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Restoration of forestry-drained boreal peatland ecosystems can effectively stop and reverse ecosystem degradation

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Ecosystem restoration will increase following the ambitious international targets, which calls for a rigorous evaluation of restoration effectiveness. Here, we present results from a long-term before-after control-impact experiment on the restoration of forestry-drained boreal peatland ecosystems. Our data comprise 151 sites, representing six ecosystem types. Species-level vegetation sampling has been conducted before, two, five, and ten years after restoration. With joint species distribution modelling, we show that, on average, not restoring leads to further degradation, but restoration stops and reverses this trend. The variation in restoration outcomes largely arises from ecosystem types: restoration of nutrient-poor ecosystems has a higher probability of failure. Yet, the ten-year study period is insufficient to capture the restoration effects in slow-recovering ecosystems. Altogether, restoration can effectively halt the biodiversity loss of degraded ecosystems, although ecosystem attributes affect the outcome. This variability in outcomes underlies the need for evidence-based prioritization of restoration efforts across ecosystems.

Ecosystem restoration is likely to become mainstream in the near future, even if the Kunming-Montréal Global Biodiversity Framework target¹ to effectively restore at least 30% of degraded ecosystems by 2030 is so ambitious that it is unlikely to be met. As 20–40% of the global land area is degraded, an even smaller percentage of the land to be restored would add to the 1 billion hectares currently committed to restoration². In general, restoration succeeds in increasing biodiversity and ecosystem functions in degraded ecosystems^{3–5}. Yet, restored ecosystems rarely fully recover^{4–6}, and the outcomes are often unpredictable^{3,5,7}. To make restoration more effective, we need to improve the predictability of restoration by identifying the causal factors behind the variation in the restoration outcomes^{7,8}.

Identification of the sources for the variation is best done with properly controlled and replicated experimental data⁹. Unfortunately, such data are relatively scarce in environmental biology. Only 23% of the biological intervention studies use randomised designs or controlled observational designs with before-impact sampling (i.e., before-after control-impact design), even though such designs are known to provide less biased estimates than simpler designs⁹. In restoration studies, the amount of experimental studies is even lower. A recent meta-analysis of restoration effects⁵

included 89 studies, of which only 10 had before-after control-impact design, and only half had both unrestored and reference controls, which are needed to estimate and verify the effect of restoration reliably. Thus, the repeated calls for properly controlled, long-term restoration experiments replicated over large spatial scales^{8,10} remain unanswered.

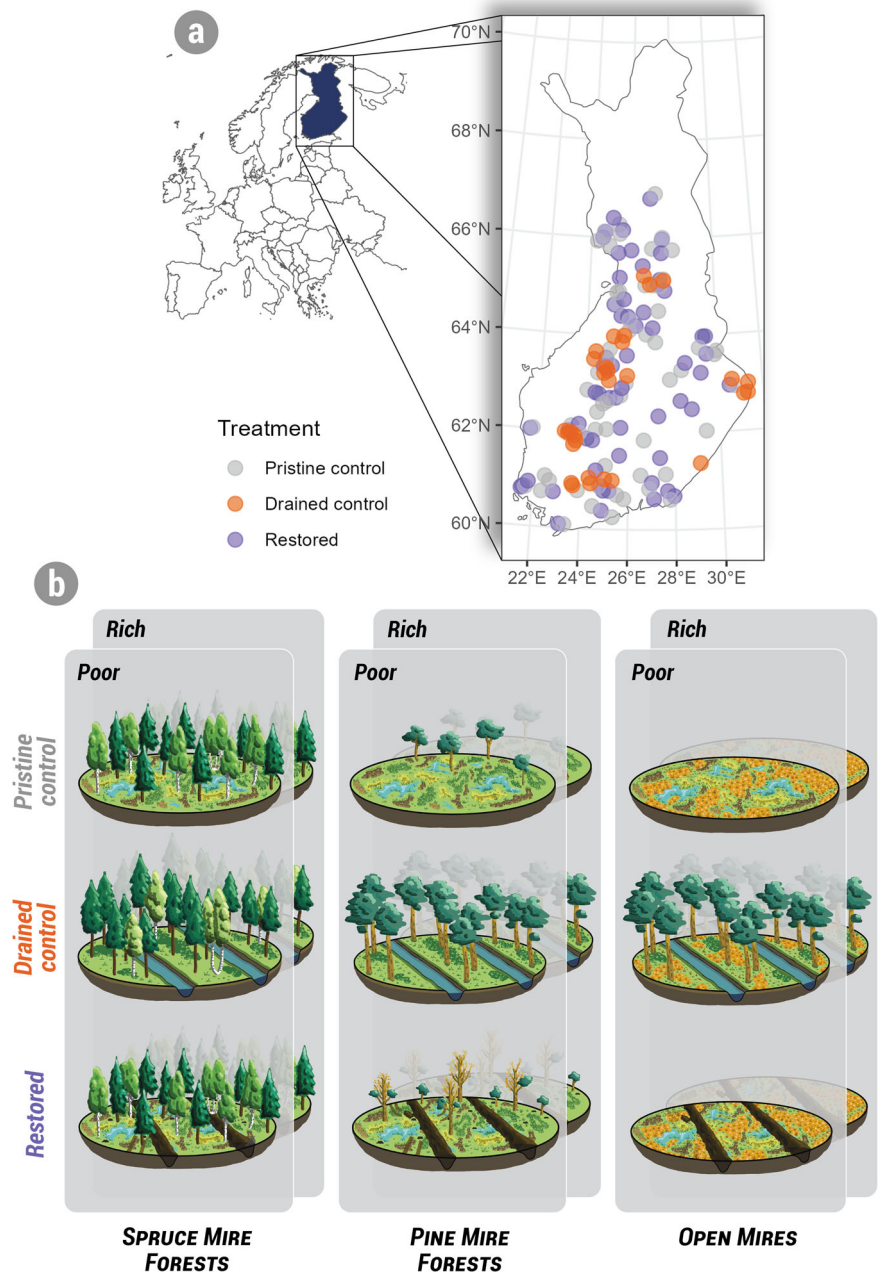
Here, we contribute to filling this gap by reporting results from a well-replicated long-term before-after control-impact experiment on the restoration of forestry-drained boreal peatland ecosystems (Figs. 1, 2). These ecosystems rely on high water table levels and are important carbon sinks and storages^{11,12}, provide numerous other ecosystem services¹³ and host unique biodiversity¹⁴ in their pristine stage. Boreal peatland ecosystems have been widely drained for agriculture, peat extraction and especially for forestry, the latter affecting ~30% of Europe's peatland ecosystem area¹⁵. Promisingly, the forestry-drained ecosystems may be more easily restored than the other uses because the vegetation is not removed, and there are likely to be source populations nearby for species that have become locally absent^{16,17}. Hence, peatland restoration in forestry-drained ecosystems could result in long-term biodiversity¹⁴ and climate benefits¹⁸.

