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Spring bryophytes in forested landscapes: Land use effects on bryophyte species richness, community structure and persistence

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Abstract

Many freshwater ecosystems face severe threats from anthropogenic disturbances, yet little is known about the degree to which their biotic communities have been degraded by human activities. We analysed temporal changes and persistence of bryophyte communities in 40 springs in eastern Finland by comparing field surveys conducted in 1986 and 2000. During that period, some springs had remained in a near-pristine state, while others had undergone varying degrees of disturbance from forest management, drainage, and water abstraction. Several spring bryophytes (e.g., *Philonotis fontana*) declined between the study years, whereas *Sphagnum* mosses (e.g., *Sphagnum warnstorfii*) increased in abundance. Species richness of spring bryophytes declined significantly from 1986 to 2000, irrespective of bryophyte group (spring vs. other bryophytes) and spring condition (severely disturbed vs. unaltered springs). Bryophyte cover also decreased dramatically from 1986 to 2000, but this effect was related to both spring condition and bryophyte type. Spring bryophytes lost much of their cover in severely altered springs, while in unaltered springs they remained relatively stable through time. No such trend was observed for other, habitat generalist bryophytes. Persistence and stability of bryophyte communities showed significant, albeit rather weak, relationships with spring condition, with communities in unaltered springs being more persistent than those in altered springs. Given the importance of springs to boreal forest and aquatic biodiversity, restoration of degraded springs is a major challenge to maintaining and conserving biodiversity of boreal landscapes.

Keywords: Biodiversity conservation; Boreal forests; Bryophytes; Community persistence; Landscape disturbance; Species richness; Springs

1. Introduction

A major challenge to conservation biologists is to estimate the degree to which natural ecosystems and their biota have been altered by landscape-scale anthropogenic disturbances. Such disturbances may be of severe concern if they threaten the key biotopes, i.e., habitats that harbour valuable components of biodiversity and have far-reaching effects on the surrounding ecosystems. In boreal forests, springs are among the most important key biotopes, because they provide suitable habitat for many rare and threatened aquatic species, and enhance the biodiversity of the surrounding terrestrial landscape (Virkkala and Toivonen, 1999). Unfortunately, the degree to which springs are influenced by anthropogenic disturbances remains largely unknown, yet such information is urgently needed given the conservation value of the spring biota

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(Fensham and Price, 2004). Studies on other types of small freshwater ecosystems (e.g., headwater streams) have shown, however, that land use practices in the catchment area may severely threaten the integrity and biodiversity of these vulnerable ecosystems (e.g., Roth et al., 1996; Harding et al., 1998; Vuori et al., 1998).

Major factors threatening the biodiversity of springs in boreal regions include forestry and agricultural activities, road construction, and water abstraction. Land use and water abstraction have considerably reduced the number of springs and altered their habitat characteristics, but knowledge of their effects on spring biota is largely lacking. Most studies to date only give approximate figures to the degree of physical degradation of spring habitats. For instance, it has been estimated that spring vegetation has been almost completely altered by drainage in southern Finland, whereas only one fourth of the springs have been similarly modified in central Finland (Eurola et al., 1991). Although these figures are only rough estimates, they nevertheless underscore the alarming rate of spring habitat loss in boreal regions.

Bryophytes are a dominant plant group in boreal springs. Spring bryophytes include both species dependent on ground water discharge, thus occurring almost exclusively in springs, and hygrophytic mosses and liverworts with a wider distribution in semiaquatic/aquatic habitats. For instance, approximately 24% of Finnish bryophytes occur in wetland habitats, such as mires, springs and streams, and a notable number (16 of 78 species) of these semiaquatic and aquatic species are red-listed (Ulvinen et al., 2002). However, the degree to which the endangerment of spring bryophytes is due to landscape-level disturbances has not been assessed rigorously.

