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The effects of drainage and restoration of pine mires on habitat structure, vegetation and ants

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Highlights

- Mire drainage shifted floristic composition and ant assemblages towards forest communities.
- Raising the water-table level by ditch filling and the thinning of trees affected mire communities positively already 1–3 years after the start of restoration.
- The extent of tree cover, the coverage of *Sphagnum* mosses and the water-table level were major determinants of ant assemblage structure.

Abstract

Habitat loss and degradation are the main threats to biodiversity worldwide. For example, nearly 80% of peatlands in southern Finland have been drained. There is thus a need to safeguard the remaining pristine mires and to restore degraded ones. Ants play a pivotal role in many ecosystems and like many keystone plant species, shape ecosystem conditions for other biota. The effects of mire restoration and subsequent vegetation succession on ants, however, are poorly understood. We inventoried tree stands, vegetation, water-table level, and ants (with pitfall traps) in nine mires in southern Finland to explore differences in habitats, vegetation and ant assemblages among pristine, drained (30–40 years ago) and recently restored (1–3 years ago) pine mires. We expected that restoring the water-table level by ditch filling and reconstructing sparse tree stands by cuttings will recover mire vegetation and ants. We found predictable responses in habitat structure, floristic composition and ant assemblage structure both to drainage and restoration. However, for mire-specialist ants the results were variable and longer-term monitoring is needed to confirm the success of restoration since these social insects establish perennial colonies with long colony cycles. We conclude that restoring the water-table level and tree stand structure seem to recover the characteristic vegetation and ant assemblages in the short term. This recovery was likely enhanced because drained mires still had both acrotelm and catotelm, and connectedness was still reasonable for mire organisms to recolonize the restored mires either from local refugia or from populations of nearby mires.

Keywords Aichi Biodiversity Target 15; ditching; ecological restoration; Formicidae; pine bogs and fens; transforming and transformed drained mires; water-table level

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1 Introduction

The Global Peatland Database of the International Mire Conservation Group (IMCG) has estimated that peatlands represent about 3% of the globe's total land mass, and that at least 80% of peatlands are located in areas with northern temperate or cold climates (Rydin and Jeglum 2006). Much of the original peatland area has already been lost (Rydin and Jeglum 2006). In Finland, peatlands cover 28% of the land mass, which is the largest share of peatlands globally (Auvinen et al. 2007). At present, of the 8.8 million ha of peatland about 4.1 million ha remain undrained and 4.6 million ha are drained (Peltola 2014).

Most of the Finnish pristine mires are situated in Lapland, whereas in southern Finland nearly 80% of peatlands have been drained (Auvinen et al. 2007). Drainage for forestry and agriculture, and peat harvesting are the main threats to the mire biota and habitat types in Finland (Kaakinen et al. 2008; Rassi et al. 2010; Working Group on a National Strategy for Mires and Peatlands 2011). Owing to drainage, the size and connectivity of mires have drastically decreased in southern Finland, which has impaired the movement and colonization of mire biota among habitats (Auvinen et al. 2010). The number of red-listed species living primarily and secondarily in Finnish mires is 223 and 197, respectively, comprising 8.5% of all red-listed species (Rassi et al. 2010). Because populations respond slowly to increased habitat loss at large spatial scales (Hanski 2008), many mire species are likely experiencing an extinction debt (Tilman et al. 1994; Hanski and Ovaskainen 2002). Furthermore, a number of mire-associated insects are habitat specialists (Spitzer and Danks 2006) and thus prone to extinction (Dunn 2005). An analysis of changes of red-list categories (i.e., degree of threat) of species in Finland between 2000 (Rassi et al. 2001) and 2010 (Rassi et al. 2010) showed that 30 mire-associated species have become more threatened, but only 4 species less threatened (Rassi et al. 2010). Also, populations of many mire bird and butterfly species have declined, which indicates an increasing number of threatened mire species (Auvinen et al. 2010).

Clearly, there is a need to safeguard the remaining pristine sites and to restore degraded ecosystems of European mires, and EU has agreed of the goal of restoring 15% of degraded ecosystems by 2020 (see the Aichi Biodiversity Target 15, CBD 2010; European Commission 2011). This target, however, seems unrealistic: heavy restoration measures must be completed across large areas and in a short time, while compensating for ongoing degradation elsewhere (Kotiaho et al. 2015; see also Kotiaho and Moilanen 2015).

Restoration is a process where the functions, structures, processes, and biotic communities of habitats and ecosystems are returned towards their pristine state (Society for Ecological Restoration International Science & Policy Working Group 2004; Rydin and Jeglum 2006) or turned into a desired state. Peatland restoration aims for the recovery of ecosystem functions: to return naturally functioning and self-sustaining, carbon-accumulating and nutrient-retaining mire ecosystems (Kuuluvainen et al. 2002; Vasander et al. 2003; Aapala et al. 2008). Important goals include the recovery of ecohydrological properties (the quantity and quality of in-flowing and out-flowing waters and naturally-fluctuating water-table levels, i.e. natural hydrology), the recovery of peat-forming vegetation (e.g. *Sphagnum* mosses) and the recovery of structural characteristics (e.g. species composition) and processes (e.g. succession) of the mire biota (Aapala et al. 2008). Many mires, even within the current conservation-area network of Finland, have been drained for forestry prior to the establishment of conservation areas. In 1989–2013 about 20 000 ha of these

peatlands have already been restored and about 18 000 ha still need to be restored to safeguard the ecological value of the protected areas (Similä et al. 2014).

The effects of peatland restoration on the biota need further investigation, especially on habitat specialists (Rydin and Jeglum 2006). Ants provide valuable information when evaluating land-management actions and assessing long-term ecosystem changes because they are sensitive to changes in habitat quality and play a pivotal role in many ecosystems (Andersen and Majer 2004; Underwood and Fisher 2006; Fagan et al. 2010). They, like many keystone plant species, shape ecosystems for other organisms. The activities of ants and their nest and trail constructions may affect other biota considerably (Hölldobler and Wilson 1990; Punttila and Kilpeläinen 2009; Finér et al. 2013, and references therein).

Mires comprise the primary or secondary habitat for at least a third of the 55 native ant species of Finland (Punttila et al. 2013). In boreal areas, a few studies have shown that drainage of mires affects mire-ant species negatively (Krogerus 1960; Collingwood 1963; 1999; Vepsäläinen et al. 2000; Punttila and Kilpeläinen 2009), but knowledge on mire ant communities and their assembly processes are scarce globally (Sveum 1978; Vepsäläinen et al. 2000; Dlussky 2001; Ellison et al. 2002; Gotelli and Ellison 2002a; b; Mabelis and Chardon 2005; Ratchford et al. 2005; Sanders et al. 2007; Bujan et al. 2010). The effects of mire restoration and subsequent vegetation succession on ants and other insect fauna are poorly understood (Laiho et al. 2001; van Duinen et al. 2003; Watts et al. 2008; Elo et al. 2015; Noreika et al. 2015).

Our primary aim is to characterize differences in mire habitats, ant assemblages and the occurrence of individual ant species among pristine, drained and recently restored mires. We focused on three questions in the short term: (1) What are the most essential differences in vegetation between pristine and drained mires, and how do restoration affect these?; (2) Does the ant-assemblage structure differ between pristine and drained mires and how does restoration affect ant assemblages?; (3) How are the ant species distributed among pristine, drained and restored mires, and what are the most important mire characteristics affecting the ants? Further, our study serves as a baseline for future monitoring of the studied mires when longer-term restoration success is evaluated.

Generally, we test if restoring the water-table level by ditch filling and reconstructing naturally sparse and low pine stands by heavy thinning and partial clear-cutting, will restore habitats to allow recolonization and recovery of the vegetation and ants of pristine mire habitats.

2 Materials and methods

2.1 Study design

Metsähallitus Parks & Wildlife Finland manages the Finnish conservation area network and aims to restore mire ecosystems that have been drained for forestry prior to the establishment of conservation areas. Restoration success is also monitored (Aapala et al. 2012). We utilized a sampling-plot network established to monitor restoration success of drained pine mires with the goal of returning the drained mires to their natural state.

The nine study mires (Table 1) are located in two regions in Finland, Northern Karelia and Central Finland, along the border between the southern and middle boreal forest vegetation zones (Ahti et al. 1968), mostly in the eccentric bog zone (*Sphagnum fuscum* raised bogs) and partly (Kiemanneva and Väljänneva in Table 1) in the southern aapa mire zone (Ruuhijärvi 1983). The mires are mainly ombrotrophic, though oligotrophy is also wide-ranging and some mire parts are mesotrophic. All mires belong partly to the Natura 2000 network of nature protection areas but parts of the mires had been drained in 1960s–1970s prior to the establishment of nature conservation

Table 1. Mire types of the pristine, drained and restored treatments prior to the start of restoration in 2003, in the nine study mires in Central Finland and Northern Karelia, and their approximate coordinates. N = number of sampling locations representing the given mire type (total = 162 sampling locations).

Region/mire	Treatment	Mire types ¹ (N)	Coordinates
Central Finland			
Kiemanneva	Pristine	IR (1), RiNR (3), TR (2)	63°23'N, 25°16'E
	Drained	muIR (3), TKg (3)	
	Restored	muIR (3), muRaR(3)	
Väljänneva	Pristine	LkN (2), RaR(1), SR (3)	63°19'N, 25°18'E
	Drained	muIR (1), muRaR (3), muTR (1), TKg (1)	
	Restored	muIR (1), muKeR (3), muRaR (2)	
Southern Kulhanvuori	Pristine	IR (1), SR (1), TR (4)	62°34'N, 24°57'E
	Drained	muIR (1), TKg (5)	
	Restored	muIR (3), TKg (3)	
Northern Kulhanvuori	Pristine	LkR (6)	62°35'N, 24°57'E
	Drained	muRaR (1), TKg (5)	
	Restored	muRaR (1), TKg (5)	
Northern Karelia			
Ristisuo	Pristine	LkR (1), RaR (5)	62°56'N, 31°20'E
	Drained	muIR (3), muKgR (1), muRaR (2)	
	Restored	muIR (4), muPsR (1), muRaR (1)	
Juurikkasuo	Pristine	LkR (1), RaR (5)	62°56'N, 31°26'E
	Drained	muIR (2), muKgR (1), TKg (2), VT (1)	
	Restored	muPsR (1), TKg (5)	
Rapalahdensuo	Pristine	LkR (4), RaR (2)	62°54'N, 29°30'E
	Drained	muIR (2), muLkR (1), muRaR (1), TKg (2)	
	Restored	muIR (4), TKg (2)	
Tiaissuo	Pristine	LkR (3), RaR (3)	62°56'N, 29°24'E
	Drained	muIR (4), TKg (2)	
	Restored	muIR (4), muRaR (2)	
Heinäsuo	Pristine	LkN (1), RaR (5)	62°54'N, 31°28'E
	Restored-a	muIR (3), muLkR (2), muRaR (1)	
	Restored-b	LkR (1), muIR (4), muLkR (1)	

¹Mire type abbreviations are according to Eurola et al. (1995), and English translations are according to Raunio et al. (2008): IR = Dwarf shrub pine bogs, LkN = Low-sedge bogs & fens, LkR = Low-sedge pine fens, muIR = Transforming Dwarf shrub pine bogs, muKeR = Transforming Ridge-hollow pine bogs, muKgR = Transforming Thin-peated pine mires, muLkR = Transforming Low-sedge pine fens, muPsR = Transforming *Carex globularis* pine mires, muRaR = Transforming *Sphagnum fuscum* bogs, muTR = Transforming *Eriophorum vaginatum* pine bogs, RiNR = Flark pine fens, RaR = *Sphagnum fuscum* bogs, SR = Tall-sedge pine fens, TKg = Transformed drained mires, TR = *Eriophorum vaginatum* pine bogs, VT = Sub-xeric heath forests.

areas (Uusitalo et al. 2006). Restoration of parts of all the studied mires started in 2003–2005 by filling the ditches and by harvesting a varying proportion of trees in 2003–2006. During harvesting, timber and pulpwood were removed, but all tree stumps and varying amounts of logging residues (branches and tree tops) were left behind.