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Fig. 1 | Location of the sites and study set-up. Map of the 151 study sites in Finland: sites that had been drained for forestry during the 1960s and 1970s and were restored during the project ('restored'; purple symbols), relatively pristine sites with no drainage ('pristine control'; grey symbols), and sites that had been drained and were not restored ('drained control'; orange symbols) (a). The sites represent three main ecosystem types: spruce mire forests, pine mire forests and open mires, which all rely on high water table levels. They are further divided into two types (poor/rich) according to the productivity level (as shown by the two overlapping panels; note that the levels 'poor' and 'rich' are not comparable between spruce mire forests, pine mire forests and open mires) (b). Hence, the six ecosystem types form a rough gradient in their productivity level and differ in their tree cover and species composition. Each site includes 10 permanent sampling plots from which vascular plant and moss species were monitored prior to restoration and 2, 5 and 10 years after restoration in restored, drained control and pristine control sites (Supplementary Fig. 1).



Indeed, restoration of forestry-drained ecosystems often succeeds in raising the water table to pristine levels^{19,20}. This often leads to recovery of the ecosystem functions, such as carbon sequestration^{21–23}, but only a partial recovery of community composition^{17,20,21,24–26}. However, similarly to the restoration studies in general, the previous studies are based on a few study sites^{20,25}, early years after restoration²⁶, or space-for-time substitutions^{17,21,24}. Moreover, the studies have often focused on only one of the many peatland ecosystem types, which may respond differently to restoration²², due to their inherent differences in nutrient levels²⁷.

We show that the forestry-drained boreal peatland ecosystems continued to degrade without restoration during the monitored 10 years. On average, the restoration of these ecosystems successfully stopped and reversed the trend of degradation of the vegetation communities and reversed the successional process. Our results reinforce the previous findings on the restoration effects in general^{4–6} as well as for the boreal forestry-drained peatland ecosystems in particular^{17,20,21,24–26}: restoration is effective in changing the community composition towards, but not all the way to, the

reference pristine community composition. However, our modelling revealed important variations in the responses of the vegetation communities between different ecosystem types. That is, restoration led to different outcomes depending on the ecosystem type. These results have profound implications for restoration planning when considering the probability of restoration success and when setting restoration priorities. Hence, the data-based evidence provided by our experiment can improve restoration's effectiveness.

Results and discussion

Overall response to restoration

In general, restoration was successful in reversing the effects of drainage: the average vegetation community composition in restored sites was more similar to pristine controls and less similar to drained controls 10 years after restoration than before restoration (Fig. 3a). This resulted from a positive response to restoration of species which had decreased after drainage, and conversely a negative response of species which had



Fig. 2 | Different peatland ecosystem types before and shortly after restoration. A spruce mire forest before (a) and after restoration (b), a pine mire forest before (c) and after restoration (d), and an open mire before (e) and after restoration (f). Note that (c) and (d) are not from the same site. Photos: (a–d) Maarit Similä, (e, f) Sakari Rehell.

increased after drainage (Fig. 4). For instance, several peat-forming *Sphagnum* mosses responded positively whereas common forest mosses (*Hylocomnium splendens*, *Pleurozium schreberi*) which tend to colonize or increase in drained peatland ecosystems¹⁶, responded negatively (Fig. 5), as also found in previous studies^{17,24}. However, many of the responses were mild (Fig. 5), and 10 years after restoration, the species abundances did not equal those in the reference pristine controls (Supplementary Fig. 6). Also, several species that had increased or decreased after drainage did not show detectable responses to restoration (Fig. 4). These responses resulted in a partial recovery of the plant communities (Fig. 3a) which suggests that our monitoring period of 10 years, although being longer than in many restoration studies^{5,6}, is not enough for a full recovery of the plant communities. This finding aligns with previous meta-analyses suggesting that full recovery, if achieved at all, takes decades rather than years^{4,6}. While communities in restored sites will

converge towards communities in pristine sites over time, they are unlikely to fully resemble the pristine communities. One reason for this is that community succession is always affected by drift. Communities will develop somewhat differently due to stochasticity^{28,29}, even if identical initially. These drift effects are expected to be more prominent when the abundances of the species are small³⁰. Given that the abundance of many peatland species has severely declined due to drainage, drift is likely to strongly affect how a community develops in the restored sites.

