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ARTICLE

Restoration of formerly afforested blanket bog: Estimating time for vegetation recovery

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Abstract

Peatland restoration aims to restore hydrology and peat-forming vegetation, supporting other ecosystem functions. However, the time required for complete vegetation recovery is generally unknown. Here, we investigate this in an experimentally restored, formerly afforested blanket bog in northern Scotland, which was plowed, fertilized, and planted with non-native conifers in the mid-1980s. Plowing created three "microforms": Ridges, Original surface, and Furrows. Restoration management took place in two stages: trees were felled and drains blocked in 1998 (Standard treatment); then parts of the area were further rewetted with additional drain-blocking in 2015/2016 (Enhanced treatment). We recorded plant species composition in permanent quadrats 0, 5, 13, and 24 years after the start of restoration. Here we use an ordination-regression-based approach (ORBA) to predict time to plant species compositional recovery compared with a reference (comparable nearby intact blanket bog). For the first 13 years, plant species composition diverged from the reference, then later started to converge. If the current speed and direction of vegetation change were maintained, predicted time to recovery varies between 50–100 years and 120–285 years applying a relaxed or strict criterion for restoration success, respectively. Seven growing seasons after Enhanced treatment, recovery speed increased only for the driest microform, Ridge. Surprisingly, this microform was not predicted to take longer to recover than other microforms under either treatment. On the landscape scale, sloping areas were harder to restore than flatter areas, having longer predicted times to recovery. Complete vegetation restoration may take a long time because of legacies from the afforestation (e.g., increased nutrient availability) and the time taken to fully restore surface morphology and water table. On the other hand, other research has already demonstrated that the site is currently acting as a net carbon sink, despite the incomplete vegetation recovery. We argue that functions may be restored without full recovery of species composition. However, approaching the full suite of species may be desirable to support long-term resilience. Successful peatland restoration needs a strong science-practice partnership, where learning gained from monitoring both damaged and comparable intact peatlands can be used to adapt management interventions.

KEYWORDS
bryophytes, dynamic reference, long-term monitoring, ORBA (ordination-regression based approach), peatland restoration, plant species composition, prediction, restoration ecology

INTRODUCTION

Restoration ecology and ecological restoration are becoming increasingly important due to accelerating human-induced land degradation and climate change (Díaz et al., 2019; Suding, 2011). This increased importance is reflected in the United Nations Decade on Ecosystem Restoration 2021–2030 (Farrell et al., 2022) and the Kunming-Montreal Global Biodiversity Framework which includes a target for 30% of degraded areas of the planet to be under effective restoration by 2030 (CBD, 2022). This presents a major challenge for several reasons, including the fact that restoration ecology is a young discipline needing methodological development (Bertuol-Garcia et al., 2023; Brudvig, 2017; Rydgren et al., 2019). Two major methodological challenges are the long timeframes typically involved in restoration (Jorgenson et al., 2010) and the tendency for successional trajectories to sometimes diverge from restoration targets (Matthews & Spyreas, 2010; Suding, 2011). A practical obstacle is that restoration monitoring, if undertaken, often ends before the restoration outcome is clear (Andersen et al., 2017). This reduces learning opportunities, either from successful or unsuccessful restorations. It also causes the practice and science of ecological restoration to be poorly aligned, reducing overall cost-effectiveness and making strategic decisions more difficult to achieve and implement (Castillo et al., 2016; Rochefort & Andersen, 2017).

Methods for predicting time to recovery of key attributes of ecosystems, such as species composition (Gann et al., 2019), can play important roles in restoration ecology by guiding the entire restoration process (Evju et al., 2023; González et al., 2013; Rydgren et al., 2020). The recently introduced ordination-regression-based approach (ORBA) uses quantitative assessments of species compositional change to predict time to recovery (Rydgren et al., 2019). This approach has shown promising results (Auestad et al., 2020; Evju et al., 2023; Iwachido et al., 2023; Kreyling, 2025; Rydgren et al., 2020), but more tests, from a wider range of ecosystems, are needed to fully evaluate its potential. Peatlands are ecosystems of high restoration priority for both climate regulation and biodiversity (Andersen et al., 2017; Gewin, 2020; Vasander et al., 2003), particularly in Europe, the continent with the largest proportional loss of peatlands (Tanneberger et al., 2021). Hence, peatlands offer good opportunities for combining methodological development with the evaluation of practical restoration measures.