For each mire, prior to the start of the restoration process in 2003, three separate study areas were selected to represent different treatments: (1) pristine mire, (2) drained mire and (3) restored mire (Table 1). In one of the mires (Heinäsuo), however, the area designated to remain drained was also restored and this mire thus provided one pristine and two restored areas but no drained area (Table 1). For each treatment per mire, two 250 m transects, on average 80 m apart, were established with three sampling locations per transect. This resulted in six sampling locations per treatment per mire (nine mires × three treatments × two transects × three sampling locations = 162 sampling locations). The treatments per mire were, on average, 600 m apart.

2.2 Vegetation, drainage and ant data collection

At each sampling location, the mire-site type was recorded prior to restoration measures in 2003 (Table 1), and several sets of data were collected: (1) tree-stand characteristics were recorded from a circular 100 m² tree-sampling plot, in the middle of which (2) tree-sapling and microsite-type data were recorded from a 25 m² sapling square. In each corner of the 25 m² sapling square, (3) the covers of vascular plant, moss and lichen species, and litter and surface water were estimated within 1 m² vegetation squares (four squares per sapling square). The coverages were estimated on a scale 0.1, 0.5, 1, 3, 5, 7, 10, 15, 20, 30, 40, 50, 60, 70, 80, 85, 90, 95, 97, 100%. Data sets 1–3 above were collected both prior to restoration in 2003, and again in 2007, when we sampled the ants. Here we mainly use the 2007 data to characterize sampling locations and to provide environmental variables for the ant analyses. Additionally, in 2007, (4) the water-table level was monitored using plastic tubes (PVC pipes, length 88 cm, diameter 20 mm) as ground water wells. The tubes were set in two opposite corners of each 25 m² sapling square. Water-table depth, i.e. distance of the water table from the mire surface, was measured with an accuracy of 1 cm at two-week intervals, six times from early June to mid-August in 2007.

Three circular tree-sampling plots (radius 5.64 m = 100 m²) were evenly placed along each transect, approximately 62.5 m apart. From each tree-sampling plot, tree (height > 150 cm) species and their stem numbers were recorded. The trees were classified into size classes according to their diameter at breast height (DBH, $d_{1.3\text{ m}}$ classes < 7, 7–20 and > 20 cm) and height (classes 1.5–3, 3–8 and > 8 m). Dead standing trees (snags) and fallen dead trees (logs) were recorded in a similar way as the living trees (at 1.3 m DBH from the ground for snags and 1.3 m from the butt end for logs).

Tree-sapling and bush (height 50–150 cm) species and their numbers were recorded from the sapling square (25 m²) within the tree-sampling plot. Within the sapling square the percentage covers of mire surface topography types, i.e. microsite types (hummock, lawn and flark) were estimated to the nearest 10 percent.

Based on a-priori knowledge of the general importance of different environmental characteristics on the occurrence of ants, we selected a set of potential explanatory variables in the analyses on ants. Variables selected relate to the degree of shading of canopy layers of different height and vegetation type, to the occurrence of potential nesting sites, and to the occurrence of potential prey and aphid colonies. Also, the most important predictor variables indicating successful restoration were included. The variables used included (1) treatment (a three-level factor; pristine, drained, restored), and several variables from (2) the 100 m² tree-sampling plots (number of low trees [1.5–3 m], tall trees [> 3m] and dead trees), (3) the 25 m² sapling squares (number of tree saplings and proportions of the microsite types hummock, lawn and flark), (4) the 1 m² vegetation squares (percentage covers of surface water and litter, the pooled cover of *Sphagnum* spp., the pooled cover of other mosses, the pooled cover of herbs, sedges and grasses (i.e. non-woody annual plants), the pooled cover of low (< 20 cm) dwarf shrubs, and the pooled cover of tall (> 20 cm) dwarf shrubs and shrubs (for details, see below); average cover of the four 1 m² vegetation squares was used) and (5) water-table depth (average of the two wells per sapling square).

Vegetation data were used to characterize the microhabitat types of the sampling locations such that they would reflect the main ecological gradients among the sampling locations. We calculated the combined cover of (1) *Sphagnum* spp. mosses, (2) other mosses, (3) herbs, sedges and grasses (sensu Euroala et al. 1995) that do not provide shade in early spring and late autumn, (4) low dwarf shrubs (species typically < 20 cm in height, *Andromeda polifolia* L., *Calluna vulgaris* (L.) Hull, *Empetrum nigrum* L., *Vaccinium myrtillus* L., *V. vitis-idaea* L.) excluding the recumbent *V. oxycoccos* L. and *V. microcarpum* (Turcz. ex Rupr.) Schmalh., and (5) tall dwarf shrubs (*Chamaedaphne calyculata* (L.) Moench, *Ledum palustre* L., *V. uliginosum* L.) pooled with shrubs (*Betula nana* L., *Salix myrsinifolia* Salisb.) that provide shade throughout the growing season.

Ants were sampled using pitfall traps. One trap (a 1 dl plastic jar with inner diameter of 56 mm and a depth of 70 mm) was set in a representative location within each 100 m² tree-sampling plot, which yielded 6 traps per treatment per mire, i.e. 162 traps in total. Trapping was continuous for six weeks, with catches collected and traps reset every second week, between May and July 2007. To remove the surface tension and preserve the arthropods caught, 5 cl of a 10% NaCl solution with a few drops of detergent was added to the traps. Ants were identified with the keys of Collingwood (1979), Seifert (2000; 2007) and Czechowski et al. (2002). On the basis of published data (Krogerus 1960; Vepsäläinen et al. 2000; Punttila and Kilpeläinen 2009) and our own field experience, all the frequently collected ant species were ranked according to their affinity for mire habitats, response to drainage and affinity for pine heath forests on a scale from 1 (strongest mire affinity) to 6 (strongest pine-forest affinity). Additionally, when analysing the effects of drainage and restoration on the number of mire-ant species, we included only those species assessed in the latest red-list work of Finland by the expert group for Hymenoptera (Rassi et al. 2010) to live primarily in mires: *Formica exsecta* Nylander, 1846, *F. picea* Nylander, 1846, *F. uralensis* Ruzsky, 1895 and *Myrmica scabrinodis* Nylander, 1846 in our data.

2.3 Statistical analyses

First, we used log-likelihood ratio tests and Kruskal-Wallis non-parametric median tests to explore variation in the tree-stand variables and other variables characterizing mire habitats, and in ant occurrence among the treatments. To control for false discovery rate in multiple testing, the original p-values were adjusted with the method in Benjamini and Yekutieli (2001) using the function `p.adjust` (method = "BY") in the package `stats` in R version 3.0.1 (R Core Team 2013). Additionally, we analysed ant occurrence among different mire types with Kruskal-Wallis non-parametric median tests to increase our limited knowledge of habitat associations of mire ants. We excluded all sampling locations on restored mires and all mire types with less than four sampling locations, which resulted in 89 sampling locations in these analyses.

Second, we applied non-metric multidimensional scaling (NMDS) to characterize differences in tree stands, floristic composition and ant-assembly composition among the treatments (pristine, drained and restored). The three NMDS ordinations were performed using the `vegan` community ecology package, version 2.0–8 (Oksanen et al. 2013) in R (R Core Team 2013). We used the `vegan` function `metaMDS` with `monoMDS` to produce two-dimensional NMDS ordinations with several hundred random starts to find stable solutions. The ordination dimensions ("axes") were scaled to half-change units. We fitted a set of environmental variables (see above) into ordinations using the `vegan` function `envfit` and tested their fit with permutation tests.

For the NMDS of the tree-stand characteristics, the Gower dissimilarity measure was used; the data were the number of sapling and tree individuals per species, the number of sapling and tree species, the number of trees in three diameter and three height classes, the number of snags in two diameter classes (<7 cm, 7–20 cm), and the number of logs in three diameter classes in the 100 m² tree-sampling plots and 25 m² sapling squares. We excluded variables with less than 8 positive values out of 162 data entries.

For the NMDS of the floristic data, the Bray-Curtis dissimilarity measure, square root transformation and Wisconsin double standardization were used.

For the NMDS of the ant data, the Raup dissimilarity measure with ant presence-absence data in the pitfall traps was used, because conspecific individuals of social insects captured in a pitfall trap are not statistically independent units and do not directly reflect assemblage structure (Melbourne 1999; Vepsäläinen et al. 2000; Gotelli et al. 2011; Higgins and Lindgren 2012). Only worker-ant data were included in the NMDS and other multivariate analyses because only workers indicate established colonies.

Third, we used generalized linear mixed models (GLMM, glmer function in the lme4 package, Bates et al. 2013) in R (R Core Team 2013) to evaluate the effects of treatment and a set of environmental variables on the occurrence of ant species. Ant presence-absence data were modeled following a binomial error distribution. Mires nested within study regions were included as a random factor. Nine species occurring in >10% of the traps were analysed individually.

GLMM analyses were subject to model selection, but treatment, *Sphagnum* cover, hummock cover and number of tall trees (>3 m) not, owing to their a-priori expected importance for the individual species analysed. The following predictor variables were, however, subject to model selection: number of dead trees (logs and snags pooled), litter cover, covers of low (<20 cm) and tall (>20 cm) dwarf shrubs and the pooled cover of herbs, sedges and grasses. These variables were removed, one at a time, if their p-values exceeded 0.1 and if AIC values (see Burnham and Anderson 2002) decreased after excluding the particular variable. All predictor variables (except treatment) were standardized to zero mean and unit variance (Schielzeth 2010) to make them comparable. Mires from which no individuals of a particular species were caught were not included in the GLMM analyses since they may be unsuitable for that species for reasons that are not considered in this study.

3 Results

3.1 Mire-site types

Prior to starting restoration in 2003, 21.6% of the 162 sample locations represented transformed drained mires where the identification of the original mire type was impossible owing to successional changes. For the 34.0% and 43.8% of the sample locations established in pristine or transforming mire types, respectively (Table 1), pine mires and pine bogs were dominating (57.4% of all 162 locations), and pine fens and rich pine fens made up 18.5%. The most common pristine types were *Sphagnum fuscum* bogs (RaR, 13.0% of all sample locations, Table 1) and low-sedge pine fens (LkR, 9.9%), and the most common transforming types were transforming dwarf shrub pine bogs (muIR, 25.9%) and transforming *Sphagnum fuscum* bogs (muRaR, 10.5%).