Some species that did not respond or even increased after drainage responded positively to restoration (Fig. 4), possibly because they benefitted from bare peat surface, increased light availability, and/or the nutrient pulse due to restoration actions¹⁷. For example, a sedge *Eriophorum vaginatum* increased strongly (Fig. 5), in concert with the increased nutrient release³¹, as observed previously^{17,22}. Likewise, birch (*Betula pubescens*) increased due to restoration (Fig. 5). In spruce mire forests, birch is a natural part of the

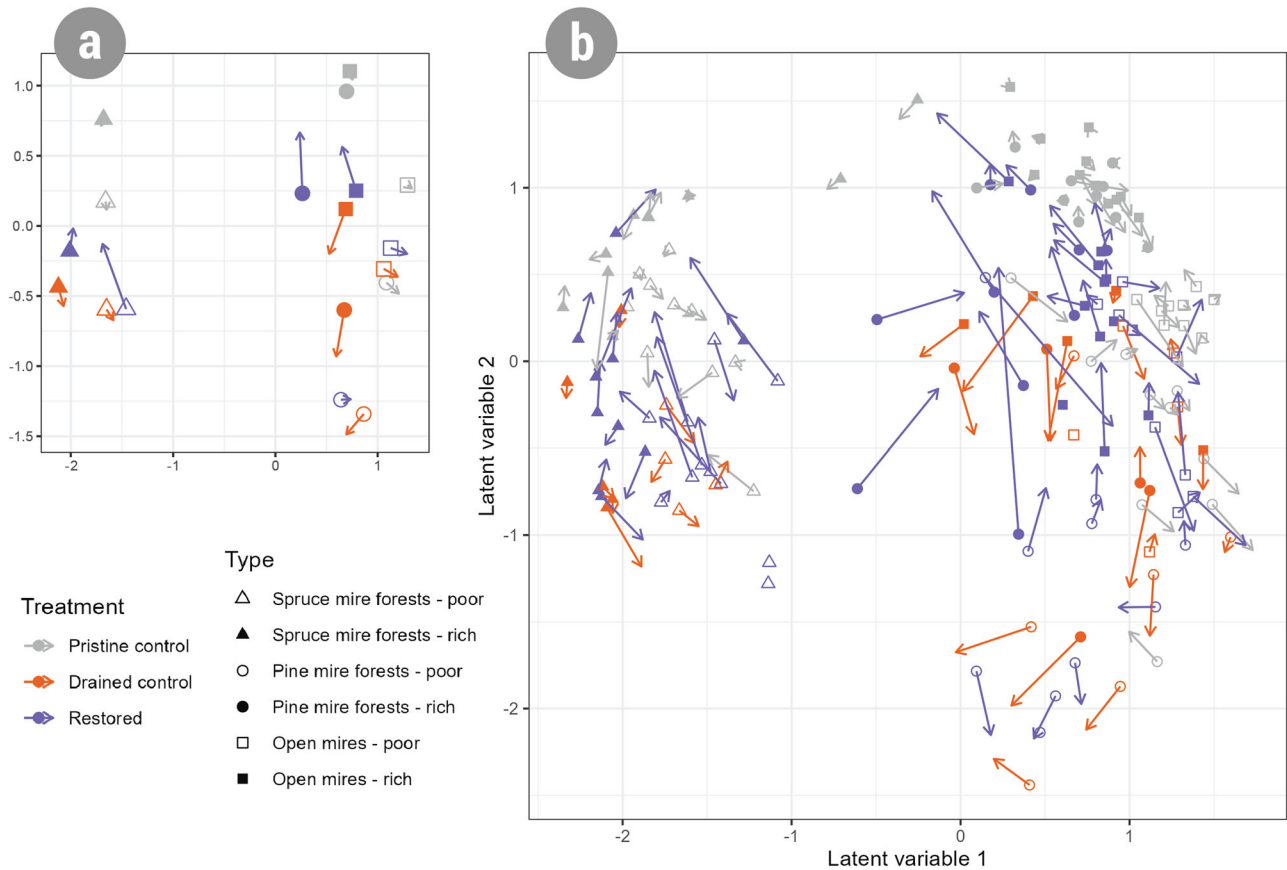


Fig. 3 | Changes in vegetation community composition from before to 10 years after restoration. Community compositions in restored sites (purple symbols) were more similar to pristine controls (grey symbols) and less similar to drained controls (orange symbols) 10 years after restoration (the head of the arrow) than how they were before restoration (symbol) on average (a) but the variation between individual sites and ecosystem types was large (b). Panel (a) shows the average values of all sites

for each treatment (restored/pristine control/drained control) per ecosystem type (poor spruce mire forests = open triangles, rich spruce mire forests = filled triangles, poor pine mire forests = open circles, rich pine mire forests = filled circles, poor open mires = open squares, rich open mire = filled squares) from a model-based ordination before restoration (symbol) and 10 years after restoration (the head of the arrow). Panel (b) shows the corresponding values for each of the 151 sites.

ecosystem and tends to increase as spruce die and light increases²⁴, but in pine mire forests, it may counteract restoration as it shades understorey and evaporates water. Among mosses, *Sphagnum* species, in particular, responded positively, likely due to their preference for wetter conditions. The exception was *S. fuscum*, which occupies drier microhabitats and consequently decreased after restoration. Many of the positive responses were for species that differed already in their initial abundances in restored and drained sites (Fig. 5). Hence, their changes may indicate site-specific differences and may not be generalised.

Although many of the species increased above the levels of pristine controls (Supplementary Fig. 6), the responses were mild, and restoration effects in general tend to attenuate with time. Thus, pronounced community divergences are not expected in the future. Ten years after restoration, the community compositions of restored sites represent the continuum from drained, dryer heath forest-type communities towards communities in pristine ecosystems (Figs. 3 and 5) without, for instance, non-native species. Thus, by contrast to what has been suggested for restored fens in Central Europe³², restoration of boreal forestry-drained peatland ecosystems does not appear to lead to self-sustaining novel ecosystems (*sensu* Hobbs et al.³³) but rather to a transforming stage between pristine and degraded ecosystems^{4,6}.