Restoring peatlands is a complex process that involves the reestablishment of hydrological, mechanical and ecological processes that are related by intricate feedback mechanisms (Bacon et al., 2017; Holden et al., 2004; Vasander et al., 2003; Waddington et al., 2015). Accordingly, peatland restoration may achieve a range of acceptable goals. These might vary depending on the degree of degradation, or stage of restoration (e.g., with interim targets in earlier stages). For example, in heavily degraded peatlands such as cutover bogs or peat-mining landscapes, the restoration aim may simply be to establish a bryophyte carpet dominated by the key genus *Sphagnum* (González & Rochefort, 2014) or with more than 50% cover of targeted species (Borkenhagen et al., 2024). In less degraded peatlands, a more ambitious aim may be to restore an ecosystem with a species composition and ecological processes that closely resemble a reference ecosystem, that is considered largely undisturbed. This aim represents the highest restoration standard, "five stars" in the terminology of Gann et al. (2019).

Plant species composition plays a key role in peatlands—and indeed in most other ecosystems—by forming the basic trophic level that strongly influences all other ecosystem attributes (Clewell & Aronson, 2013). Successful restoration of the native, specialist plant species composition will likely also imply that other key ecological functions of the peatland, such as the formation of peat, have been successfully restored (Allan et al., 2024). However, monitoring programs often use simple metrics across various ecosystems such as species richness or vegetation cover (of single species or genera) to assess restoration progress and success (e.g., Ruiz-Jaén & Aide, 2005; Waldén & Lindborg, 2016). Whole-community responses are rarely monitored (Allan et al., 2024). And yet, species composition is arguably a more ecologically relevant indicator of ecosystem condition and, hence, ecosystem recovery, than simpler attributes (cf. Matthews, Spyreas, & Endress, 2009; Rydgren et al., 2020). For peatlands, simpler metrics have often suggested rapid initial recovery, for example, within a decade (Alderson et al., 2019), while post-restoration recovery of species composition and associated processes may take much longer (Anderson & Peace, 2017; Haapalehto et al., 2011; Hancock et al., 2018; Kreyling et al., 2021). We need to better understand the temporal scale of full recovery of these low-productivity and slow-responding ecosystems. We believe that predictive approaches such as ORBA are useful to fill such knowledge gaps (Evju et al., 2023; Kreyling, 2025; Rydgren et al., 2020).

The Flow Country of Caithness and Sutherland, in northern Scotland, is covered by extensive blanket bogs, a globally rare type of peatland limited to cool and/or coastal regions at high latitudes (Joosten et al., 2016; Lindsay et al., 1988; Lindsay & Clough, 2017). Due to its "outstanding universal value," approximately 190,000 ha of the 400,000 ha of the Flow Country was designated in 2024 as the first and only peatland UNESCO World Heritage Site. However, in the Flow Country, as in other parts of Western Europe (particularly Ireland), over 67,000 ha of peatlands were deep-plowed, fertilized, fenced (to exclude wild deer) and planted with non-native conifers in the 1970s–1980s (Andersen et al., 2017; Lindsay et al., 1988). This fundamentally changed the hydrology, light, and litterfall conditions (Gaffney et al., 2018; Howson et al., 2021, 2023) and vegetation (Hancock et al., 2018). Deep plowing also radically changed the surface topography of the peatland, creating three different "microforms": plow ridges, the original surface (a strip remaining between the plow ridges), and plow furrows (Hancock et al., 2018).

Following a recognition of the negative impact of afforestation on the biodiversity of the Flow Country (Lindsay et al., 1988; Warren, 2000), restoration attempts were initiated in the late 1990s (Anderson & Peace, 2017; Wilkie & Mayhew, 2003). These included early experimental restoration areas, with permanent vegetation quadrats (Anderson & Peace, 2017; Hancock et al., 2018). Initial "standard" forest-to-bog restoration efforts of felling trees into plow furrows and dam collector drains (Wilkie & Mayhew, 2003) were supplemented with an additional "enhanced" blocking of plow furrows for parts of the area from the winter of 2015/2016 onward.