3.2 The effects of drainage and restoration on tree stand and vegetation

Drainage led to a four-fold increase in the number of tree stems relative to pristine mires, and the increase in birch reduced the dominance of pines and led to mixed pine-birch stands in the drained mires (Table 2). Tree growth and thus growing stock increased, as reflected especially by the greater abundance of larger trees ($d_{1.3} > 7$ cm or $h > 3$ m) in drained than in pristine mires. Restoration harvesting successfully converted stand structure (in terms of stem number, tree-size distribution and tree-species composition) closer to pristine conditions (Table 2). Similarly, there were more birch saplings in the drained than pristine mires, whereas restored mires had intermediate numbers (Table 2). The amount of dead trees was generally low and rather similar among the treatments, but the amount of small-sized logs was higher in drained and restored than pristine mires (Table 2).

The microsite-type distribution of drained and pristine mires differed considerably from one another: the surface of drained mires was almost completely (97%, Table 2) covered by hummock, whereas more than half of the surface of pristine mires was covered by lawn (38%) and flark (16%). The microsite-type distribution in restored mires resembled that of pristine mires, but the share of hummock was larger (67%) than in pristine mires (46%).

Table 2. Mean ($\bar{x} \pm SE$) tree-stand and sapling characteristics, microsite-type coverage, mire-surface coverage and water-table levels of the sampling locations in pristine, drained and restored mires. Differences in variables among the treatments were tested with Kruskal-Wallis rank sum test (H, $df = 2$; treatments not sharing the same letter differed significantly according to a posteriori test with critical $\alpha = 0.05$). We adjusted the original p-values (p adj. in the Table) to control false discovery rate in multiple testing using the method in Benjamini and Yekutieli (2001). h = height, $d_{1.3}$ = diameter at breast height (1.3 m from the mire-surface level or 1.3 m from the butt end of logs), and N = number of sampling locations. Data on living and dead trees are from the 100 m² tree-sampling plots, data on tree saplings and microsite types are from the 25 m² sapling squares, data on mire-surface coverage are from the 1 m² vegetation squares, and data on water-table depth are from the ground-water wells.

Variable	Treatment						Test statistics				
	Pristine (N = 54)			Drained (N = 48)			Restored (N = 60)				
	\bar{x}	SE		\bar{x}	SE		\bar{x}	SE		H	p adj.
Living trees (h > 1.5 m):											
Total number of stems	5.8	1.0	a	23.1	2.5	b	9.2	1.2	a	60.47	<0.0001
No. of pines	5.8	1.0	a	14.9	1.3	b	8.0	1.2	a	42.03	<0.0001
No. of birches	0.1	0.0	a	7.4	2.3	b	1.2	0.4	a	42.95	<0.0001
No. of stems $d_{1.3} < 7$ cm	4.7	0.8	a	13.8	2.3	b	7.1	1.1	a	17.65	0.0007
No. of stems $d_{1.3} 7-20$ cm	1.0	0.3	a	8.2	0.8	b	1.8	0.3	a	67.34	<0.0001
No. of stems $d_{1.3} > 20$ cm	0.0	0.0	a	1.1	0.2	b	0.3	0.1	a	32.44	<0.0001
No. of stems h 1.5-3 m	4.1	0.7		3.5	0.8		3.5	0.8		2.05	1.0000
No. of stems h 3-8 m	1.7	0.3	a	12.5	2.0	b	4.9	0.7	c	40.24	<0.0001
No. of stems h > 8 m	0.0	0.0	a	7.0	1.2	b	0.8	0.4	a	68.29	<0.0001
Number of species	0.9	0.1	a	1.8	0.1	b	1.0	0.1	a	53.10	<0.0001
Dead trees:											
Total number of snags	0.7	0.2		1.1	0.2		0.9	0.3		1.49	1.0000
No. of snags $d_{1.3} < 7$ cm	0.6	0.1		0.9	0.2		0.8	0.3		0.96	1.0000
No. of snags $d_{1.3} 7-20$ cm	0.1	0.1		0.2	0.1		0.1	0.0		1.16	1.0000
Total number of logs	0.0	0.0	a	0.4	0.2	a	0.6	0.2	a	10.24	0.0354
No. of logs $d_{1.3} < 7$ cm	0.0	0.0	a	0.4	0.2	a	0.6	0.2	a	11.15	0.0235
No. of logs $d_{1.3} 7-20$ cm	0.0	0.0		0.1	0.0		0.1	0.0		1.57	1.0000
No. of logs $d_{1.3} > 20$ cm	0.0	0.0		0.0	0.0		0.0	0.0		1.70	1.0000
Tree saplings (h 50-150 cm):											
Total number of saplings	1.9	0.3		2.6	0.6		1.7	0.3		1.02	1.0000
No. of pines	1.9	0.3	a	1.4	0.4	b	1.2	0.2	ab	8.60	0.0736
No. of birches	0.0	0.0	a	0.9	0.4	b	0.3	0.1	ab	17.14	0.0014
Number of species	0.7	0.1		0.9	0.1		0.8	0.1		1.31	1.0000
Microsite types (%):											
Hummock	46.1	3.6	a	96.6	2.0	b	66.9	4.1	c	71.47	<0.0001
Lawn	37.8	4.0	a	1.1	0.7	b	24.8	3.8	c	58.68	<0.0001
Flark	15.5	3.6	a	0.0	0.0	b	6.3	1.7	a	27.05	<0.0001
Mire-surface coverage (%):											
Water	0.0	0.0	a	0.0	0.0	a	2.4	1.0	a	14.20	0.0052
Litter	2.4	1.2	a	12.1	3.1	ab	15.5	2.4	b	27.30	<0.0001
<i>Sphagnum</i> spp.	90.0	1.7	a	30.7	3.8	b	46.0	3.9	b	83.39	<0.0001
Other mosses	3.1	0.6	a	38.4	3.9	b	22.7	2.8	c	64.53	<0.0001
Herbs, sedges and grasses	14.0	1.1	a	8.2	1.0	b	20.9	2.2	a	22.51	<0.0001
Low dwarf shrubs	9.6	1.2	ab	16.6	2.1	a	8.6	1.3	b	8.92	0.0655
Tall dwarf shrubs	3.7	0.6	a	6.2	0.8	ab	9.5	1.0	b	19.39	0.0007
Water-table depth (cm below the mire-surface)	15.1	1.3	a	38.0	1.5	b	16.0	1.3	a	74.34	<0.0001

Similarly, the surface cover of drained mires was dramatically different from pristine mires: the moss layer was dominated by *Sphagnum* mosses (90%, Table 2) in pristine mires, in drained mires 31%, with a higher cover of other mosses (38%). Differences in the herb layer were clear: the pooled cover of herbs, sedges and grasses was lower and the cover of tall dwarf shrubs higher in drained than pristine mires (Table 2). Pristine mires had higher cover of *Sphagnum* mosses but lower cover of other mosses, litter and tall dwarf shrubs than restored mires (Table 2).

The water-table level was lower in the drained (at a depth of 38 cm, Table 2) than in the pristine (15 cm) and restored (16 cm) mires.

Tree-stand and sapling characteristics of the drained mires differed clearly from those of the pristine and restored mires in the NMDS ordination (treatment, $r^2=0.205$, $p<0.001$): sampling locations of the drained mires were to the right in the ordination and displayed large scatter, whereas locations of the pristine and restored mires were to the left with small scatter (Fig. 1 A). Drained mires were characterized by a birch mixture and an abundance of large trees, but pristine and restored mires by pines and smaller trees (Fig. 1 B). The scatter of the restored sampling locations, however, was larger than that of the pristine ones (Fig. 1 A). Five of the 15 a-priori selected and fitted environmental variables showed significant correlations ($p<0.001$) with the NMDS-ordination space: the number of tall trees, water-table depth and the cover of hummock microsite type had higher values in the drained mires than elsewhere (Fig. 1 A). The values of pooled cover of *Sphagnum* mosses and those of herbs, sedges and grasses were higher in the pristine and restored mires than in the drained ones (Fig. 1 A).

The floristic composition of the drained mires differed clearly from both the pristine and restored mires in the NMDS ordination (treatment, $r^2=0.352$, $p<0.001$, Fig. 2 A). Sampling locations of the drained mires were mostly to the right in the ordination, whereas those of the pristine mires were mostly to the left, and those of the restored mires mostly in between (Fig. 2 A). Sampling locations to the right, the drained mires and many of the restored ones had higher cover and occurrence rate of forest species such as *Vaccinium myrtillus*, *V. vitis-idaea*, *Pleurozium schreberi* (Willd. ex Brid.) Mitt. and *Dicranum polysetum* Sw. ex anon., whereas species characterizing pristine mires such as *Carex limosa* L., *C. pauciflora* Lightf., *Drosera rotundifolia* L., *Sphagnum balticum* (Russow) C.E.O.Jensen, *S. fallax* (H.Klinggr.) H.Klinggr., *S. fuscum* (Schimp.) H.Klinggr., *S. papillosum* Lindb., *S. rubellum* Wilson and *V. microcarpum* were to the left in ordination (Fig. 2 B, Appendix 1, available at <http://dx.doi.org/10.14214/sf.1462>). Restoration seemed to have increased the covers and occurrence rates of mire species such as *Sphagnum russowii* Warnst., *S. fallax* and *Polytrichum commune* Hedw. in the short term as seen by their locations in the top half of the ordination (Fig. 2 B, Appendix 1).

A number of species located in the top half of the ordination have benefitted from recent disturbances during restoration, e.g. *Carex globularis* L., *Polytrichum commune*, *Sphagnum squarrosum* Crome and *Straminergon stramineum* (Dicks. ex Brid.) Hedenäs (Fig. 2 B, Appendix 1). Additionally, the cover of especially *Eriophorum vaginatum* L. seemed to have increased considerably in restored mires relative to both drained and pristine mires although there were no great differences in its occurrence rate among the treatments (Appendix 1).

The same five a-priori selected environmental variables as in the tree-stand NMDS showed significant correlations ($p<0.001$) here and correlated similarly with the vegetation ordination space as above, but also five additional variables correlated significantly with the ordination (Fig. 2 A): low dwarf shrubs and litter tended to increase in cover towards the drained mires, other mosses than *Sphagnum* spp. tended to increase in cover towards the drained and restored mires, and the cover of the microsite type flark increased towards the pristine mires and that of lawn towards both pristine and restored mires. Generally, the ordination revealed a gradient from more wet and fertile conditions characterized by a high cover of lawn and flark microsites to drier and poorer conditions with a high cover of hummock microsites (Fig. 2 A).