Variation in the responses to restoration

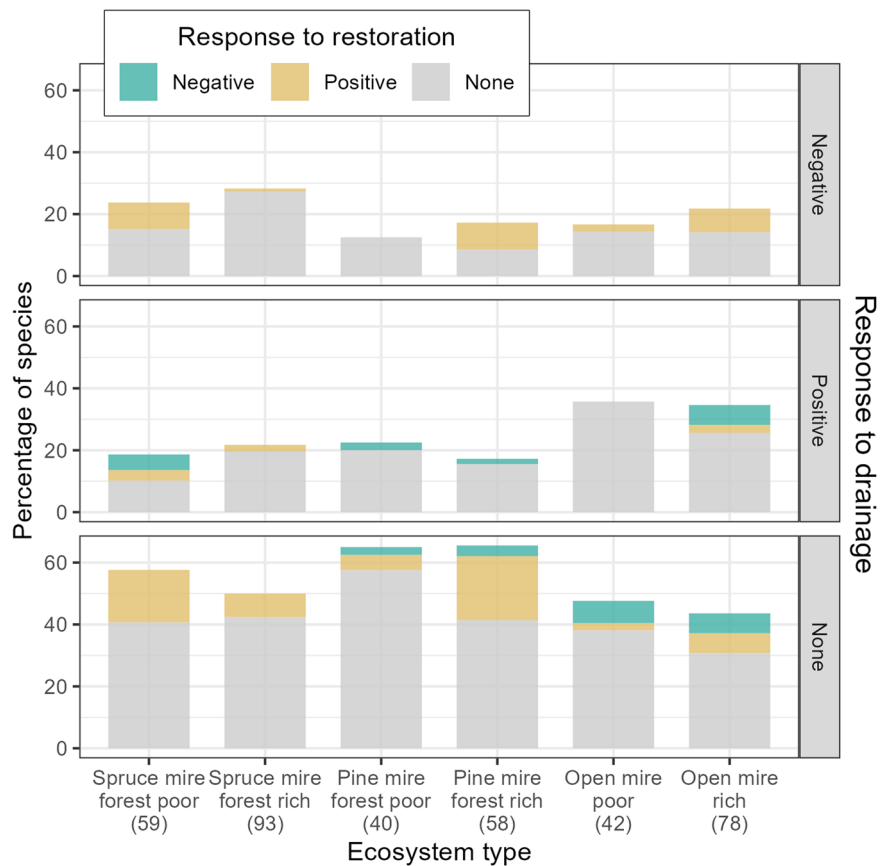
In all ecosystem types, there was considerable variation in response to restoration (Figs. 3b and 6). However, restoration was more effective in certain ecosystem types than in others. Approximately one-third of the species responded (either positively or negatively) in poor spruce mire

forests, rich pine mire forests, and rich open mires (34%, 34% and 29% of the species showed statistically supported responses, respectively). By contrast, only 10–12% of the species showed statistically supported responses in poor pine mire forests, poor open mires and rich spruce mire forests (Fig. 4). This corresponds to only four species in poor pine mire forests and five in poor open mires (Fig. 5). The negligible mean response to restoration of poor pine mire forests and open mires (Figs. 3a, 4 and 5) resulted partly due to opposing restoration outcomes among sites within these ecosystems (Fig. 6). For poor pine mire forests, some restored sites recovered well but the restored sites which had very similar communities to the drained sites before restoration, did not recover but instead followed the trajectory of the drained controls after restoration (Fig. 3b). The same but to a lesser extent applied to poor open mires.

There are several possible reasons for the variation in the restoration effect, which are not mutually exclusive. First, the variation in restoration outcome was likely affected by the technical success of restoration. As the nutrient-poor sites are usually situated on raised bogs, receiving their water and nutrients only from rain, filling in the ditches does not necessarily result in increased water table level, particularly if the drainage has caused peat subsidence near ditches. Indeed, a study using a subset of the sites considered here, showed that two out of the three poor pine mire forest sites were considered not as effectively restored in terms of water-table level 5 years after restoration¹⁹. However, all poor open mires were considered well-restored. Hence, while technical failure is likely to be part of the reason, it does not seem to explain all the variations.

The restoration effect was greatest at oligo-mesotrophic sites (Fig. 6) in the middle of our trophic gradient from ombrotrophic to meso-eutrophic

Fig. 4 | Species response to drainage and restoration. The bars show the percentage of species according to their response to drainage (negative/positive/none) and response to restoration (negative=green/positive=yellow/none=grey) in each ecosystem type (the number of analysed species is shown in parentheses). The response to drainage is negative if species predicted abundance (occupancy x cover given presence, as predicted from the joint species distribution modelling) is smaller in both restored sites and drained controls than in pristine controls before restoration with high statistical support (>95% posterior probability), and positive if larger. The response to restoration is the change in abundance before restoration to 10 years after restoration in restored sites in relation to drained controls. Hence, response to restoration is positive (in the figure with high statistical support >95% posterior probability) either if abundance in restored sites increases and abundance in drained sites increases less, is stable or decreases, or if abundance in drained sites decreases and abundance in restored sites is stable or decreases less. Similarly, response to restoration is negative either if abundance in restored sites decreases and abundance in drained sites decreases less, is stable, or increases, or if abundance in drained sites increases and abundance in restored sites is stable or increases less.



sites. In our rough scale, the trophic level also reflects nutrient level and relates to productivity. It has previously been suggested that passive restoration is most likely to succeed in medium productivity levels because resource depletion restricts species responses at low-productivity sites, and competition among species increases at high-productivity sites. In a short-term study where two forestry-drained ecosystems were compared 2 years after restoration, the nutrient-rich site recovered faster than the nutrient-poor site²². This is in line with the effect of drainage: relatively wet and nutrient-rich types change faster after drainage than drier and nutrient-poor types¹⁶. Hence, our results support the idea that productivity level is an important factor in explaining the restoration outcome. Thus, future studies on peatland restoration should consider nutrient level as a key factor in explaining restoration outcomes³⁴.

The restoration outcome may also depend on the pre-restoration community composition, which can lead to unpredictable variation if unaccounted for. These so-called priority effects are known to be important determinants of the community succession pathways and to interact with productivity levels³⁵. In peatland ecosystems, priority effects may particularly influence poor pine mire forests and open mires. When species of drier conditions are abundant enough before restoration, they may prevent the re-colonisation of the original species. In the same line, drainage can cause irreversible changes in peat hydraulic conditions, such as increased surface compaction and peat density^{36,37}, which may prevent the pristine-like hydrological conditions in a site from recovering³⁸.

Regardless of the specific reason(s), the increase in similarity with the pristine sites was variable, and the amount of change, in general, was small, suggesting that the restoration success in nutrient-poor pine mire forests and open mires is uncertain. Although their restoration could be easily justified from the economic point of view, as drainage of these ecosystem types has often failed to yield economically valuable tree growth³⁹, it has a lower probability of producing benefits for biodiversity when compared to nutrient-richer pine mire forests and open mires.