We studied spring bryophyte communities in eastern Finland in relation to anthropogenic, landscape-level disturbances. Our study was based on re-sampling a set of 40 springs previously sampled in the mid-1980s by Saastamoinen (1989). Between these two sampling periods, more than half of the springs and their surroundings were severely impacted by human activities, while the rest had remained in a relatively unaltered state. Our main objectives were to examine (1) whether the spring bryophyte flora of the study region had undergone (1a) any changes, and (1b) changes that could be related to anthropogenic disturbances in the catchment area. We further assessed (2) whether these disturbances had influenced the persistence (invariability of species composition) and stability (invariability of species abundances; see e.g., Scarsbrook, 2002) of the bryophyte communities.

2. Material and methods

The study springs are located in eastern Finland (63–64°N, 28–31°E) in the middle boreal vegetation zone (Ahti et al., 1968). The vegetation is dominated by a mosaic of mires and coniferous forests (mainly Norway spruce *Picea abies* and Scotch pine *Pinus sylvestris*). Deciduous vegetation (mainly alder *Alnus incana*, birch *Betula pubescens*, and willows *Salix* spp.) characterises productive stream valleys. The landscape is hilly, but relative differences in elevation are modest (<100 m). The dominating soil type is glacial till, but some eskers occur particularly in the south-eastern part of the study area. Water pH of the study springs ranged from 5.0 to 6.6, alkalinity from 0.03 to 0.43 mmol/L, and conductivity from 2.1 to 8.5 mS/m. Preliminary analyses showed, however, that none of these environmental variables explained significantly variability in spring bryophyte diversity and community structure (Virtanen, unpublished data). Furthermore, there were no appreciable changes in spring water pH, conductivity, and nutrients between 1986 and 2000, based on standardised water sampling, so these factors are unlikely to be associated with the overall changes in bryophyte assemblages during this period.

Most of the springs were close to a natural state in 1986, but some of them had undergone varying degrees of anthropogenic change by 2000. In 2000, the springs ranged from totally degraded to near-natural. Accordingly, we scored each spring during the 2000 survey on a scale of 0–3, ranging from completely destroyed to unaltered springs. This assessment combined multiple observations on the degree of forestry, ditching, water abstraction, and construction in, and adjacent to, each spring, using methods commonly employed in biodiversity surveys of springs in Finland (Ohtonen et al., 2005). Thus, for example, when a spring had been destroyed by drainage, distinct points of groundwater discharge with associated moss vegetation were still often detected, and such a spring obtained a score of 1. When moderately altered, only part of a spring was disturbed by, for example, water abstraction (score 2). Intermediate stages (scores 0.5, 1.5, 2.5) were also possible.

Bryophyte sampling was conducted following the same, strictly standardised scheme in each spring in both years. We studied 1–6 quadrats ($0.25\,m^2$) in each spring, the number of quadrats depending on spring area and length of the runoff channel. The first quadrat was placed at the outflow point and subsequent samples were taken along the runoff channel at regular intervals of 1, 2, 3, 5 and 10 m. It should be noted, however, that no attempt was made to sample exactly the same plots on both sampling years. We identified all bryophyte species and estimated their cover (%) for each quadrat. Cover values were averaged over such quadrats, and pooled species counts from all quadrats of each pond were equal to species richness in this paper.

The bryophyte data included 60 species. Some highly sporadic and rare species (those occurring at a single site in one year) were omitted, leaving 56 species for the analysis. The species were divided in two major groups following Eurola et al. (1984): (i) spring bryophytes – species growing mainly in springs and in rich, ground-water affected fens; (ii) other bryophytes – species of nutrient-poor mires and wetlands, including all *Sphagnum* species. The nomenclature follows Ulvinen et al. (2002).