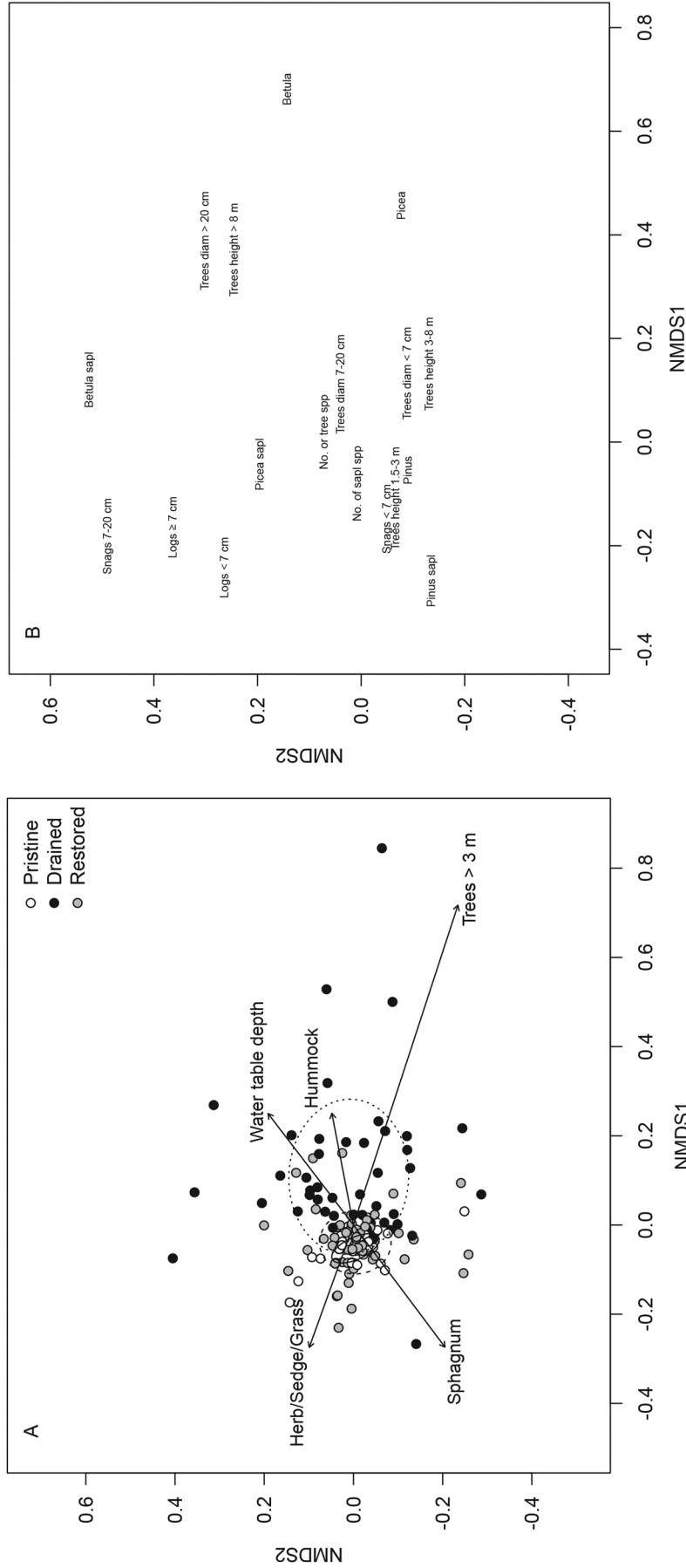


Fig. 1. NMDS ordination plots of the tree-stand variables presenting (A) sampling locations of the pristine (white dots), drained (black dots) and restored (grey dots) mires and (B) tree and sapling variables within the sampling locations. The dispersion ellipses in plot A indicate 1 SD of the weighted average of the site scores of pristine (solid line), drained (dotted line) and restored (dashed line) mires. The arrows in plot A indicate the environmental variables fitted to the ordination space such that only variables with highly significant p-values are shown ($p < 0.001$); the direction of the arrow indicates the direction of the gradient, and the length of the arrow indicates the strength of the correlation).

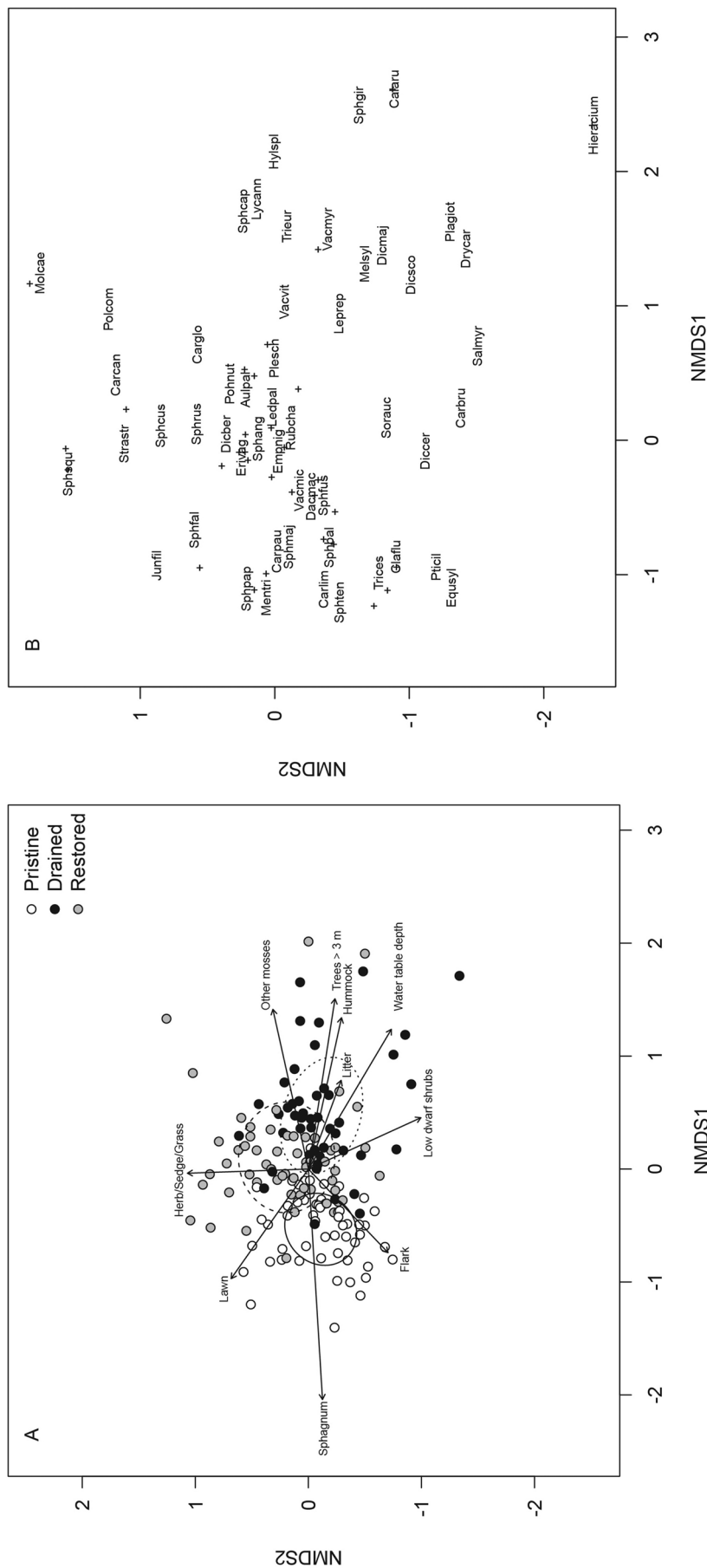


Fig. 2. NMDS ordination plots of the floristic data presenting (A) sampling locations of the pristine (white dots), drained (black dots) and restored (grey dots) mires and (B) moss, lichen and vascular plant species within the sampling locations (note the differences in the scales of axes between plots A and B). The dispersion ellipses in plot A indicate 1 SD of the weighted average of the site scores of pristine (solid line), drained (dotted line) and restored (dashed line) mires. The arrows in plot A indicate the environmental variables fitted to the ordination space such that only variables with highly significant p-values are shown ($p < 0.001$). The species names indicated in plot B are such that for overlapping labels, priority is given to the most abundant species and the rest are indicated with “+”. After this, 14 frequent species (occurring in > 9% of sampling locations) remained without labels. These species are located as follows: *Dicranum polysetum* ca. 0.7 units right from the origin, *Vaccinium uliginosum*, *Chamaedaphne calyculata*, *Polytrichum strictum* Menzies ex Brid., *Vaccinium oxycoccos*, *Benula nana*, *Sphagnum magellanicum* Brid. and *Andromeda polifolia* within ca. 0.3 units left from the origin, *Carex rostrata* Stokes ca. 0.5–1.0 units toward the ca. lower left corner from the origin, *Pinus sylvestris* L., *Calluna vulgaris*, *Myrica anomala* (Hook.) Gray, *Drosera rotundifolia* and *Sphagnum rubellum* within ca. 0.5–1.0 units toward the ca. lower left corner from the origin. For species abbreviations, see Appendix 1 (abbreviations represent the first three letters of the genus name and the first three letters of the species name).

Table 3. Mean (\bar{x} , range 0–1) and total (\bar{fr}) occurrence rates of ant workers and queens, and the mean number ($\bar{x} \pm SE$, standard error given in column \bar{fr}) of mire ant species and all ant species in the sampling locations representing different mire types in pristine and drained mires (mire types with less than four sampling locations in pristine and drained mires, and all sampling locations in restored mires were omitted). In the table, mire types within both pristine and the transforming and transformed mires are ordered by increasing growing stock from left to right (mire types to the left tend to have lower growing stock than types to the right). Differences in the occurrence rate (\bar{fr}) of ant species among the mire types were tested with log-likelihood ratio test (G^2 , $df = 6$), and differences in the numbers of species were tested with Kruskal-Wallis rank sum test (H , $df = 6$; a posteriori test was unable to locate differences among mire types at $\alpha = 0.05$ for the variable “number of mire ant species”). We adjusted the original p-values (p adj.) in the Table) to control false discovery rate in multiple testing using the method in Benjamini and Yekutieli (2001). N = number of sampling locations (total N = 89).

Species	Mire type ¹												Test statistics			
	Pristine						Transforming and transformed									
	LkR (N = 15)		RaR (N = 21)		SR (N = 4)		TR (N = 6)		muRaR (N = 7)		muLR (N = 16)		TKg (N = 20)		G ²	p adj.
\bar{x}	\bar{fr}	\bar{x}	\bar{fr}	\bar{x}	\bar{fr}	\bar{x}	\bar{fr}	\bar{x}	\bar{fr}	\bar{x}	\bar{fr}	\bar{x}	\bar{fr}			
Ant workers																
<i>Formica picea</i>	0.5	7	0.3	7	0.8	3	0.3	2	0.0	0	0.0	0	0.1	1	27.30	0.0010
<i>Formica uratensis</i>	0.1	2	0.0	0	0.0	0	0.2	1	0.3	2	0.2	3	0.2	3	8.66	0.7269
<i>Myrmica scabrinodis</i>	0.6	9	0.9	18	0.8	3	0.7	4	0.9	6	0.6	10	0.4	7	13.90	0.1592
<i>Lasius platythorax</i>	0.3	4	0.4	9	0.5	2	0.5	3	0.3	2	0.5	8	0.5	10	3.25	1.0000
<i>Formica sanguinea</i>	0.1	2	0.4	9	0.3	1	0.0	0	0.4	3	0.1	1	0.1	1	16.86	0.0579
<i>Leptothorax acervorum</i>	0.2	3	0.4	9	0.5	2	0.2	1	0.1	1	0.1	1	0.1	2	11.43	0.3491
<i>Myrmica rubra</i>	0.1	2	0.1	2	0.3	1	0.0	0	0.0	0	0.1	1	0.2	3	4.43	1.0000
<i>Myrmica ruginodis</i>	0.3	5	0.4	9	0.0	0	0.3	2	0.9	6	0.9	15	0.9	18	36.74	<0.0001
<i>Camponotus herculeanus</i>	0.1	1	0.0	0	0.0	0	0.2	1	0.1	1	0.8	12	0.7	14	51.34	<0.0001
Ant queens																
<i>Myrmica scabrinodis</i>	0.2	3	0.3	7	1.0	4	0.5	3	0.1	1	0.3	4	0.0	0	25.74	0.0017
<i>Myrmica ruginodis</i>	0.1	2	0.0	0	0.0	0	0.0	0	0.3	2	0.6	9	0.5	9	29.93	<0.0001
Mean number of species															H	p adj.
Mire ants	1.3	0.2	1.2	0.1	1.8	0.3	1.3	0.4	1.1	0.1	0.9	0.2	0.6	0.1	20.45	0.0158
All ants	2.4	0.3	3.0	0.3	3.3	0.5	2.5	0.8	3.3	0.4	3.5	0.3	3.6	0.3	8.82	0.7269

¹Mire type abbreviations are according to Euroala et al. (1995), and English translations are according to Raunio et al. (2008): LkR = Low-sedge pine fens, RaR = *Sphagnum fuscum* bogs, SR = Tall-sedge pine fens, TR = *Eriophorum vaginatum* pine bogs, muRaR = Transforming *Sphagnum fuscum* bogs, muLR = Transforming Dwarf shrub pine bogs, TKg = Transformed drained mires.