The continuing effect of drainage for forestry

The effect of restoration should be interpreted not only by the increasing similarity of the restored communities towards the pristine controls but also by their increasing dissimilarity from the drained controls⁵. Thus, the effect of restoration is either larger or smaller than estimated from the state of the ecosystem at the time of restoration if the unrestored sites continue to degrade or start to recover passively. Continued degradation was the case in our experiment: on average, drained sites increasingly differed from the pristine sites during the study period (Fig. 3a and Supplementary Fig. 7). This resulted from the continued increase of forest mosses in poor spruce mire forests and forest dwarf shrubs in poor pine mire forests and rich open mires (Supplementary Fig. 8). Altogether, these changes resulted in drier, more heath forest-like conditions in drained sites, highlighting that drained sites do not necessarily recover passively without restoration⁴⁰. Detecting continuous degradation with our experiment is somewhat remarkable because the sites had been drained for as long as 50–60 years ago, and only in three sites have the ditches been re-opened since. For rich spruce and pine mire forests, species responses behind the increasing dissimilarity from the pristine controls could not be dissected, possibly because of large variations in species composition and site-specific responses (Supplementary Fig. 8). By contrast, species-specific changes indicate some passive recovery.

While our experimental set-up is a large-scale and long-term well-replicated before-after control-impact design, we acknowledge it also has features that affect the generalisation of the results. First, it was not possible to randomise the restoration and control treatments among the drained sites. This constraint is evident in the difference in initial abundances between restored treatment and drained control sites for many species (Fig. 5), which adds uncertainty to our estimates of species responses. Second, restored sites were often located in protected areas near pristine peatlands. On average, their connectedness and pre-restoration naturalness may be higher compared to many drained peatlands outside protected areas or not yet chosen for restoration. In addition, the watersheds where the

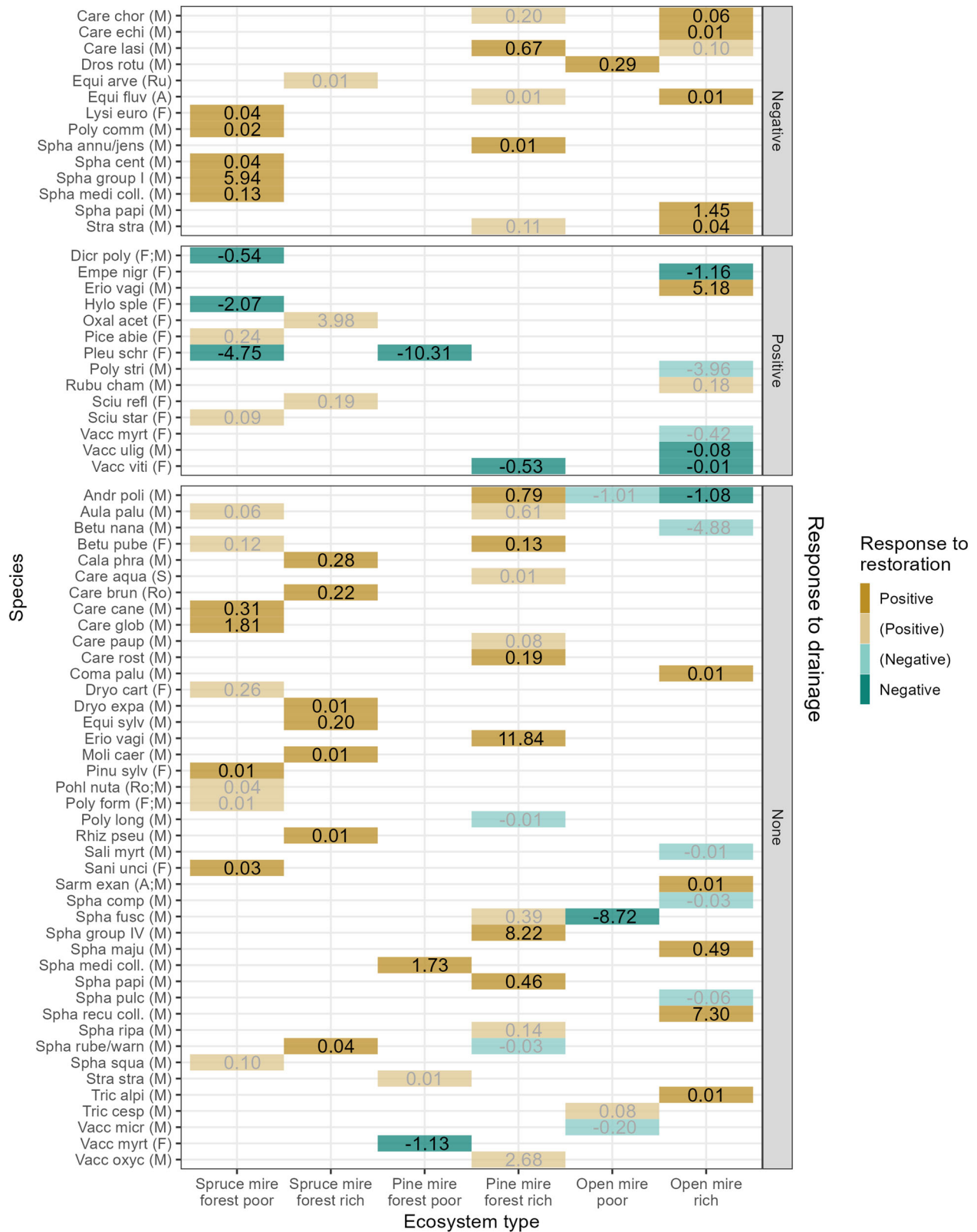
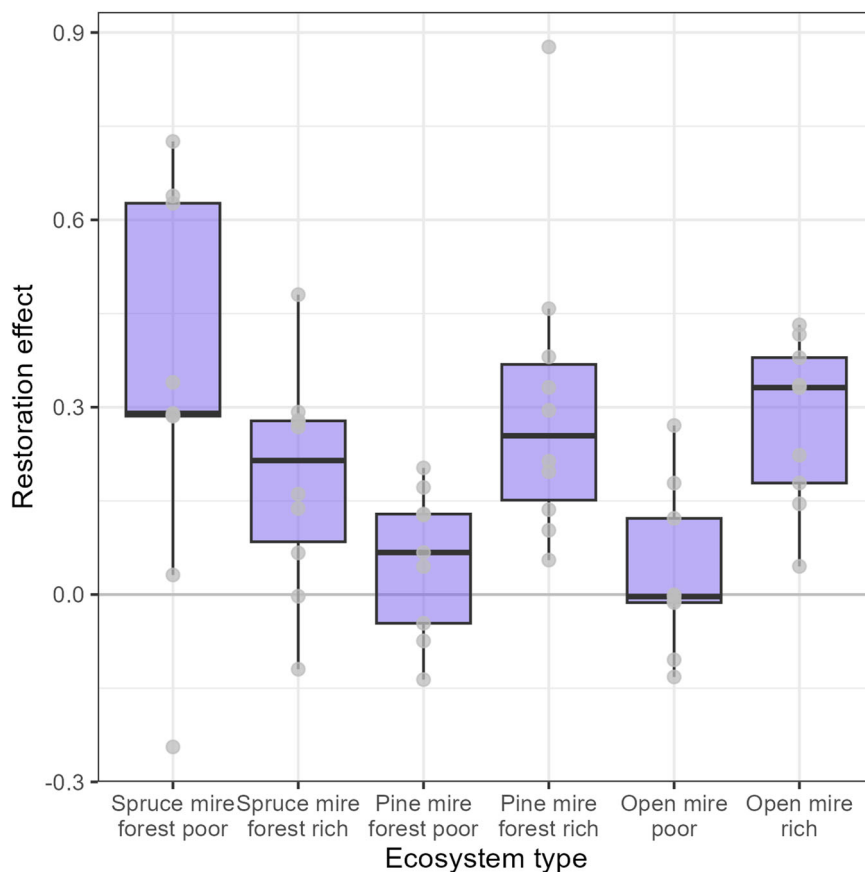