2.1. Statistical analyses

Temporal changes in mean bryophyte cover and species richness (pooled across individual plots in each spring) in relation to status score were examined using generalised linear mixed effects modelling (Pinheiro and Bates, 2000). Mixed effects models are particularly suitable for analysing data with repeated measures, and they allow modelling with categorical and continuous covariates. Generalised mixed effects models also allow definition of appropriate error structures. Here, Poisson error structure was used for species richness, and normal error structure for percent cover (square-root transformed). Analyses were run using glmmPQL [generalised linear mixed effects model with Penalised Quasi-Likelihood], as implemented in the statistical software R (version 1.7.1., The R Development Core Team, 2003). Models included year and intercept as random factors. The explanatory variables included year (1986 or 2000), status score (0–3) and bryophyte group (spring bryophytes vs. other bryophytes). We tested (i) whether the cover/richness of spring bryophytes and/or other bryophytes changed from 1986 to 2000, and (ii) if such changes occurred, were they related to changes in spring condition (i.e., status score) between the years. For this purpose, we first constructed a model with all explanatory variables and their interactions. The presence of significant interactions would lead to rejection of the null hypothesis of no changes between the years, or that these changes were independent of status score and bryophyte group. In model simplification, we thus first tested whether the third or second order interaction terms were significant; if not, the terms were removed from the model. Akaike information criterion (AIC) was also used in selecting the model (best model having the lowest AIC value).

Changes in species composition (persistence) and in bryophyte species cover (stability) in relation to spring condition were examined using linear regressions on similarity indices. We first calculated a similarity index (1986 vs. 2000) for each site, separately on presence–absence (Sørensen's coefficient; persistence) and cover data (Czekanovski's coefficient; stability). The relationship between the similarity indices and the status score were then examined using simple linear regressions.

3. Results

Only eight of the 40 springs studied remained in close to a natural state (status score 3) by year 2000, whereas 10 springs were moderately (score 2) and 22 severely (score 0–1) altered. Forestry activities, consisting mainly of wetland drainage, ranked as the most common cause of alteration (24 sites), followed by water abstraction (9 sites) and agricultural activities (7 sites).

Several spring bryophytes decreased from 1986 to 2000, four of them significantly (i.e., *Bryum pseudotriquetrum*, *Philonotis fontana*, *Scorpidium revolvens*, and *Warnstorfia exannulata*) (Table 1). Across the study sites, 17 spring bryophytes showed a 5% or larger change in cover: 13 of these decreased, four increased in abundance. Corresponding figures for other bryophytes were five and four, respectively (Table 1). Most species did not show significant among-year differences in mean cover, but for several species, the low number of observations (frequency less than 0.1) limited the chance of detecting a difference. Three species, *Sphagnum warnstorfii*, *Sphagnum girgensohnii, and Polytrichum commune*, increased significantly from 1986 to 2000 (Table 1). The mean cover of all *Sphagnum* species combined increased from 3.7% in 1986 to 15.0% in 2000 (paired *t*-test for the difference, $p = 0.015$), while their frequency of occurrence did not change accordingly (0.78 vs. 0.60, respectively).

Bryophyte species richness was significantly related to year, with more species in 1986 than in 2000 (Table 2, Fig. 1). The interaction term status score × bryophyte group was also significant, implying that bryophyte groups differed in their response to spring degradation: species richness increased with status score, but only for spring bryophytes (Fig. 1). Percent cover also differed between the bryophyte groups, spring bryophytes being generally more abundant (Table 3, Fig. 2). Significant interaction term (year × group) implies that the bryophyte groups had different patterns of temporal change. Significant three-way interaction (year × status × group) reflected the fact that spring bryophytes declined drastically in degraded springs, but no changes were observed in springs that remained in good condition by year 2000. No corresponding changes related to spring condition were observed for other bryophytes (Fig. 2).

Bryophyte community persistence was related to status score. Both presence–absence data (persistence, Sørensen's coefficient) and abundance data (stability, Czekanovski coefficient) showed that communities remained more similar through time in unaltered than in disturbed springs. It must be emphasised though that the status score explained only a minor portion of variability in bryophyte community persistence (Table 4, Fig. 3).