3.3 Ant occurrence among mire-site types

The ant data comprised 20 species: 10 579 workers of 17 species, 169 queens of 13 species and two males of one species (Appendix 2, available at <http://dx.doi.org/10.14214/sf.1462>). The most abundant species in the worker data were *Lasius platythorax* Seifert, 1991, *Formica uralensis*, *Myrmica ruginodis* Nylander, 1846, *M. scabrinodis* and *F. sanguinea* Latreille, 1798, and the most frequently caught species were *M. ruginodis* (66% of the 162 sampling locations), *M. scabrinodis* (65%), *L. platythorax* (49%), *Camponotus herculeanus* (Linnaeus, 1758) (33%), and *Leptothorax acervorum* (Fabricius, 1793) (22%).

The species ranked a-priori to have the strongest pine-forest affinities, *C. herculeanus* and *M. ruginodis*, were more frequent in transforming and transformed than in pristine mire types (worker data, Table 3). Species ranked to have the strongest mire affinities showed more variable pattern: *F. picea* occurred almost exclusively in pristine mire types, whereas *F. uralensis* and *M. scabrinodis* were found frequently in both pristine and transforming and transformed mire types (Table 3). The rest of the species seemed to occur more evenly among the mire types (Table 3). Queens of the forest species *M. ruginodis* were more frequent in the transforming and transformed than in the pristine mire types, whereas queens of *M. scabrinodis* showed the opposite pattern (Table 3). The number of all ant species did not differ among mire types, whereas the number of mire ant species was higher in pristine mire types than in transforming and transformed types, and seemed to decrease with increasing growing stock (Table 3).

Table 4. Mean (\bar{x} , range 0–1) and total (fr) occurrence rates of ant workers and queens, and the mean number ($\bar{x} \pm \text{SE}$, standard error given in the column fr) of mire ant species and all ant species in pristine, drained and restored mires. Differences in the occurrence rate (fr) of ant species among the treatments were tested with log-likelihood ratio test (G^2 , $df = 2$), and differences in the number of species were tested with Kruskal-Wallis rank sum test (H , $df = 2$; treatments not sharing the same letter differed significantly from each other according to a posteriori test with critical $\alpha = 0.05$). We adjusted the original p-values (p adj. in the Table) to control false discovery rate in multiple testing using the method in Benjamini and Yekutieli (2001). N = number of sampling locations (total N = 162).

Species	Treatment						Test statistics				
	Pristine (N = 54)		Drained (N = 48)		Restored (N = 60)		G^2	p adj.			
	\bar{x}	fr	\bar{x}	fr	\bar{x}	fr					
Ant workers:											
<i>Formica picea</i>	0.44	24	0.02	1	0.02	1	48.63	< 0.0001			
<i>Formica uralensis</i>	0.07	4	0.19	9	0.08	5	3.76	0.6328			
<i>Myrmica scabrinodis</i>	0.74	40	0.52	25	0.67	40	5.49	0.2918			
<i>Lasius platythorax</i>	0.35	19	0.50	24	0.60	36	7.13	0.1431			
<i>Formica sanguinea</i>	0.22	12	0.13	6	0.23	14	2.44	1.0000			
<i>Leptothorax acervorum</i>	0.30	16	0.15	7	0.20	12	3.52	0.6513			
<i>Myrmica rubra</i>	0.09	5	0.13	6	0.10	6	0.30	1.0000			
<i>Myrmica ruginodis</i>	0.37	20	0.92	44	0.72	43	37.34	< 0.0001			
<i>Camponotus herculeanus</i>	0.06	3	0.67	32	0.30	18	47.23	< 0.0001			
Ant queens:											
<i>Myrmica scabrinodis</i>	0.41	22	0.10	5	0.18	11	14.25	0.0061			
<i>Myrmica ruginodis</i>	0.04	2	0.42	20	0.28	17	24.99	< 0.0001			
<i>Camponotus herculeanus</i>	0.11	6	0.02	1	0.20	12	9.68	0.0450			
Mean number of species:											
Mire ants	1.3	0.1	a	0.8	0.1	b	0.8	0.1	b	22.59	< 0.0001
All ants	2.7	0.2	a	3.6	0.2	b	3.1	0.1	ab	10.23	0.0390

3.4 The effects of drainage and restoration on ants

The mean number of mire-ant species was highest in pristine mires, but the number of all ant species was highest in drained mires (Table 4). The mire species *Formica picea* occurred almost exclusively in the pristine mires, and the queens of another mire species, *Myrmica scabrinodis*, were most frequent in pristine mires, but this pattern was not observed for its workers (Table 4). The workers of the forest species *Camponotus herculeanus* and *M. ruginodis* – and queens of the latter – were most frequent in drained mires and common also in restored mires. Occurrence rate peaked in restored mires only for *C. herculeanus* queens (Table 4). The occurrence rates of the rest of the species did not differ statistically significantly among the treatments (Table 4).

Of the nine species analysed individually with GLMM, three were ranked a priori to have the strongest mire affinities (rank 1: *F. picea*, *F. uralensis* and *M. scabrinodis*), two were ranked a priori to have the strongest pine-forest affinities (rank 6: *M. ruginodis* and *C. herculeanus*), and the remaining four species to be more generalists in their habitat affinities (rank 2: *L. platythorax*, *F. sanguinea* and rank 3: *L. acervorum*, species that occur both in mires and forests but disappear with tree-canopy closure during forest succession, and rank 4: *M. rubra* (Linnaeus, 1758), which is known to tolerate tree-canopy shading). Below, we focus on the overall trends of occurrence of species along the mire-forest continuum, rather than statistically significant differences in the occurrence rate of individual species.

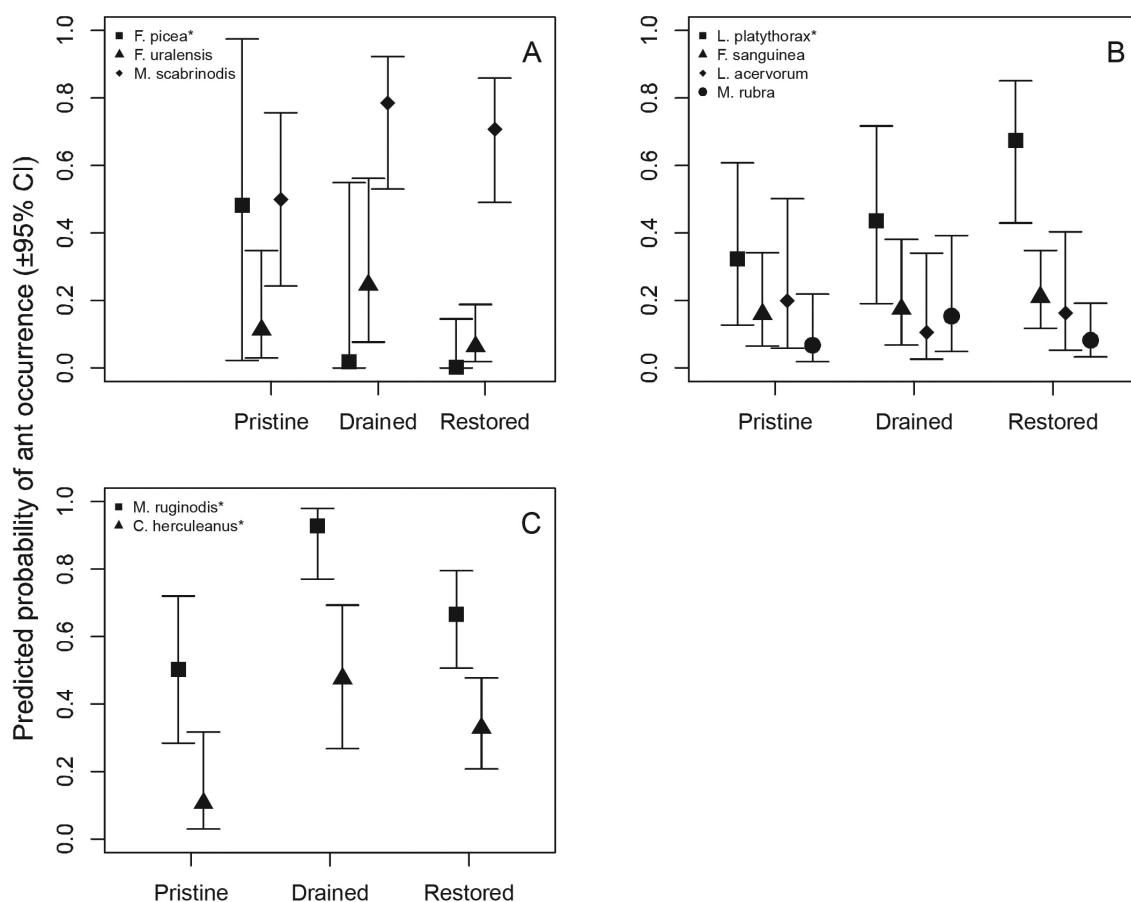


Fig. 3. Statistical responses of individual ant species to mire treatment (A = mire specialist species, B = generalist species, C = forest species). * = statistically significant ($p < 0.05$) responses (see Table 5).

Mire specialist species showed variable responses to treatment (Fig. 3 A, Table 5). *Formica picea* responded statistically significantly and negatively to restored sites, and the trend for *F. uralensis* suggests negative association with restored mires. Interestingly, *M. scabrinodis* and *F. uralensis* tended to associate with drained sites. The fairly generalist species, *L. platythorax* responded statistically significantly and positively to restored sites, and the trend for *F. sanguinea* suggests that it associates with restored sites (Fig. 3 B, Table 5). *Myrmica rubra* behaved like the forest-associated species, whereas *L. acervorum* responded more as a mire specialist (Fig. 3 B).

As expected, the two forest-associated species, *C. herculeanus* and *M. ruginodis*, occurred statistically significantly more often in drained sites, less in restored sites and least frequently in pristine sites (Fig. 3 C).