In this study, we use ORBA (Rydgren et al., 2019) to predict time to recovery of the plant species composition in one of these areas, after Standard treatment and Enhanced treatment were initiated, that is, 24 and 6.5 years after restoration respectively. Our experimental setup addresses two treatments in a factorial manner: two restoration measures (Standard and Enhanced) × three microforms (Ridge, Original surface, and Furrow). Given that the hydrological conditions had already improved after 13 years (Hancock et al., 2018), we hypothesize that the plant species composition would have started converging toward the reference after 24 years, regardless of treatment. Furthermore, we hypothesize that the rate of change would be highest for quadrats within Enhanced restoration areas, and lowest for the (driest) Ridge microform. More specifically, we aim to evaluate the following hypotheses:

> **H1.** During the 11 years between the two vegetation surveys of quadrats in the experimental area (pre- and post-Enhanced restoration), the pattern of species compositional change has shifted, from diverging from the reference, to converging toward the reference.
>
> **H2.** The Enhanced restoration reduces the predicted time to recovery compared to the Standard restoration, for all microforms.
>
> **H3.** The predicted time to recovery is longer for Ridge than for the two other microforms (Furrow and Original surface), for both restoration treatments.

METHODS

Study area

The study was conducted in the Talaheel restoration area (Figure 1a,b), formerly a conifer plantation (58°25′ N, 3°49′ W, 160–200 m asl) within Forsinard Flows National Nature Reserve (NNR), now managed by the Royal Society for the Protection of Birds. Forsinard Flows NNR is situated centrally in the Flow Country (Joosten et al., 2016; Lindsay et al., 1988) where the topography is gently undulating with peat ranging in depth from <50 cm to >6 m (Chapman et al., 2009) over syenite and granite (Searle et al., 2019). The climate is cool and oceanic, with mean annual (1991–2020) precipitation of 949 mm, days with ≥1 mm rainfall of 183, air temperatures maximum and minimum of 11.7 and 3.6°C respectively, taken at Kinbrace station (Met_Office, 2023), approximately 20 km southwest of the study site.

The Flow Country peatlands were more or less treeless from c. 4000 BP (Charman, 1994) until the 1970s and 1980s, when the American conifer species, *Pinus contorta* Douglas ex Loudon and *Picea sitchensis* (Bong.) Carrière, were widely planted in the area (Lindsay et al., 1988; Warren, 2000). These plantings included the establishment