4. Discussion

Present-day biodiversity crisis urges conservation biologists to measure the rates of decline in taxonomic and functional biodiversity in various ecosystems (Tilman and Lehman, 2001). There are, however, alarmingly

Table 1
Mean cover at occupied sites and frequency of occurrence (proportion of springs occupied by a species across whole region) of bryophyte species in the studied springs in 1986 and 2000

	1986 Cover	1986 Frequency	2000 Cover	2000 Frequency	*P*
Spring bryophytes					
Brachythecium rivulare	29.06	0.23	16.87	0.30	
Breidleria pratensis	0.25	0.03	0.25	0.03	
Bryum pseudotriquetrum	10.79	0.28	4.09	0.25	*
Bryum weigelii	7.71	0.33	8.40	0.33	
Calliergon cordifolium	15.19	0.15	0.93	0.08	
Calliergon giganteum	13.33	0.03	31.67	0.05	
Calliergon richardsonii	0.10	0.08			
Chiloscyphus polyanthos	17.80	0.28	12.48	0.33	
Fissidens adianthoides	0.13	0.03			
Fissidens osmundoides	0.04	0.03			
Harpanthus flotovianus	4.68	0.10	1.19	0.10	
Marchantia polymorpha	9.67	0.10	15.42	0.05	
Paludella squarrosa	1.73	0.05	6.78	0.08	
Philonotis fontana	17.06	0.43	12.23	0.30	*
Plagiomnium ellipticum	21.48	0.28	7.63	0.40	
Pseudobryum cinclidioides	25.69	0.35	12.61	0.33	
Rhizomnium magnifolium	16.33	0.30	12.31	0.25	
Rhizomnium pseudopunctatum	29.21	0.20	10.21	0.43	
Rhizomnium punctatum	16.94	0.08	6.67	0.03	
Riccardia multifida	0.10	0.08	0.53	0.10	
Scapania irrigua	11.48	0.20	4.66	0.25	
Scapania paludicola	0.13	0.03	4.17	0.05	
Scapania paludosa	66.67	0.03	71.67	0.03	
Scapania undulata	9.00	0.05	17.50	0.05	
Scorpidium revolvens	27.75	0.10	6.96	0.08	*
Warnstorfia exannulata	34.21	0.63	18.07	0.48	**
Warnstorfia sarmentosa	55.00	0.03	10.88	0.03	
Other bryophytes					
Aulacomnium palustre	0.17	0.10	0.21	0.05	
Brachythecium salebrosum	1.33	0.23	7.01	0.10	
Calliergonella cuspidata	0.17	0.03	5.70	0.05	
Climacium dendroides	0.58	0.13	2.14	0.10	
Dicranum scoparium	0.05	0.03			
Helodium blandowii	0.04	0.03			
Hylocomium splendens	0.25	0.03	0.35	0.08	
Mnium hornum	2.63	0.05	1.30	0.05	
Plagiochila asplenioides	0.04	0.03			
Pellia epiphylla	7.28	0.28	0.34	0.05	**
Pellia neesiana	1.56	0.18			
Plagiomnium medium	16.61	0.15	4.76	0.15	
Plagiothecium denticulatum	1.08	0.13	0.15	0.13	
Pohlia nutans	0.04	0.08			
Polytrichum commune	0.40	0.08	2.06	0.15	*
Rhytidiadelphus subpinnatus	0.17	0.05	0.15	0.05	
Sanionia uncinata	14.03	0.05	0.96	0.18	
Sphagnum angustifolium	10.00	0.03	13.08	0.10	
Sphagnum centrale	5.00	0.03	3.75	0.03	
Sphagnum contortum	0.17	0.03	1.38	0.03	
Sphagnum girgensohnii	0.19	0.05	11.09	0.13	*
Sphagnum magellanicum	25.00	0.03	3.42	0.10	
Sphagnum riparium	1.77	0.10	15.66	0.10	
Sphagnum russowii	3.75	0.08	4.78	0.08	
Sphagnum squarrosum	2.50	0.23	0.07	0.08	*
Sphagnum teres	6.15	0.10	6.79	0.10	
Sphagnum warnstorfii	1.02	0.20	8.59	0.38	*
Straminergon stramineum	10.14	0.40	1.80	0.18	*

Significance of among-year difference in cover values was tested using Wilcoxon signed rank test (*$P < 0.05$, **$P < 0.01$). Nomenclature follows Ulvinen et al. (2002).