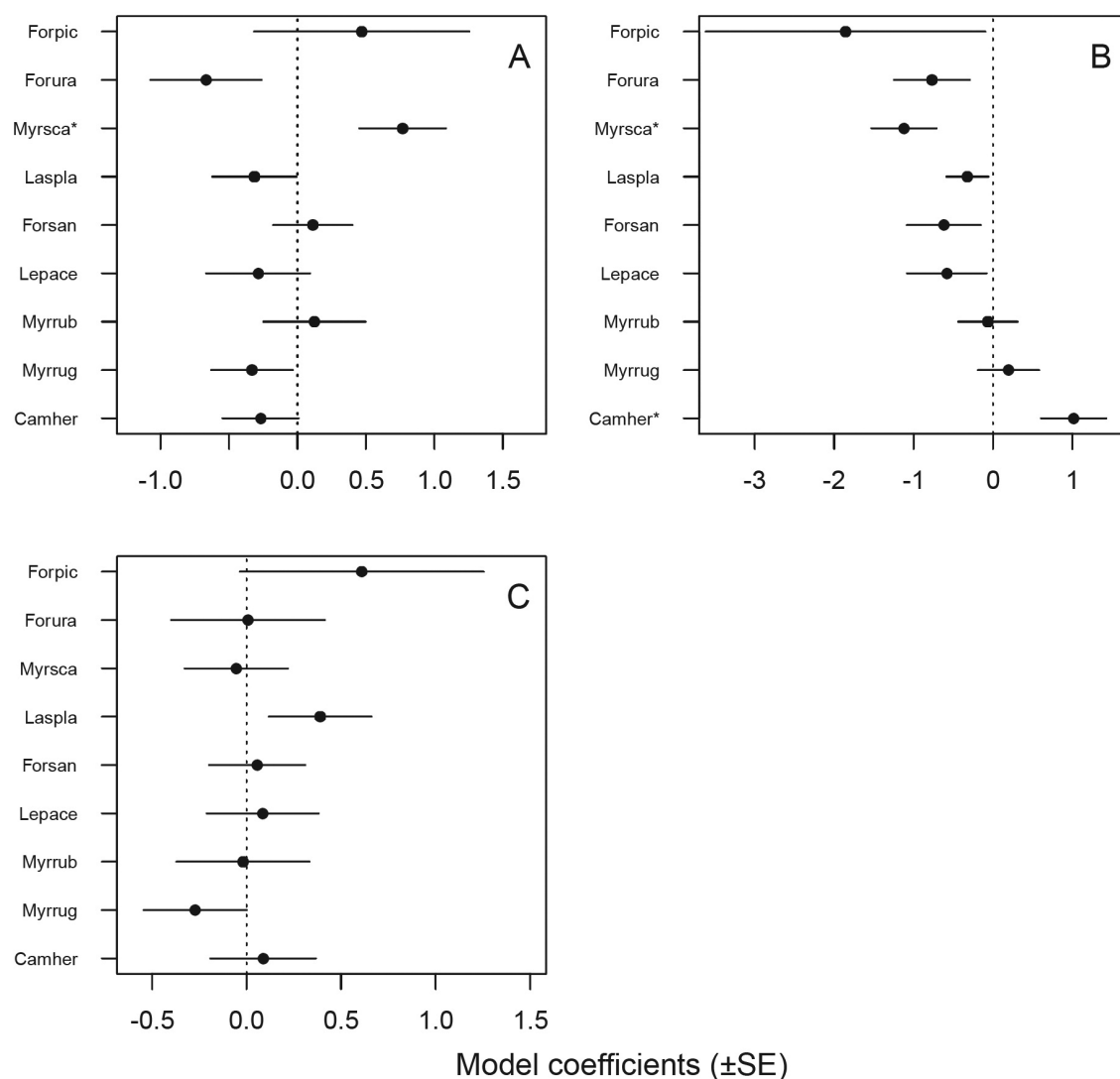


Fig. 4. Statistical responses (model coefficients ±SE, see Table 5) of individual ant species to environmental variables: A = *Sphagnum* moss cover, B = number of tall trees (> 3 m), C = hummock cover. * = statistically significant ($p < 0.05$) responses. Species were listed a priori (based on expert opinion and the literature: Krogerus 1960; Vepsäläinen et al. 2000; Punttila and Kilpeläinen 2009) from the most mire-associated (mire specialist) species at the top of each plot to species with the strongest forest affinities (forest species) at the bottom of each plot; generalist species are located in-between.

Table 5. Generalised linear mixed model results of ant mire specialists, generalists and forest species. Model estimates, standard errors (SE) and p-values of terms retained in the models are given. Treatment, *Sphagnum* cover, hummock cover and number of trees (> 3 m) were a priori chosen as important environmental variables for the ant occurrences and were retained in all final models. Other variables were subject to model selection and their values are only given when they remained in the final model. Statistically significant p-values (<0.05) are in bold. The intercept represents prediction in the pristine mire treatment. Est. = Estimate. * = mire specialist species, ** = generalist species, *** = forest species, all according to our a priori evaluations.

Species	Intercept	Drained	Restored	<i>Sphagnum</i>	Hummock	Trees > 3 m	Low dwarf shrubs	Tall dwarf shrubs	Annual plants	Litter	Dead trees
<i>Formica picea</i> *	Est.	-0.071	-3.913	-6.032	0.610	-1.855					
	SE	1.859	2.514	1.894	0.645	1.762					
	p	0.970	0.120	0.001	0.551	0.345	0.292				
<i>Formica uralensis</i> *	Est.	-2.066	0.946	-0.630	0.007	-0.769					
	SE	0.718	1.166	0.947	0.406	0.476					
	p	0.004	0.417	0.506	0.100	0.985	0.106				
<i>Myrmica scabrinodis</i> *	Est.	-0.004	1.304	0.887	0.768	-1.120	0.461				0.449
	SE	0.568	0.873	0.651	0.318	0.411	0.242				0.236
	p	0.995	0.135	0.173	0.016	0.006	0.057				0.057
<i>Lasius platythorax</i> **	Est.	-0.743	0.485	1.472	-0.314	-0.322		-0.410		-0.467	
	SE	0.591	0.763	0.607	0.309	0.272	0.267	0.221		0.232	
	p	0.208	0.525	0.015	0.308	0.153	0.228	0.064		0.044	
<i>Formica sanguinea</i> **	Est.	-1.664	0.111	0.343	0.112	-0.619					
	SE	0.503	0.867	0.582	0.291	0.468					
	p	<0.001	0.898	0.555	0.700	0.186					
<i>Leptothorax acervorum</i> **	Est.	-1.391	-0.754	-0.248	-0.287	-0.582			-0.527	-0.626	
	SE	0.698	0.872	0.631	0.381	0.503			0.309	0.337	
	p	0.046	0.387	0.694	0.451	0.247			0.088	0.063	
<i>Myrmica rubra</i> **	Est.	-2.630	0.923	0.215	0.124	-0.064	-0.622				
	SE	0.678	1.111	0.815	0.375	0.375	0.376				
	p	<0.001	0.406	0.792	0.741	0.955	0.098				
<i>Myrmica ruginodis</i> ***	Est.	0.011	2.540	0.679	-0.333	0.195	0.541	0.552	0.492		
	SE	0.467	0.932	0.586	0.300	0.387	0.268	0.251	0.242		
	p	0.982	0.006	0.246	0.267	0.614	0.043	0.028	0.042		
<i>Camponotus herculeanus</i> ***	Est.	-2.13	2.034	1.414	-0.269	1.016					-0.473
	SE	0.680	0.93	0.759	0.279	0.411					0.239
	p	0.002	0.029	0.062	0.336	0.754	0.014				0.048

Ants responded statistically significantly to a number of variables tested, although the species seemed to differ in sensitivity (Table 5). Only the mire specialist *M. scabrinodis* responded significantly and positively to *Sphagnum* moss cover, although there is a suggestive trend of mire specialist species being positively associated with *Sphagnum* cover and forest species the opposite way (Fig. 4 A). The number of tall trees (>3 m) seemed to affect the majority of species as expected a priori: the probability of occurrence of mire specialist species tended to decrease and that of forest species to increase with an increase in the number of tall trees (Fig. 4 B). Two species responded statistically significantly to the number of tall trees: as predicted, the mire specialist *M. scabrinodis* negatively and the forest species *C. herculeanus* positively. None of the species responded statistically significantly to hummock cover, although the mire specialist *F. picea* and the generalist *L. platythorax* appeared to respond positively and the forest species *M. ruginodis* negatively to hummock cover (Fig. 4 C, Table 5). Additionally, a few other variables remained in the final models, but for only two species the responses were statistically significant: *C. herculeanus* showed a negative response to dead trees, and *M. ruginodis* responded positively to low and tall dwarf shrubs and annual plants (Table 5).

The ant-assemblage structure of the drained mires differed from the pristine mires in the NMDS ordination (treatment, $r^2=0.221$, $p<0.001$), but the scatter of the sampling locations was large in each of the three treatments, and the locations of the restored mires overlapped with those of both pristine and drained ones (Fig. 5 A). There seems to be a naturalness gradient from the sampling locations of pristine mires (to the right) towards those of drained mires (to the left), with the locations of restored mires in-between (Fig. 5 A). Seven of the 15 fitted environmental variables correlated significantly ($p<0.001$) with the NMDS-ordination space: the cover of *Sphagnum* mosses and that of the microsite type flark increased towards the pristine locations, whereas the rest of the statistically significant variables were related to drainage and correlated approximately in the opposite direction, towards the drained and restored mires (Fig. 5 A). Ant assemblages differed from each other such that the more forested mires seemed to be located to the left-hand side (correlation with tall trees) and the more open mires with abundant lower trees more to the top of the ordination.

Differences in ant assemblages among the non-pristine mires were expressed such that the shade-tolerant forest species *C. herculeanus* and *M. ruginodis* occurred in the more heavily forested sampling locations at the bottom left of the ordination, whereas species of open-canopy forests and mires – such as *L. platythorax*, *Leptothorax acervorum*, *Formica sanguinea* and *F. exsecta* – characterized the less densely forested sampling locations to the top right (Fig. 5 B). Open pristine mires were characterized by the occurrence of the mire species *F. picea* and *M. scabrinodis*, at the bottom right of the ordination (Fig. 5 B). Another mire species, *F. uralensis*, however, had benefited from drainage at least temporarily, and is located closer to the forest species *C. herculeanus* and *M. ruginodis* in ordination (Fig. 5 B). Indeed, half of the occurrences of *F. uralensis* were from drained mires (Table 4).