Fig. 5 | Species-specific responses to restoration. For each species responding to restoration with high statistical support (95% posterior probability), the posterior median of the response is shown separately according to their response to drainage in the given ecosystem type. Positive responses are shown in yellow and negative in purple. The lighter colour and grey font are for species that differ in the initial abundance in drained and restored sites. For response median values between 0.01

and 0, the value 0.01 is used, and for response median values between 0 and -0.01, -0.01 is used. Species full names can be found from Supplementary Table 2. Species primary habitat type⁶¹ is shown in parentheses [F = forests, M = mires (including mire forests and open mires), A = aquatic habitats, S = shores, Ro = rock outcrops and boulder fields, Ru = rural biotopes and cultural habitats]. Median responses and their posterior probabilities for all species: see Data availability statement.

Fig. 6 | Restoration effect among ecosystem types. The restoration effect (based on the latent variables from the model-based ordination in Fig. 2) for each restored site is positive if species composition in a site changed more towards pristine sites than drained sites from before restoration to 10 years after restoration. Conversely, the restoration effect is negative if species composition changes more towards drained rather than pristine sites. The thick line corresponds to the median, and the lower and upper hinges to the 25th and 75th percentiles. The upper/lower whisker extends to the largest/smallest value that is at a maximum 1.5× distance between the 25th and 75th percentiles. Data are shown as grey points.



study sites (both pristine and drained controls as well as restored sites) were located may be less drained in total, helping to secure the effect of the raised water table by restoration. Third, the vegetation sampling plots were situated at least 10 m from the ditch line. Both the effect of the drainage and the effect of the restoration are likely to be smaller at this distance. Consequently, the vegetation community develops more directly towards pristine communities compared to vegetation closer to or within the ditch itself¹⁷. The vegetation may change fast in the ditch, but not necessarily towards the pristine reference community composition (often a wetter peatland type in the restored ditch)¹⁷. However, this kind of variation in restoration outcome can also increase the resilience of the restored peatland ecosystems through habitat heterogeneity, especially by providing habitats for the characteristic peatland species occupying pits, hollows, and wet surfaces¹⁷.

Finally, we highlight that our results also have implications for understanding the future changes in peatland ecosystems due to climate change. Climate change is expected to magnify the drying of peatlands because of increased temperatures and especially the more frequent and prolonged droughts^{41–43}. As drying may have more prominent effects in peatland communities than warming itself⁴⁴, the effects of climate change are likely to be similar and possibly synergistic with drainage for forestry, being stronger in drained sites. Hence, restoration may help prevent further ecosystem degradation, increase ecosystem resilience to climate change, and mitigate climate change by preventing even further oxidation of the deeper peat layers⁴⁵.

Conclusions

Restoration of forestry-drained boreal peatland ecosystems is, on average, effective in stopping and reversing further degradation. Our large-scale and long-term monitoring effectively revealed variation in restoration outcomes and suggested that ecosystem characteristics, including productivity level, can explain some of this variation. These results have implications for peatland restoration planning and prioritisation, as well as to predict the

future effects of climate change on these ecosystems. Overall, our study emphasises the importance of large-scale and long-term restoration monitoring to guide our actions from single-site planning to strategic decisions in the era of ecosystem restoration.

Methods

Study system and experimental design

The data include 151 sites located in the southern, central and northern boreal climatic-phytogeographical zones in Finland (Fig. 1a; please see a detailed description of the mires and peatlands in Finland from Lindholm & Heikkilä⁴⁶). The sites represent six main ecosystem types: (i) poor and (ii) rich spruce mire forests, (iii) poor and (iv) rich pine mire forests, and (v) poor and (vi) rich open mires. All the ecosystems are characterised by high water table levels and the presence of peat-forming plant species, but they differ in their tree cover and species composition (Fig. 1b). Although the sites have been originally classified as poor-rich in the floristic sense, correlating with pH⁴⁷, they form a rough gradient also in their nutrient level (note that ‘poor’ and ‘rich’ are comparable within but not between spruce mire forests/pine mire forests/open mires).

