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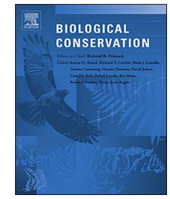

Anthropogenic habitat disturbance induces a major biodiversity change in habitat specialist bryophytes of boreal springs

Kaisa Lehosmaa[a,*], Jussi Jyväsjärvi[a], Risto Virtanen[a,b,c], Jari Ilmonen[d], Jouko Saastamoinen[e], Timo Muotka[a,f]

[a] University of Oulu, Department of Ecology and Genetics, P.O. Box 3000, FI-90014 Oulu, Finland
[b] Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Permoserstr. 15, Leipzig 04318, Germany
[c] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig D-04103, Germany
[d] Metsähallitus, P.O. Box 94, FI-01301 Vantaa, Finland
[e] Kainuu Regional Environment Centre, P.O. Box 115, FI-87101 Kajaani, Finland
[f] Finnish Environment Institute, Natural Environment Centre, FI-90014 Oulu, Finland

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ABSTRACT

Land-use is a major driver of global biodiversity loss. Despite much evidence of land-use impacts on freshwater biodiversity, long-term changes to groundwater-dependent ecosystems, and their post-disturbance recovery, remain largely unknown. We examined long-term changes of bryophyte communities in 34 boreal springs from 1987 to 2015. In 1987, all the study springs were in near-pristine condition, but 29 of them were disturbed by peatland drainage in the late 1980s and early 1990s. Five sites retained their natural status throughout the study and were used as reference sites. We aimed to assess whether bryophyte vegetation, particularly spring specialist bryophytes, showed gradual recovery toward near-pristine conditions or whether the drainage-induced habitat degradation had caused delayed extinctions of specialists, leading to dominance by generalist taxa. Bryophyte diversity showed no signs of recovery about 20 years since the initial disturbance. In disturbed springs, the abundance of specialists first decreased, then remained relatively stable. Specialist richness decreased steadily and their community composition shifted gradually from the pre-disturbance state. Abundance of habitat generalists did not change but generalist richness also decreased with a time lag. At the same time, both groups remained unaltered in undisturbed springs. We conclude that without restoration measures that improve groundwater hydrology the self-recovery potential of springs is very low. As little is currently known about the effectiveness of spring restoration in halting spring biodiversity loss, the safest management strategy is to refrain from land use within broad buffers around springs.

1. Introduction

Many ecosystems are globally threatened due to intensified land use and other human activities, challenging ecologists to provide reliable estimates about the degree of biodiversity loss and change attributable to anthropogenic causes. The imprints of land-use disturbance on the physical environment are often conspicuous, yet its impacts on biodiversity and ecosystem functioning are much harder to detect, partly because there is often a considerable time lag until the biological effects of land use become apparent (Hylander & Ehrlén 2013; Essl et al. 2015). While there is wide consensus about the unprecedented rate of species loss globally, the magnitude and even direction of biodiversity loss at local scales have been much debated (Dornelas et al. 2014; Gonzalez et al. 2016). Two recent meta-analyses found no evidence for systematic species loss at local scales but the pattern was highly context-dependent (Vellend et al. 2013; Dornelas et al. 2014). Other researchers have concluded that any generalized arguments about net species loss (or gain) at local scales are premature (Cardinale 2014; Gonzalez et al. 2016). There is evidence, however, that even if human disturbance may not cause systematic species loss, community composition may change (Dornelas et al. 2014).

Freshwater ecosystems have suffered a disproportionally high biodiversity loss (Dudgeon et al. 2006; Strayer & Dudgeon 2010), with habitat modification being the main anthropogenic driver of freshwater biodiversity (Pimm et al. 2014). Arguably, biodiversity trends, and particularly the role of human actions to those, in groundwater-dependent ecosystems (GDEs) are even less well known than those of other freshwater ecosystems (Barquín & Scarsbrook 2008). Such

* Corresponding author.
E-mail address: Kaisa.Lehosmaa@oulu.fi (K. Lehosmaa).

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information is urgently needed, however, as many GDEs harbour valuable components of regional biodiversity but are increasingly threatened by human activities, such as land drainage, agriculture, urbanization, water abstraction and global warming (Ilmonen et al. 2012; Jyväsjärvi et al. 2015). Although implementation of the European Water Framework Directive (EC 2000) and Groundwater Directive (EC 2006) have improved management of groundwater resources, monitoring and assessment of the ecological status of GDEs are still at their infancy.

GDEs support diverse biota with a high proportion of habitat specialists (i.e. crenophilous and crenobiontic species) adapted to the unique environmental conditions provided by continuous groundwater inflow (Cantonati et al. 2012). Bryophytes (aquatic mosses and liverworts) are the dominant plant group in boreal cold-water springs, and the occurrence and abundance of many bryophyte species are strongly governed by the quantity and quality of groundwater (Kuglerová et al. 2016). Anthropogenic impacts often lead to a non-random sequence of species loss, with habitat specialists being extirpated first (Pimm et al. 2014). Replacement of specialists by generalist species may result in taxonomic and functional homogenization, and to changes in ecosystem functions, particularly if specialists perform non-redundant functional roles in ecosystems (Clavel et al. 2011). Habitat specialists with limited dispersal capacity suffer disproportional losses from reduced connectivity caused by land-use disturbance and are therefore under the greatest risk of local extinction (Kuussaari et al. 2009; Pimm et al. 2014). Therefore, their recovery may remain slow even after the initial stressor is no longer present, potentially causing delayed extinctions several decades or generations after the initial disturbance (extinction debt; Kuussaari et al. 2009). Habitat specialists and generalists should therefore be examined separately because amalgamation of species with different habitat affinities may hinder the detection of patterns of conservation interest (‘assemblage deconstruction approach’; Matthews et al. 2014). Studies assessing delayed extinctions mostly focus on community-level metrics although species are known to exhibit individualistic responses to habitat disturbance (Hylander & Ehrlén 2013). We were therefore also interested in species-specific responses, based on the assumption that not all spring specialist bryophytes have suffered equally from land-use disturbance.