4 Discussion

In general, our results showed predictable responses in both habitat structure – including vegetation – and ant assemblages to mire drainage and restoration. This conclusion is similar to the results in a mire restoration study dealing with a number of solitary invertebrate groups (Noreika et al. 2015). Taken together, our results are consistent with the Field of Dreams hypothesis (Palmer et al. 1997), which suggests that if you rebuild the habitat structure, the flora and fauna will return; here mire restoration resulted in rapid recovery of mire vegetation and ant assemblages (see also

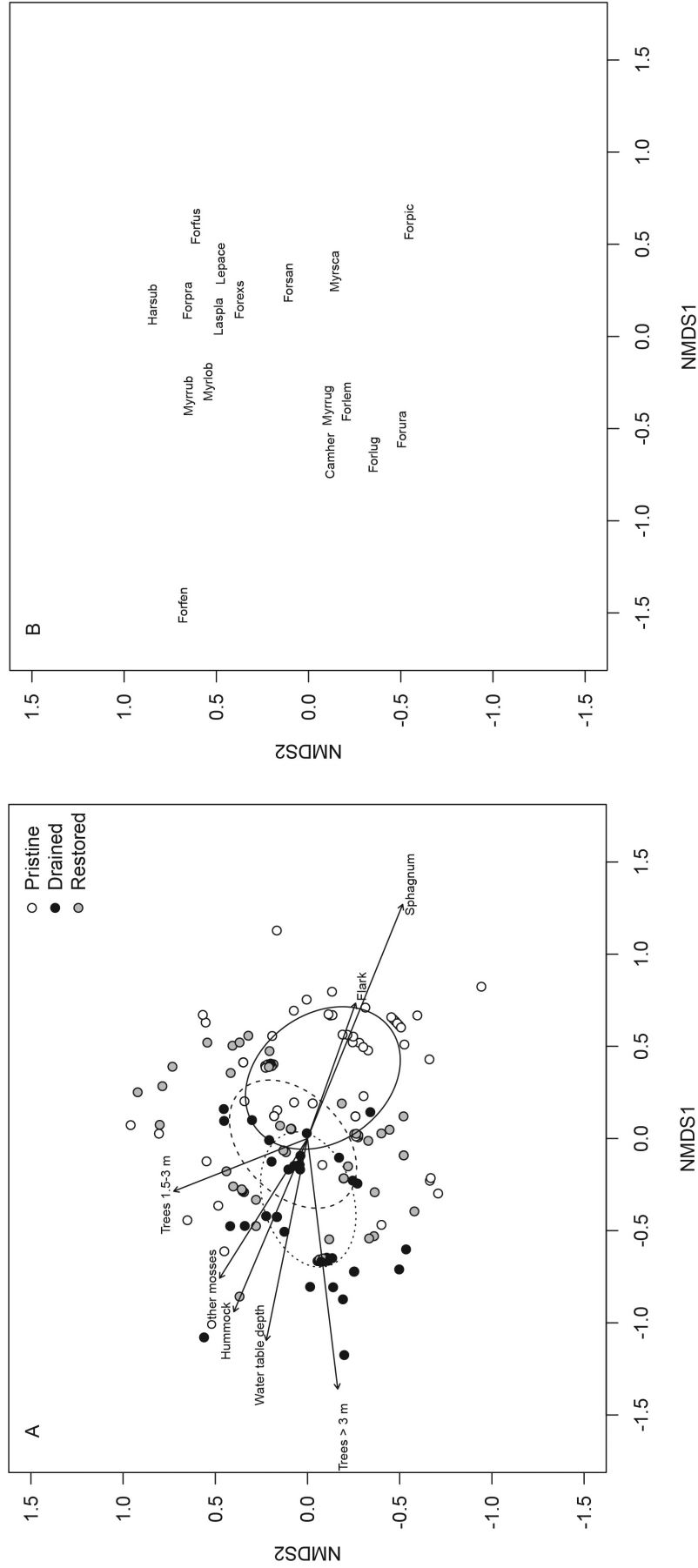


Fig. 5. NMDS ordination plots of the ant data presenting (A) sampling locations of the pristine (white dots), drained (black dots) and restored (grey dots) mires and (B) ant species within the sampling locations. The dispersion ellipses in plot A indicate 1 SD of the weighted average of the site scores of pristine (solid line), drained (dotted line) and restored (dashed line) mires. The arrows in plot A indicate the environmental variables fitted to the ordination space such that only variables with highly significant p-values are shown ($p < 0.001$). For species abbreviations, see Appendix 2 (abbreviations represent the first three letters of the genus name and the first three letters of the species name).

Noreika et al. 2015). However, for mire-specialist ant species the results were variable and longer-term monitoring is needed to evaluate the success of restoration. Considerable time lag – relative to solitary insects with shorter generation times – is expected in the response of ants, which form long-lived perennial colonies with long colony cycles.

4.1 Effects of drainage and restoration on mire-habitat structure

Restoration measures – the filling of ditches, heavy thinning and partial clear-cutting of tree stands – were successful in that both the water-table level and stand structure of restored mires matched those of pristine mires, although heavier cuttings of larger trees would have been required to accord better with pristine mires in terms of tree-canopy shading. The amount of dead wood was generally low in all mires, and the amount of small logs was only slightly higher in drained and restored mires than in pristine ones indicating that tree mortality due to competition had not yet started in drained mires, and that coarser logging residues (felled trees) were not left behind in restored mires in large quantities.

We showed that tree stand structure was more variable in the drained than in the pristine or restored areas (Fig. 1 A), which followed probably both from drainage and forest management activities. In the long run, forest management tends to homogenize stand structure by, e.g. decreasing variation in stem size distribution, whereas forest stands in pristine mires exhibit multi-modal structure (Utterä et al. 1997).

The pristine microsite-type distribution was re-established a few years after restoration: the mire surface was almost completely covered by the hummock microsite type in drained mires, but was reduced to two thirds in restored mires, whereas it was 46% in pristine mires. Although habitat structure of the restored mires had clearly changed towards pristine conditions in a few years after restoration, the cover of *Sphagnum* mosses was still lower (similarly as 10 years after restoration in Haapalehto et al. 2011), and the cover of e.g. tall dwarf shrubs was still higher in restored than pristine mires (see Fig. 3 in Laine et al. 1995a).

Drainage seemed to have led to similar successional changes of mire vegetation as in earlier studies – increased occurrence and cover of forest species and the disappearance or decline of mire species (Laine et al. 1995a; b; Jauhiainen et al. 2002; Haapalehto et al. 2011; Haapalehto 2014). Similarly, a rapid change towards pristine floristic composition in restored mires has been observed in earlier studies. The strength of the response depends on the severity of degradation of the drained mires, and on mire fertility. Rapid responses have been restricted to less heavily degraded sites within restored mires, whereas no or only minor changes have been reported from heavily degraded sites (Komulainen et al. 1999; Jauhiainen et al. 2002; Haapalehto et al. 2011; Haapalehto 2014). In our data, the rapid recovery may have been enhanced by a lack of dispersal barriers, as the restored mires were parts of larger mires with varying proportions of unditched areas. These likely provide refugia for mire species in close proximity of the drained and restored mires, and thus they also serve as potential areas for recolonization of restored mires.

Similarly to earlier studies, some species, e.g. *Eriophorum vaginatum*, responded strongly by increasing in cover (Komulainen et al. 1999; Jauhiainen et al. 2002; Haapalehto et al. 2011). On the other hand, some bog species of wet hollows, e.g. *Carex limosa* and *Scheuchzeria palustris* L., seemed to be missing from restored mires in the short term (similarly as 10 years after restoration in Haapalehto et al. 2011), and in another study these species seemed not to have colonized restored mires even after half a century, despite the existence of nearby populations (Soro et al. 1999). Laine et al. (2011) monitored the effects of restoration on vegetation of oligotrophic pine fens in a more northern area in Kainuu, eastern Finland for two years. They showed that the vegetation of drained mires had not changed much from pristine conditions during 30 years of drainage: only the typical

hollow species *Sphagnum majus* (Russow) C.E.O.Jensen, *S. balticum* and *Scheuchzeria palustris* were missing. Laine et al. (2011), however, also found that there were only minor differences in the floristic composition before vs. after restoration in the two-year monitoring period: the only statistically significant restoration-related change was that the cover of sedges increased in restored and decreased in pristine fens.

4.2 Ant occurrence in mire-site types

Knowledge on the ant fauna of mire types is limited (Oinonen 1956; Krogerus 1960). We showed the importance of tree cover on the occurrence of ant species among mire types: the occurrence rates of mire species tended to decrease with increasing growing stock, whereas forest species showed the opposite pattern (Table 3).

A NMDS analysis of the data of Krogerus (1960) revealed a clear gradient in the composition of ant assemblages from open fens and rich fens through pine mires and pine bogs to spruce mires (Punttila et al. 2013). Dlussky (2001) found a similar openness gradient within an oligotrophic bog in the Novgorod district, Russia. The ant assemblages of the open central parts of the bog were characterized by true (“endemic”) mire species (*F. picea*, *F. uralensis* and *F. forsslundi* Lohmander, 1949) and some “forest species” (*L. platythorax*, *M. rubra*, *M. scabrinodis* and *L. acervorum*), whereas pine forests of the mire edges were occupied by forest species (*C. herculeanus*, *L. platythorax*, *M. rubra* and *F. polycytena* Förster, 1850). This openness gradient resembles our NMDS-ordination results (Fig. 5 B), which showed that assemblages at the open end of the gradient were characterized by the mire species *F. picea*, *M. scabrinodis* and *F. uralensis*. On the other hand, the assemblages in sparsely forested areas with low trees were distinguished by species that colonize recently disturbed or naturally open forest areas (e.g. *L. platythorax*, *L. acervorum*, *F. sanguinea*, *F. exsecta*). Finally, the more heavily forested areas with tall trees were characterized by forest species that are capable of persisting through the whole cycle of forest succession, i.e. *C. herculeanus* and *M. ruginodis* (Niemelä et al. 1996).

4.3 Drainage and ants

The succession of tree stands on drained mires with increased growing stock of large trees and increased deciduous mixture of birch with pine result in shaded conditions. This change decimated colonies of mire-ant species requiring sun exposure, which prevails in pristine conditions of pine mires whereas shade-tolerant forest species, such as *Camponotus herculeanus* and *Myrmica ruginodis*, benefitted similarly as in earlier studies and thus, the ant assemblages of drained mires differed clearly from those of pristine mires (Krogerus 1960; Collingwood 1963; 1999; Vepsäläinen et al. 2000; Punttila and Kilpeläinen 2009). The mire specialist *Formica picea* in particular suffered from drainage and this is also expected in the long term for *F. uralensis* (which seems to benefit from the early stages of drainage) and *M. scabrinodis* (Krogerus 1960; Vepsäläinen et al. 2000). Krogerus (1960) found that *F. picea* inhabited the moistest parts of pine mires but *F. uralensis* the driest sites. Punttila and Kilpeläinen (2009) found that the occurrence rates of the three mound-building species restricted to mires in their data are highest in undrained pristine mires, lower in transforming mires and lowest in transformed ones (*F. uralensis*), or the species are missing from transformed mires (*F. fennica* Seifert, 2000 and *F. forsslundi*), whereas the most common species of forests on mineral soils, the wood ant *F. aquilonia* Yarrow, 1955, showed the opposite pattern. Similar results have been obtained in southern Sweden where the slow drying-out of bog areas has decimated the prevalence of the mire species *F. uralensis*, *F. forsslundi* and *F. picea* in only one decade (Collingwood 1999).

In our data, ant species of drier open habitats (e.g. open early successional forests after disturbances) and generalist ant species benefitted from the early phases of mire drainage. Most of these species disappeared with tree-canopy closure also during forest succession on mineral soils (Punttila et al. 1991), but in the early stages of drainage they seem to replace mire species. For instance, *M. ruginodis* replaced *M. scabrinodis* (Vepsäläinen et al. 2000) although *M. scabrinodis* appeared to be more resilient than other mire species (see also Collingwood 1999), and especially *Lasius platythorax* (Collingwood 1999; Dlussky 2001) but possibly also *Formica fusca* Linnaeus, 1758 and *F. lemani* Bondroit, 1917 seemed to replace *F. picea*, and in the later successional stages, *F. aquilonia* replaced territorial mound-building mire species (Vepsäläinen et al. 2000; Punttila and Kilpeläinen 2009). Open treeless mires or sparsely forested, drained open mires do not necessarily provide any habitat for wood ant species of the *Formica rufa* group (*F. aquilonia*, *F. lugubris* Zetterstedt, 1838, *F. rufa* Linnaeus, 1758, *F. polycтена* and *F. pratensis* Retzius, 1783) because arboreal aphid colonies providing nourishment for wood ants are scarce, and the foraging activity of wood ants may cease for long periods of time during high day-time temperatures in open mires and, finally, wood ants cannot find suitable below-ground overwintering sites deep enough because of the high water-table level (Vepsäläinen et al. 2000). In wooded and drained mires the situation is different which enables colonization of wood ants: when mire drainage proceeds, territorial wood-ant species of mineral soils also start to dominate transformed mires (Punttila and Kilpeläinen 2009). In our data, the wood ants *F. lugubris* and *F. pratensis* were missing from pristine mires, but these species occurred in seven (15%) and two (4%) sampling locations in drained, and in three (5%) and one (2%) locations in restored mires, respectively (Appendix 2).