Spruce mire forests (Fig. 2a,b; roughly corresponding EUNIS (European Nature Information System) habitat type T3K⁴⁸, spruce swamp forests *sensu* Rydin & Jeglum⁴⁷) are characterised by high tree cover, dominantly spruce (*Picea abies*) for poor types, mixed with deciduous trees, especially in rich types. They are highly diverse, mosaic-like habitats containing species typical for forests as well as peatland species that occur at the transition zone between mire massif and mineral soil forests. Hence, they have significantly higher species richness⁴⁹ compared to pine mire forests or open mires. Poor spruce mire forests are oligotrophic, and rich spruce mire forests are meso-eutrophic. Most spruce mires are *Sphagnum*-dominated, but moving along the gradient from oligotrophic to eutrophic types, the cover of other mosses and vascular plants increases, decreasing the cover of *Sphagnum*.

In pine mire forests (Fig. 2c, d; roughly corresponding EUNIS habitat type T3J⁴⁸, pine bog forests *sensu* Rydin & Jeglum⁴⁷), the dominant tree is pine (*Pinus sylvestris*), which may be accompanied by birch (*Betula pubescens*) in rich types. Pine mire forests have typically thick peat layer covered and dominated by peat-forming *Sphagnum* species, accompanied by other mosses. The poor types are ombrotrophic, while the rich types vary on a gradient from oligotrophic to mesotrophic sites.

Open mires have absent or substantially sparser tree cover than mire forests (Fig. 2e, f). The poor open mires (bogs *sensu* Rydin & Jeglum⁴⁷) are ombrotrophic and receive their nutrients mainly from rainwater, whereas rich open mires (poor and intermediate fens *sensu* Rydin & Jeglum⁴⁷) are oligo-mesotrophic as they receive nutrients also from the surrounding mineral land. The study does not include eutrophic open mires (rich fens *sensu* Rydin & Jeglum⁴⁷). Open mires are typically *Sphagnum* dominated, but when moving along the gradient from ombrotrophic to mesotrophic types, the cover of other mosses and, for example, sedges (*Carex* sp.) increases, decreasing the cover of *Sphagnum*.

The sites were chosen to reflect natural variation within each ecosystem type. The selection was based on the Finnish protected area network spatial database for habitats and an extensive search of old pre-drainage and recent aerial photographs. Pine mire forests and open mires including high coverage of open water surface, were excluded from the site selection. All sites were visited to confirm the observations. When considered necessary, the peatland type was confirmed based on the occurrence of indicator species, following Euroala et al.⁵⁰ Hydrological independency of the sites was confirmed from topographic data and with field observations. As the study sites are spread across Finland, the general environmental conditions (e.g., annual heat sum, average precipitation) vary within the network along a latitudinal gradient. The latitudinal gradient is also reflected as small differences in the vegetation composition among the study sites inside the ecosystem type categories.

Each ecosystem type includes (i) sites that had been drained for forestry during the 1960s and 1970s and were restored when included in the monitoring network ('restored treatment,' approx. 10 sites per ecosystem type), (ii) relatively pristine sites with no drainage ('pristine control,' ~10 sites), and (iii) sites that had been drained and were not restored ('drained control,' approx. 5 sites) (Supplementary Fig. 1a and Fig. 2). The treatment, pristine control and drained control sites within each ecosystem type are dispersed in a similar pattern compared to each other. When successful, drainage for forestry results in a decrease of 35–55 cm in the water table level, resulting in complex changes in nutrient regime and acidity and enhanced tree growth⁵¹. To counteract these changes, restoration was carried out on sites by filling in the ditches and logging the trees that had grown after drainage (if needed)⁵². The restoration was implemented during autumn–winter between 2007–2014⁵³.

In restored sites, moss and vascular plant species were monitored prior to restoration (0-year sampling), 2 (2-year sampling), five (5-year sampling) and 10 (10-year sampling) years after restoration. A similar interval was used in pristine and drained sites, although the time interval between the samplings varies across sites⁵³. The full series of four samplings was completed for 144 sites in total (Supplementary Fig. 1a). In each site, monitoring was done during the growing season (June–August) in 2007–2022 in 10 permanent 1 m² plots (Supplementary Fig. 1b). The plots were systematically situated in two parallel lines, 4 m apart. In restored and drained sites, the lines ran parallel to ditches, and the minimum distance to the nearest ditch was 10 m. The location of the lines represented the typical vegetation of each site, and the location of the first plot was randomised, given the criteria above. For all vascular plant and moss species on each plot, a percent cover was visually estimated at an accuracy of one percent. Exceptions were species with a cover of 0.5–0.9% for which a cover of 0.5% was used, and species with a cover of <0.5% for which a cover of 0.2% was used. Species were identified on-site; when not possible, a specimen was taken and later identified under the microscope. Prior to analysis, we removed observations that did not reach species-level resolution, including hybrids. Because

identifying particular *Sphagnum* species can be challenging, we grouped these species to avoid uncertainty due to misidentification (Supplementary Methods 1 and Supplementary Table 1).

Statistical analysis

We analysed the effect of restoration on individual species occurrences with joint species distribution modelling using the Hierarchical Modelling of Species Communities framework (HMSC^{54,55}). To assess whether the responses to restoration were consistent across ecosystem types, we fitted separate models for each of the ecosystem types. As response variables, we selected the species with at least 10 occupancies for poor spruce mire and pine mire forests, as well as poor and rich open mires (Supplementary Table 2). As rich spruce mire forests and pine mire forests showed a higher number of species, we selected their species with at least twenty occupancies to avoid convergence issues resulting from including a vast number of species. We modelled species occupancy (presence/absence) by a probit model, and conditionally on the presence, cover % (log-transformed, normalised to zero mean and unit variance within each species) with a normal model. Both models had the same structure, as follows. To account for the spatio-temporal structure of the study design, where plots are nested within sites that were visited across different years, we included the sampling year, site and plot as random effects. The sampling year and plot were included as unstructured random effects, and site was included as a spatially explicit random effect. As fixed effects, we included the treatment (a factor with three levels: drained/restored/pristine), time (a continuous variable; 0, 2, 5, 10), and its second-order polynomial to allow for unimodal responses, as well as the interaction of treatment and time².