Species' relative abundances respond to human disturbances much earlier than species go extinct (Hillebrand et al. 2008). Therefore, although it can be argued that species richness goes a long way toward characterizing a biological community (May 1975), the key limitation of using mere richness to detect human impacts is that it weighs all species equally, rare and common (Jost 2007). Interspecific abundance-occupancy relationships (AOR) can be particularly informative about anthropogenic alteration of community composition (for a review, see Matthews & Whittaker, 2015). While species' abundances and distributions vary naturally, considerable evidence suggests that human disturbance (and subsequent recovery from it) can shape AORs greatly by reducing the occupancy of rare species or increasing the dominance by already common species (Verberk et al. 2010; Guedo & Lamb 2013; Simons et al. 2015).

Springs are ubiquitous and numerous throughout the boreal region and they are an integral component of boreal forest ecosystems. In Finland, there are over 32,000 mapped springs, but the actual number is likely much higher. Springs are distinct ecotones between groundwater and surface water, as well as between aquatic and terrestrial ecosystems, and they provide diverse habitat structure and continuous influx of groundwater, being thus hotspots of forest biodiversity (Cantonati et al. 2012). Their value for national forest biodiversity conservation was acknowledged in the Finnish National Forest Act 1997 where springs were included among the 13 woodland key habitats. Nevertheless, guidelines for sustainable management of spring ecosystems are still lacking (Lehosmaa et al. 2017). This study helps filling this gap, as it not only examines the long-term consequences of intensive land use on spring bryophyte flora but also provides information about the potential for self-recovery of spring ecosystem after land-use disturbance.

We documented the rate of change of bryophyte communities in a set of boreal springs from the late 1980s to 2015. In 1987, most of the springs were in near-pristine condition but were strongly disturbed by peatland drainage in the late 1980s and early 1990s. Drainage is known to alter groundwater-surface water dynamics, thermal regime and habitat structure of springs (Lehosmaa et al. 2017). Drainage ditching was declined in 1997 and we therefore expected that, following revegetation of old drainage ditches (see Holden et al. 2004), spring bryophyte communities should show distinct signs of recovery since the initial disturbance more than two decades ago. Specifically, we assessed whether (i) bryophytes, particularly spring specialist species, had recovered from the initial land-use disturbance, or whether (ii) habitat disturbance had caused delayed local (or regional) extinctions of habitat specialists. We also tested whether (iii) generalist peatland bryophytes had assumed greater dominance through time, posing an additional threat to habitat specialists. Finally, we assessed (iv) whether (and how) drainage disturbance, and recovery from it, may have shaped AORs, and (v) whether changes in AORs through time differed between spring specialist and generalist bryophytes.

2. Materials and methods

2.1. Study area

Study region and methodology are described in detail in Heino et al. (2005) and we thus only provide a short summary here. The study was conducted in Kainuu and North Karelia regions, eastern Finland (63–64°N; 28°–31°E). The area is characterized by coniferous forests and peatlands, the main land use being silviculture, particularly drainage of peatlands to improve forest growth, with limited agricultural activities. Initially, 40 springs were selected for the pre-disturbance survey in 1987, based largely on their accessibility (Saastamoinen 1989). In our resurveys, six springs were omitted due to uncertainty of their location. We thus focus here on five springs that retained the initial near-pristine condition throughout the study (1987 to 2015) (henceforth, reference springs) and 29 springs altered by land drainage (disturbed springs). Drainage ditching was the only major land use in the vicinity of the study springs (i.e. no harvesting of trees within a few hundred meters from the springs). Reference and disturbed springs were spatially interspersed (Appendix A). All study springs were comparable in habitat structure, containing a spring pool and an outflowing channel. Spring size varied from 1 m^2 to 100 m^2, the majority of springs being smaller than 10 m^2. Habitat structure (e.g. proportion of minerogenic and organogenic substrate) varied initially little among the springs but the disturbed springs and their riparian areas harbored distinct signs of drainage on later surveys. In 1987, all 34 springs were in pristine condition (or nearly so), while in the 2000 survey (Heino et al. 2005), most springs were altered by land drainage, often with a ditch flowing directly into the spring pool or outflow. Five sites also had man-made structures for water abstraction. Water quality was measured only sporadically and was therefore excluded from data analysis. However, these data suggested negligible changes in water quality during the study period. Spring water conductivity (mean ± 1SD) was lowest in 2010 (6.1 ± 4.5 mS/m) and highest in 1987 (6.8 ± 5.1 mS/m). Water pH varied little across years, mean values being 5.8 (1987) to 5.9 (all other years).

2.2. Data collection

Field data were collected four times in each of the 34 springs (in 1987, 2000, 2010 and 2015) and, apart from the 1987 survey, by the same person (RV). In each year, quality of the spring habitat and its immediate surroundings was assessed with a four-scaled classification procedure (Heino et al. 2005; Lehosmaa et al. 2017). Sites assigned