4.4 Restoration and ants

We are not aware of any other study on the effects of mire restoration on ants, but with the results of the present study and the results of earlier studies concerning drained mires, together with information about the autecology, competitive capacity and dispersal of different ant species, we can outline some general principles to be taken into account when planning mire restoration.

The rewetting of mires and removal or strong thinning of the growing tree stock are key components in successful restoration of mire ants. A high water-table level prevents the overwintering of top-competitors of the territorial *Formica* ants of heath forests in mire habitats and thus leaves the terrain free for typical mire-ant assemblages to develop with their own top-competitors of other territorial *Formica* ants, such as *F. uralensis*, *F. exsecta* and *F. forsslundi* (see Punttila and Kilpeläinen 2009).

Another important issue in mire restoration for ants is the treatment of logging waste, i.e. tree stems, tops, branches and cut stumps after logging in naturally treeless or sparsely forested mires: whether these are left behind or harvested (Punttila et al. 2013).

Despite the fact that the amount of dead trees in our study was generally low in all treatments, the amount of small logs was somewhat higher in drained and restored mires than in pristine ones, thus providing more nesting sites for forest ants there. Most of the boreal forest ant species can nest in or even require dead wood for establishing new colonies, and for many species in many habitat types a large share of ant nests are located in dead wood (e.g. Oinonen and Wuorenrinne 1976; Franch and Espadaler 1988; Punttila and Haila 1996; Włodarczyk et al. 2009; Persson et al. 2013). Thus, leaving stumps, felled trees or logging residues in restored mires may enhance colonization of non-desired forest species in the restored mire habitats. Dead wood provides elevated microhabitats that may offer the only sun-exposed and warm above-ground nesting sites for forest ants. Such conditions are found in habitats where dense, shading herb-layer vegetation prevents sun exposure of the ground. In forested habitats, this may happen shortly after the crea-

tion of tree-canopy openings by wind throws, fire or cuttings, but this may also take place after disturbances – e.g. ditching or restoration – in mires.

Although the rapidly recovering moss layer of the restored mires may overgrow logging residues and cut stumps within a few years following restoration, they nevertheless provide luxuriant nesting substrates for a large variety of forest and generalist ant species. These newcomers may later prevent or slow down the colony establishment of mire specialist ant species by predation pressure on the dispersing mire-ant queens attempting colony founding, and through nest-site competition and pre-emption of nesting sites – such priority effects are exemplified, e.g. in the colonization by ants of small land uplift islands of the Baltic Sea (see Vepsäläinen and Pisarski 1982). These types of nesting substrates are missing almost entirely from pristine open mires and thus, their creation should be minimized in the restoration process. Ant species of open successional forests may also be capable of replacing the few remaining but weakened mire ant populations of restored mires. These forest species are also able to inhabit logging residues in the middle of larger restored mires, as the dispersing females of some of these species are rather strong fliers (Vepsäläinen and Pisarski 1982; Czechowski et al. 2013). The colonization of many aggressive and territorial *Formica* species is dependent on the occurrence of species in whose nests they start new colonies by temporary parasitism (Gösswald 1951; 1952; Kutter 1969; Wilson 1971; Collingwood 1979; Seifert 2000; 2007; Czechowski et al. 2012). These species can often utilize both mire specialist species remaining in the area, and generalist species of mineral soils, which have colonized the drained mire. Thus, their colonization may be enhanced in areas where both mire and forest species occur together (Collingwood 1979; Seifert 2007). Another option for logging-residue harvesting is to girdle the trees and let them die standing, which reduces the amount of potential dead-wood nesting sites for forest ant species by spreading the increase of logs on the ground over a longer time span.

In restoration planning, the surrounding terrestrial environment should also be taken into account to inhibit possible colonization of forest ants in restored mires. Restoration efforts can be timed to years when there are no larger regeneration cuttings or young sapling stands in close proximity to the restored areas. For instance, in southern Sweden, the eradication of *Formica picea* from slowly drying bogs was accelerated by colonization pressure and subsequent competitive exclusion by *Lasius platythorax*, which immigrated from the surrounding fresh thinning cuttings performed a few years earlier. In the cut area, the forest floor was covered by logging residues, fallen trees and sun-exposed cut stumps. Nearly all the cut stumps were occupied by flourishing *L. platythorax* colonies, and these ants were also seen in large quantities in bog tussocks in the mires (Collingwood 1999).

Our knowledge on the dispersal capacity and competitive ability of mire ants is scanty (but see Collingwood 1979; Vepsäläinen et al. 2000). Thus, it is difficult to predict the recolonization of restored mires by mire ants. Apparently dispersal among different habitat patches by winged females is rather limited at least in many polygynous ant species and populations (Sundström et al. 2005; Seppä 2008), but generally the dispersal capacity seems to vary widely from very strong dispersers (e.g. *L. niger*, *C. herculeanus*) to seemingly poor ones (see Vepsäläinen and Pisarski 1982). There is evidence that the dispersal of the mire ant *Formica picea* is weak, not only between different mires but also within mires (Mabelis and Chardon 2005; Rees et al. 2010). In our data, this species seemed to be almost exclusively confined to pristine mires. The recolonization of *F. picea* in restored mires probably depends heavily on the closeness of healthy populations. This may be critical for restoration because successful colonization of the rewetted mires by *F. picea* is a prerequisite for the subsequent colonization of the other true mire species, *F. forsslundi* and *F. uralensis*, which establish their new colonies through temporary parasitism in the nests of *F. picea*.

4.5 Habitat disturbance and ant colonization

Habitat disturbance often opens up new colonization possibilities for boreal ants in forested areas. Disturbances create favourable climatic conditions for species that require warm and well-lit conditions at least during the colonization stage. Large disturbances in mature forests also open competition-free terrain by often wiping out the territorial wood-ant colonies, whereas these colonies seem to tolerate smaller disturbances (Punttila et al. 1991; Punttila et al. 1994; Punttila 1996; Punttila et al. 1996; Sorvari and Hakkarainen 2005; 2007; Kilpeläinen et al. 2008; Punttila and Kilpeläinen 2009; Sorvari et al. 2011). In our data > 60% of *Camponotus herculeanus* queens were found in the samples of restored mires. Restored mires, however, should be inferior habitat for this wood-inhabiting species, because most of the trees have been removed from there, and the cut stumps are probably rather quickly buried under the growing mire mosses. Such colonization attempts may, however, be explained by possible attractiveness of recently disturbed open areas following restoration measures. Flying *Camponotus* queens might orientate towards light reflecting from disturbed habitat patches similarly as many other ant species do (Brian 1952; Pontin 1960; Brian et al. 1966; Wilson and Hunt 1966; Fowler 1987; Tschinkel 1987). In forested areas, recently disturbed areas devoid of territorial wood ants (*Formica rufa* group) are presumably optimal habitats for colony founding, and high queen numbers have indeed been observed in fresh clear-cuts following cutting and prescribed burning (Punttila et al. 1991; Punttila and Haila 1996). Also *Lasius platythorax* probably benefitted from recent disturbances in restored mires as suggested by our data.

Disturbed forested boreal areas are quickly colonized by many ant species requiring open conditions in at least the colony-founding stage, and thus the habitat becomes crowded such that the only options remaining for colony founding are nest parasitism and – for queens in established colonies – colony budding (Punttila et al. 1991). Such crowded conditions, however, seem not to be reached often in open pristine mires although these are long-lived habitats. Our own experience is that open pristine mires are often sparsely inhabited by ant colonies. The reason why apparently suitable nesting sites often remain uninhabited is not known, but presumably any larger ant-free terrain can be created by extreme events such as long-term flooding that drowns the ant colonies, or severe winters with thin snow cover lowering the overwintering survival of colonies, or wildfires in exceptionally dry years. The commonness of such events might ultimately determine the nest density of the mire. If this were the case, polygyny and subsequent budding, leading to multinest colonies, would increase the resilience of mire ant colonies in the long run, as the risk of extirpation of an extensive nest network should be smaller than that of a single nest (Mabelis and Chardon 2005).

On the other hand, ant assemblages in drained mires in our data had become more crowded than in pristine mires, as they housed populations of both forest and mire species. Thus, in both pristine and drained mires, nest budding (leading to multinest colonies) and nest parasitism are most likely as important modes of nest-founding as in successional boreal forests. In our data, the high frequency of *Myrmica* queens – *M. scabrinodis* in pristine and *M. ruginodis* in drained mires – indicated the occurrence of polygynous colonies, where the queens are moving or transferred among the nests of multinest colonies (Punttila et al. 1991; Seppä et al. 1995). Our data were, unfortunately, insufficient for making any observations on nest parasites because our sampling window was outside the dispersal period of most species, which is in the late season.

4.6 Conclusions

Generally, we tested whether restoring simple but crucial habitat characteristics, the water-table level by ditch filling and the naturally sparse and low pine stand by thinning and clear-cutting, would lead to recolonization and recovery of the characteristic vegetation and ant assemblages of pristine mire habitats. Here we cannot yet evaluate long-term restoration success, but our short-term results are consistent with predictions of the Field of Dreams hypothesis (Palmer et al. 1997), which does not necessarily apply to more heavily degraded mire ecosystems. The recovery of our study mires was fast because the drained mires still had an acrotelm (the surface layer of mire soil) and catotelm (core of peat), and mire organisms could recolonize the restored mires either from local refugia or from populations of nearby mires (see the discussion in Komulainen et al. 1999; Vasander et al. 2003). The connectedness of mire habitats, however, has been severely reduced especially in southern Finland; consequently, recolonization has become unlikely for many mire specialist species, which have become locally threatened (Rassi et al. 2010). Such demanding species in boreal areas may include the workerless social parasite *Myrmica karavajevi* (Arnoldi, 1930) and the temporary parasite *M. vandeli* Bondroit, 1920. Both species require dense colonies of their host ant *Myrmica scabrinodis* for which, especially within the boreal mainland areas of Finland, the most important habitat is mires (Vepsäläinen et al. 2000; Punttila et al. 2013). Degradation of mire habitats and their fragmentation may lead to the disappearance of these highly specialized rare social parasites and other mire specialist species from large areas. In Finland, the threat is most acute in the south, where almost 80% of mires have been drained and the distances between restored mires and pristine mires housing potential source populations are increasing with decreasing connectedness, which weakens the recolonization prospects of specialist species once they have disappeared (Vepsäläinen et al. 2000; Auvinen et al. 2007; Punttila et al. 2013).

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Total of 109 references.

Supplementary files

Appendix 1 and 2 are available at <http://dx.doi.org/10.14214/sf.1462>.