We ran the models with R package Hmsc 3.0.11⁵⁶, using the Bayesian framework with Gibbs Markov chain Monte Carlo (MCMC) sampling. We assumed the default prior distributions, except for α_1 and α_2 parameters for the random effect site, which were set to 100 to increase the shrinkage and thus avoid modelling noise in the site-level association matrix. We sampled the posterior distribution with four chains, each for 250 samples with a thinning of 1000, using a transient phase of 125,000 and adaptation (the number of MCMC steps at which the adaptation of the number of latent factors is conducted) of 100,000. We evaluated the chain convergence by assessing the effective size of the posterior sample as well as the potential scale reduction factors for each of the estimated parameters (Supplementary Fig. 2). We evaluated model fitting by assessing the difference between the explanatory power (Supplementary Fig. 3) and predictive power through two-fold cross-validation (Supplementary Fig. 4) with Tjur's R² (occupancy) and R² (cover) metrics.

Based on the fitted models, we predicted the abundance of each species (probability of presence × cover given presence) in time for different treatments. From these predictions, we calculated the following five measures informing the different aspects of the effects of restoration on the plant communities.

First, to interpret which species were affected by drainage in the past, we calculated the difference in species abundance in restored versus pristine sites at the initial stage of the experiment:

$$\text{Resp}_{D1} = ab_R^0 - ab_P^0 \quad (1)$$

and similarly drained versus pristine sites:

$$\text{Resp}_{D2} = ab_D^0 - ab_P^0 \quad (2)$$

where ab_R^0 , ab_D^0 and ab_P^0 are species' abundance on plots at time 0 in restored, drained control and pristine control sites, respectively. We calculated the median and the posterior probability for the median being larger than zero, and we considered species having a positive/negative response to drainage if the median for both 1a and 1b were positive/negative with at least 85% posterior probability.

Next, we calculated species response to restoration:

$$\text{Resp}_R = (\text{ab}_R^{10} - \text{ab}_R^0) - (\text{ab}_D^{10} - \text{ab}_D^0) \quad (3)$$

where ab_R^0 and ab_R^{10} are species' abundance on plots in restored sites on the time 0 and 10, respectively; ab_D^0 and ab_D^{10} represent corresponding values in drained sites. Resp_R takes positive values if abundance change is positive in relation to change in drained sites and negative values if abundance change is negative in relation to change in drained sites.

Species abundances in drained and restored sites may differ as they were not randomly selected. To assess the reliability of inferences of how species respond to restoration, we calculated whether species abundance at the beginning of the experiment differed between the drained and restored sites:

$$\text{Diff}_{RD}^0 = \text{ab}_R^0 - \text{ab}_D^0 \quad (4)$$

where ab_R^0 and ab_D^0 are species' abundance on plots in drained control and restored sites at time 0, respectively.

We calculated whether species abundances were similar in restored and pristine control sites 10 years after restoration:

$$\text{Diff}_{PR}^{10} = \text{ab}_P^{10} - \text{ab}_R^{10} \quad (5)$$

where ab_P^{10} and ab_R^{10} are species' abundance on plots in pristine control and restored sites at time 10, respectively.

Finally, we calculated whether species abundances change in drained sites:

$$\text{Change}_D = \text{ab}_D^{10} - \text{ab}_D^0 \quad (6)$$

And whether the difference between drained and pristine control sites grew smaller or larger during the study period:

$$\text{Diff}_{DP} = \text{abs}(\text{ab}_P^{10} - \text{ab}_D^{10}) - \text{abs}(\text{ab}_P^0 - \text{ab}_D^0) \quad (7)$$

where ab_P^{10} and ab_D^{10} are species' abundance on plots in pristine and drained control sites at time 10, respectively, and ab_P^0 and ab_D^0 represent corresponding values at time 0. For all measures from Eq. (2)–(6), we calculated the median as well as posterior probability for the median being larger than zero. We considered the measure to have high support for the median being positive/negative if the posterior probability is >95% and moderate support if the posterior probability is >80%.

To illustrate the variation in community composition among and within ecosystem types and treatments, we produced a model-based ordination using generalised linear latent variable models. The model was fitted with R package *gllvm*⁵⁷ for species with at least 10 observations using hurdle beta response model⁵⁸ and two latent random variables for each site and monitoring year. We assessed model fitting by evaluating the difference between the explanatory and predictive power (based on four-fold cross-validation) (Supplementary Fig. 5). Further, we calculated a restoration effect for each site based on the latent variables in the ordination, which represent similarities in the species compositions among sites. The restoration effect for each site is the change in average distance to drained sites (time 10 - time 0) minus a change in average distance to pristine sites (that in 10 years, the species composition of time 10 - time 0). Thus, a positive restoration effect means the restored site changed more towards pristine sites than drained sites. Conversely, a negative restoration effect means that in 10 years, the species composition of restored sites changed more towards drained sites than pristine sites.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Site-specific species data generated and analysed in the study, species-specific responses as outputs from the joint species distribution modelling as well as source data to produce the graphs have been deposited openly available in Zenodo⁵³.

Code availability

All analyses were carried out with the functions and additional packages specified in the “Methods” section in the free and open-source environment R (version 4.3.0)⁵⁹. The specific codes to reproduce the results are openly available in Zenodo⁶⁰.

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Author contributions

Merja Elo analysed the data and wrote the first draft. Santtu Kareksela oversaw the maintenance of the monitoring network, lead the field work and contributed to writing. Otso Ovaskainen, Jenni Niku, Nerea Abrego and Sara Taskinen all analysed the data and contributed to writing. Kaisu Aapala and Janne S. Kotiaho designed the monitoring network, oversaw the maintenance and obtained funding to maintain the monitoring network, and contributed to the writing.

Competing interests

The authors declare no competing interests.

Additional information

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