Table 2
Parameter estimates for the generalized mixed effects model, fitted by maximum likelihood, for temporal changes in spring bryophyte species richness

	Value	SE	d*f*	*t*	*P*
Intercept	0.532	0.162	117	3.29	0.001
Year	−0.317	0.111	117	−2.87	0.005
Status score	−0.059	0.091	38	−0.65	0.520
Group	0.251	0.201	117	1.25	0.220
Status × group	0.281	0.112	117	0.251	0.014

Fitted values are plotted in Fig. 1.

Table 3
Parameter estimates for the generalised mixed-effects model, fitted by maximum likelihood, for temporal changes in bryophyte cover (square root transformed)

	Value	SE	d*f*	*t*	*P*
Intercept	3.198	0.639	114	5.01	<0.001
Year	−0.300	0.905	114	−0.33	0.740
Status	−0.423	0.363	38	−1.16	0.250
Group	5.792	0.903	114	6.41	<0.001
Year × status	−0.105	0.515	114	−0.20	0.840
Year × group	−5.499	1.278	114	−4.30	<0.001
Status × group	0.574	0.514	114	1.12	0.270
Year × status × group	1.866	0.727	114	2.57	0.012

Fitted values are plotted in Fig. 2.

few rigorous studies estimating these rates, and the situation is even worse for freshwater ecosystems, which have traditionally received little attention from the mainstream conservation biologists (Abell, 2002). The same certainly applies to springs, and to our knowledge, no studies to date have examined temporal changes in spring bryophyte communities in relation to landscape-level disturbances. Nevertheless, acquiring such information is critical for the conservation of these key habitats of boreal forests. Clearly, the approach used in this study was not optimal. The "snapshot" approach (sampling the same set of springs a number of years apart) suffers from the lack of temporal replication, and the "trajectory" approach whereby the same sites are sampled repeatedly over time would give more reliable information of bryophyte community persistence (see Hildrew and Giller, 1994). Despite these limitations, several patterns likely to be important for the conservation of spring biodiversity emerged from our study.

Several spring bryophytes declined during the study period. Even species that were frequent and abundant in 1986 had decreased dramatically by year 2000 (Table 1), probably because of the loss of suitable spring habitat through the alteration of wetland hydrology. In such altered conditions, formerly subordinate species may attain greater dominance. Indeed, the increase of *Sphagnum* mosses in our study springs paralleled the decrease of spring bryophytes. Observational and experimental studies have shown that, in altered conditions, *Sphagnum* mosses are superior competitors to habitat specialist bryophytes (Kooijman, 1992; Kooijman and Bakker, 1993). Through overgrowing and associated microenvironmental changes, they may even turn a fen mire into a nutrient-poor bog (Van Breemen, 1995). Our data thus provide circumstantial evidence that, due mainly to man-induced changes in spring hydrology, true spring bryophytes were replaced by more generalist species. A similar declining tendency of spring bryophytes and other fen species has been detected in Central Sweden (Gunnarson et al., 2000). It is unclear, however, whether the decline of spring bryophytes in our study area was caused by environmental changes, increase of *Sphagnum*, or interaction between these two factors. Clarifying these relationships would require long-term monitoring of individual springs, because competitive interactions are more likely to be detected at the scale of individual springs than in large-scale, among-spring surveys.