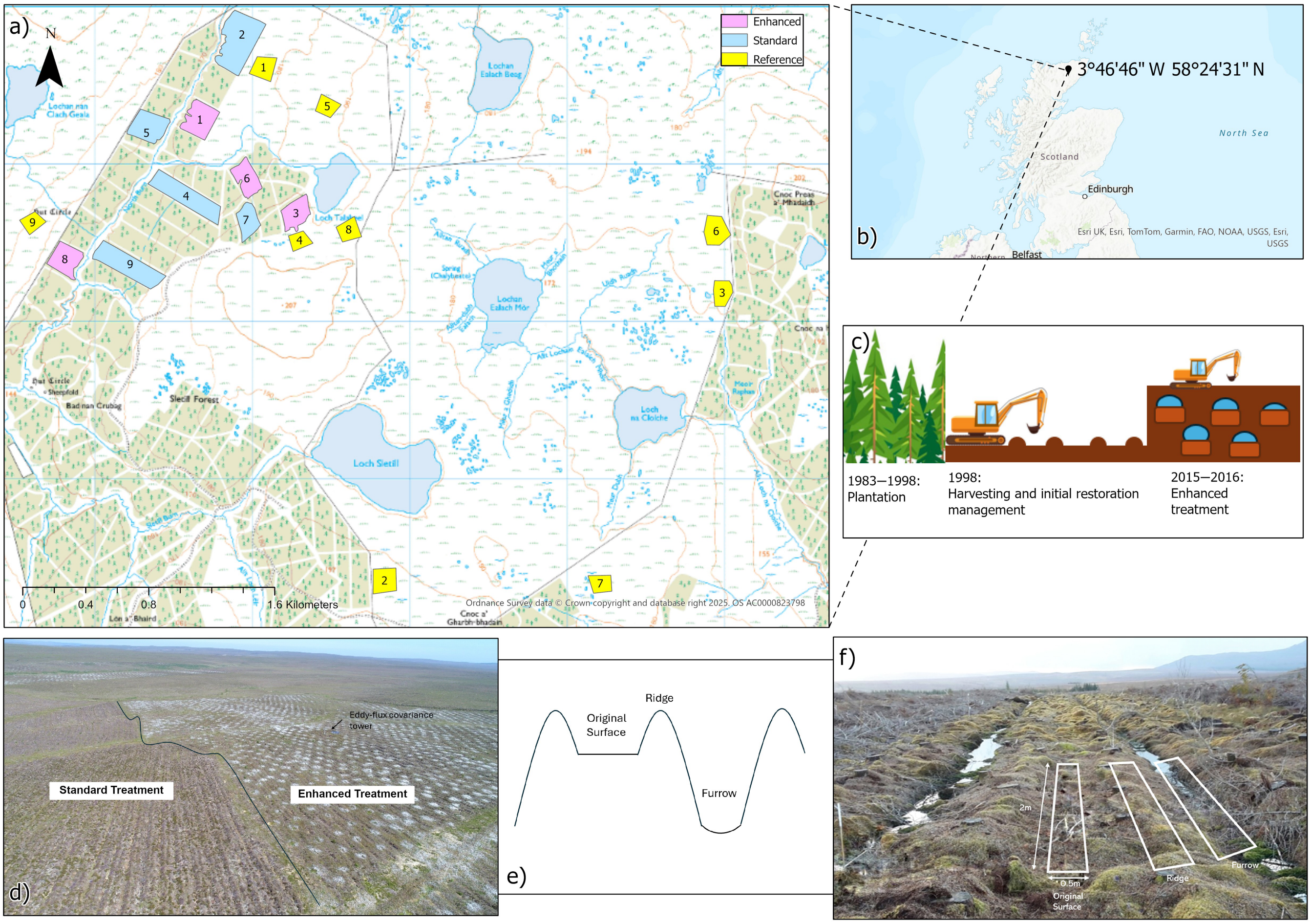

FIGURE 1 (a, b) Location of the Talaheel study site in northern Scotland with restoration plots 1–9 (blue and pink), and their matched reference (bog control) plots (yellow) with corresponding numbers. (c) An illustration showing the restoration history of the study site. (d) Aerial photo showing an area in 2019, with Standard treatment (left) and Enhanced treatment (right). In the latter, pools formed behind dams are visible from the seed heads of *Eriophorum vaginatum* (white patches). Note the alternate dams in adjacent furrows. (e) A sketch showing a cross section of the three microforms. (f) An example from an earlier stage of restoration in a different ex-forestry area, of the three microforms Ridge, Original surface, and Furrow, resulting from the afforestation. Photo credits: (c) Robert D. Hughes, using licensed stock image from Canva (Canva Pro, licensed for commercial and academic use) (d) Paul Turner; (f) Robert D. Hughes.

of the 150-ha Talaheel plantation during 1983–1985. Before planting, as was typical of these plantations, the Talaheel site was plowed to c. 1 m depth with c. 2.5 m spacing of furrows. This resulted in the creation of three "microforms" (Figure 1e,f): plow ridges (hereafter Ridge), Original surface, and plow furrows (hereafter Furrow). "Collector drains," typically longer, wider and deeper than furrows, were plowed alongside afforested compartments, approximately perpendicular to furrows, to remove water draining from multiple furrows. After site preparation, conifer saplings were planted on plow ridges. At that time and in later years, fertilizers were added to enhance conifer establishment. The area was fenced to exclude native wild red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. Nevertheless, over time deer found their way into the fenced area; hence, some deer browsing occurred in the afforested area but less than in the surrounding blanket bog landscape.

In 1998, restoration started (Figure 1c), with felling the (relatively small) trees well before harvesting age; depositing stems and other logging residues in furrows, which to some extent impeded drainage; and damming of collector drains (Hancock et al., 2018) (hereafter, Standard treatment). Conifer seedlings that colonized the area from seed sources nearby were manually cleared in 2003–2004 and 2010–2012. In the winter of 2015/2016, parts of the study area were subjected to additional restoration treatments to accelerate rewetting, hereafter referred to as the Enhanced treatment (Figure 1c,d). In Enhanced areas, additional peat dams were placed every c. 20 m along furrows, further impeding drainage. Dams were staggered on alternate furrows. A limited amount of surface re-profiling was also achieved by driving a low-ground-pressure excavator along the furrow ridges while constructing the peat dams, reducing the height of the ridges and the width of the furrows.