Interestingly, year was a significant factor in the generalised linear mixed effects model, indicating that bryophyte richness was higher in 1986 than in 2000. This

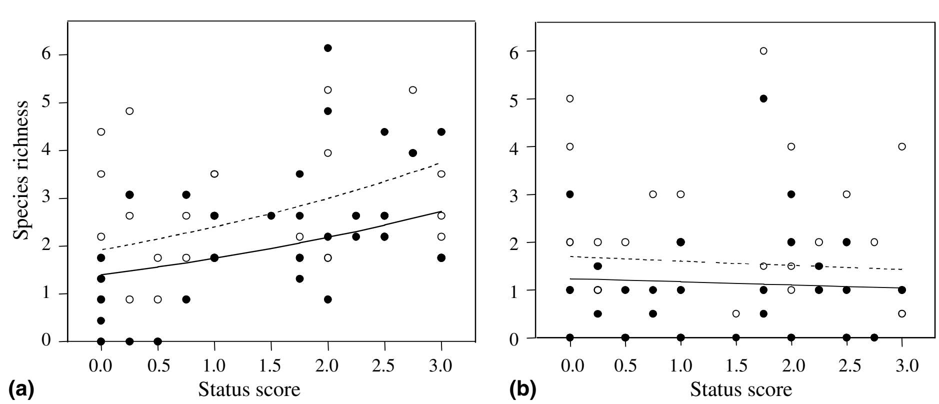

Fig. 1. Changes in the species richness of spring bryophytes (a) and other bryophytes (b) in relation to year and spring condition (status score). Status score was defined in the 2000 survey, using an ordinary scale of 0 to 3 (0 = completely altered, 3 = undamaged springs). Open circles, dashed line = 1986, filled circles, solid line = 2000. Fitted lines are based on back-transformed predictions of the model given in Table 2.

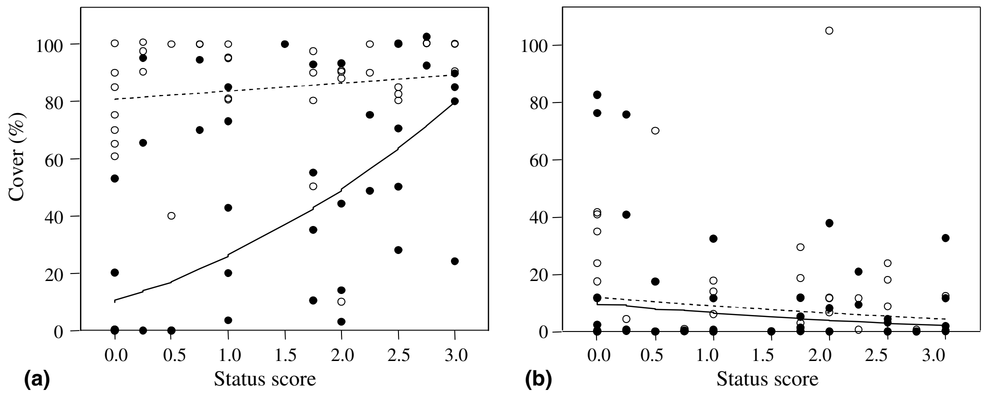

Fig. 2. Changes in percentage cover of spring bryophyte species (a) and other bryophytes (b) in relation to year and status score. Open circles, dashed line = 1986, filled circles, solid line = 2000. Fitted lines are based on back-transformed predictions of the model given in Table 3.

Table 4
Linear regressions of bryophyte community persistence (presence–absence data, Sørensen's coefficient) and stability (% cover data, Czekanovski coefficient) to spring status score

	Value	SE	t	P	R^2
Sørensen					
Intercept	0.384	0.057	6.787	<0.001	
Status score	0.087	0.032	2.691	0.011	0.16
Czekanovski					
Intercept	0.128	0.033	3.834	<0.001	
Status score	0.055	0.019	2.897	0.006	0.18

Similarity coefficients were calculated for each site to describe the degree of persistence and stability of bryophyte communities between 1986 and 2000.