Sampling design and data collection

In 1998, an experimental area was established in the blanket bog landscape centered on the former Talaheel forestry plantation, to monitor the effects of the restoration measures. Within this area, nine plots (Figure 1a) were randomly selected, stratified by planting year, that varied in size between 1.6 and 4.8 ha (Hancock et al., 2018). The plots encompassed different topographic positions and probably also different initial hydrological conditions: from more strongly sloping, concave valley sides adjacent to the River North Burn in the southwest (plots 8 and 9), to very gently sloping, plane or convex topography west of Lake Talaheel (plots 3 and 7).

In each plot, nine recording locations, each approximately 2 × 2 m (Hancock et al., 2018), were selected at random. Within each location, three permanent quadrats of 0.5 × 2 m were established to represent the three microforms: Ridge, Original surface (hereafter referred to as Original), and Furrow. Of the nine plots, four, chosen at random, were subjected to the Enhanced treatment in winter 2015–2016 (Figure 1a,c). Thus, the quadrats in these plots experienced seven growing seasons following the Enhanced treatment before being resurveyed in 2022.

The plant species composition of the quadrats was recorded shortly before tree felling in 1998, which constitutes our year 0, and again 5, 13 and 24 years later, that is, in 2003, 2011 and 2022. In 2011–2015, nine plots were selected in intact blanket bog, 100 m to several km from the forestry fence surrounding the experimental area at Talaheel (Figure 1a). These plots were situated in very gently sloping, plane or convex terrain. They were used as bog controls by Hancock et al. (2018) and are used in our study as a dynamic reference (Rydgren et al., 2019) for intact blanket bog vegetation. In each reference plot, five permanent 1 × 1 m quadrats were established. The species composition of the 45 quadrats in the nine control plots was surveyed at establishment in 2011–2015, and again in 2022. The nine reference plots and the nine restoration plots had similar peat depths (mean ~2.7 m, range 1.3–4.8) and slopes (mean ~1.9–2.1°, range 0.88–3.7) (Hancock et al., 2018).

The total dataset comprised 1062 quadrat × time combinations (QTCs) with a total of 100 recorded plant taxa. The nomenclature of vascular plants and mosses follows Clapham et al. (1987) and Smith (2004), respectively. Of these, 90 QTCs represented the reference quadrats, Reference 2011–2015 ($n = 45$) and Reference 2022 ($n = 45$). The remaining 972 QTCs represented the six combinations of restoration measure and microform, hereafter referred to as Microform × Treatment combinations (MTCs) (Table 1): Furrow Standard ($n = 180$), Furrow Enhanced ($n = 144$), Original Standard ($n = 180$), Original Enhanced ($n = 144$), Ridge Standard ($n = 180$), and Ridge Enhanced ($n = 144$).

The plant species composition of the QTCs was recorded from July to December in each monitoring year. The abundance of each taxon was visually estimated as percentage cover. Most taxa were determined to the species level, and some to the genus level. Ferns, liverworts, and lichens were aggregated to a group.

Data analyses

All statistical analyses were performed in R version 4.3.0 (R Development Core Team, 2023). The vegan package version 2.6-2 (Oksanen et al., 2022) was used for all ordination analyses. Prior to analyses, we modified the relative weight given to qualitative and quantitative information (Økland, 1990b) by applying a power function to each percentage cover value in each QTC (van Son & Halvorsen, 2014). A value $w = 0.5$ was used for the weighting parameter as suggested by Rydgren (1993), to set the range of the abundance scale, that is, the ratio between the highest and lowest abundance value, to 10.

Ordination analyses were used to extract gradients in species composition from the 1062 QTC × 100 species data matrix with weighted abundances for all taxa. Detrended correspondence analysis (DCA; Hill & Gauch, 1980) and global nonmetric multidimensional scaling (GNMDS; Minchin, 1987) as implemented in the vegan package version 2.6-2 (Oksanen et al., 2022) were used in parallel to confirm that the ordination axes were structure axes (Økland, 1999). See Appendix S1: Section S1 for ordination specifications (options and settings) and other details of the analyses. The two- and three-dimensional GNMDS ordinations were relatively similar to each other and to the corresponding axes of the DCA ordination (Appendix S1: Section S1), except for a more distinct outlier QTC in the DCA ordination. We therefore used the three-dimensional GNMDS solution for all subsequent statistical analyses. Estimates of the relative positions of species optima in GNMDS ordination space were obtained as weighted mean sample scores using the function *wascores* in vegan (Oksanen et al., 2022). These “relative species optima” are not expressed on the same scale as QTC scores, because weighted averaging places them within

TABLE 1 The distribution of quadrats among treatments, microforms, and time periods.