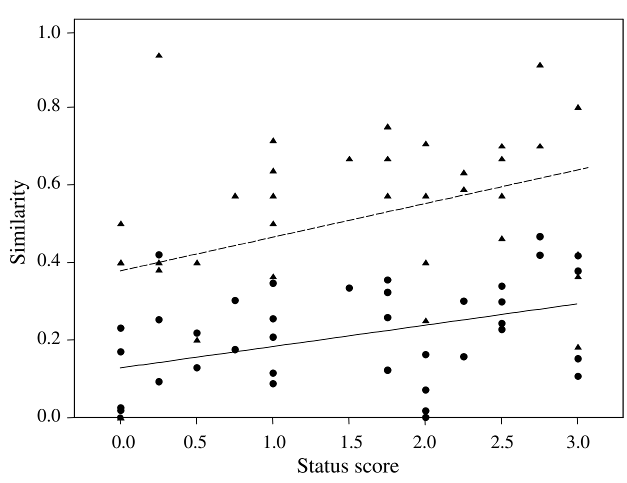

Fig. 3. Persistence (triangles, dashed line; Sørensen's coefficient) and stability (circles, solid line; Czekanovski coefficient) of bryophyte communities in relation to spring status score. Associated regression analyses are summarized in Table 4.

suggests the presence of some regional-scale factor that could not be detected based on our sampling design. Obviously, however, intensified land use due mainly to forestry activities has generally impaired the status of springs in our study region, leading to decreased frequency of occurrence of many spring bryophytes. Eventually, such human-induced changes in local communities may feed back to the regional level, resulting in an impoverished regional species pool. Year × status × group interaction was non-significant, showing that the gradient in spring condition detected in year 2000 was already present, to some degree at least, by the mid-1980s. Forestry activities and water abstraction had certainly affected many of the springs before our first survey, but owing to the lack of historical data, we are unaware of the degree of impairment before 1986. Nevertheless, dramatic changes in spring habitats occurred between the two surveys, and these changes were easily detectable in the field.

The cover of spring bryophytes declined strongly with declining spring status in 2000, but not in 1986, whereas no effect of status on other bryophytes was observed in either of the study years. A related pattern emerged when the persistence and stability of bryophyte community structure were considered, i.e., communities in springs that had undergone severe disturbance were, on average, less persistent and stable than those in relatively undisturbed springs. However, only a minor portion of variability in persistence and stability was accounted for by spring condition. The low explanatory power most likely resulted from heterogeneity in the type of disturbance or from some unmeasured sources of variability in environmental conditions among the springs. Our scoring system mainly described disturbance severity, while the exact nature of disturbance varied somewhat. Most of the disturbed springs were, however, affected by forest drainage. Furthermore, there were likely some unmeasured sources of variability in spring characteristics. The springs varied in size, off-flow stability, and nutrient concentrations, all of which could affect the persistence of bryophyte communities (see Warncke, 1980). For instance, larger springs with stable off-flow might support more persistent communities, owing to reduced probability of extinction and increased probability of recolonisation. This reasoning remains speculative, however, because little is known about these aspects of aquatic bryophyte biology (Stream Bryophyte Group, 1999).

As springs are considered key biotopes in boreal forests (Virkkala and Toivonen, 1999), preservation of their biota and ecological integrity should be a foremost goal in landscape level conservation planning. It is hardly surprising that severe landscape-level disturbances may affect the spring biota, although, lacking historical data, it may prove difficult to estimate how large a portion of spring biodiversity has already been lost through anthropogenic influences. Nevertheless, if the figures presented for Finnish springs (see Eurola et al., 1991) are in the right direction, spring biodiversity appears to be in great jeopardy, due mainly to extensive habitat loss. Thus, given that a majority of springs has already been degraded by human activities, preservation of spring biodiversity may require active restoration of these key biotopes. Establishing guidelines for ecologically sound restoration of springs remains a major challenge for the conservation of spring biodiversity and, even more, the overall biodiversity of boreal forest landscapes.

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