		Years since restoration began			
Restoration measure	**Microform**	**0**	**5**	**13 (−17)**	**24**
Standard	Ridge	45	45	45	45
	Original	45	45	45	45
	Furrow	45	45	45	45
Enhanced	Ridge	**36**	**36**	**36**	36
	Original	**36**	**36**	**36**	36
	Furrow	**36**	**36**	**36**	36
Reference	Original	0	0	45	45

Note: Numbers in bold indicate that, at these time points, the quadrats had not yet been subjected to Enhanced restoration, which was conducted in the winter of 2015/2016, 17.5 years after restoration. Reference quadrats in nearby intact blanket bog were surveyed 13–17 years and 24 years after restoration. “Original” means “original blanket bog surface.”

the range spanned by QTC scores along the axes (Økland, 1990b).

We conducted two different tests of QTC positions in the GNMDS ordination. First, we tested whether the centroids of the six MTCs differed from the reference (data from 2011 to 2015) along each of the three GNMDS axes at the start of the restoration in 1998. Next, we tested if the centroids of the six MTCs differed between the four periods (1998, 2003, 2011 and 2022) for each of the three GNMDS axes. Tests were done using generalized linear mixed models (GLMMs; Bates et al., 2015) with an identity link and Gaussian error distribution, in the R packages lme4, version 1.1.21 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2016). In the first test, the random factor was location nested within plot. In the second test, to account for repeated measurements, quadrat number was included as an additional random factor. We followed the principle of parsimony and simplified the models into a minimal adequate model, using a backward elimination procedure with likelihood ratio tests (Crawley, 2013).

We used ORBA to predict time to species compositional recovery (Rydgren et al., 2019). We first obtained a consensus ordination (the three-dimensional GNMDS) by the procedures described above. Secondly, for each MTC and time point, we used QTC positions along each GNMDS axis to calculate successional distance ($d_{jt,0}$) (Rydgren et al., 2019), or successional displacement when it holds negative values, from an appropriate reference. For the first three time points (0, 5, and 13 years after restoration began), we used the mean position of the reference QTCs in 2011–2015 as reference for all restored QTCs, while the mean position of the reference QTCs in 2022 was used as reference for QTCs analyzed in 2022. Thus, we used reference data that were collected nearest in time, as our comparator for the restoration data. The variation of the reference for each GNMDS axis was calculated as the SD of distances along each axis from single QTC positions to the centroid of appropriate reference QTCs at the time point in question. The variation of the reference for three-dimensional GNMDS was calculated as the SD of variance for the sum of three variables:

$$\begin{aligned}\mathrm{var}(a1+a2+a3) =& \mathrm{var}(a1)+\mathrm{var}(a2)+\mathrm{var}(a3)\\ &+2\mathrm{cov}(a1,\, a2)+2\mathrm{cov}(a1,\, a3)\\ &+2\mathrm{cov}(a2,\, a3)\end{aligned}$$

where $a1$ = GNMDS axis 1, etc.

Finally, we modeled the successional distances in three-dimensional GNMDS ordination space (because no single axis represented the strongest successional gradient) at the two time points, 13 and 24 years after restoration, as a function of time since restoration, for each of the six MTCs, and each of the nine plots and the three microform combinations ($n = 27$). The response was logarithmically transformed because successional rates generally decrease over time (Anderson, 2007; Myster & Pickett, 1994; Rydgren et al., 2004; Rydgren et al., 2019). The spatially nested sampling structure was accounted for by specifying quadrats nested within locations (but not for the plot data where all quadrats come from the same plot) and plots as random intercepts. All models were parameterized with an identity link and a Gaussian error distribution using the R package lme4, version 1.1.21 for GLMM (Bates et al., 2015). From the model, we derived two different time-to-recovery predictions for each MTC (Rydgren et al., 2019): $\mathrm{TR}_{\mathrm{As}+1}$ (restoration target: predicted successional distance = +1 SD off the centroid of reference QTC scores) and $\mathrm{TR}_{\mathrm{Af}+0.01}$ (restoration target: predicted successional distance = +0.01 SD off the centroid of reference QTC scores). The terms “Relaxed” and “Strict” are used for the “+1 SD model” and the “+0.01 SD” model, respectively.

RESULTS

Overview of species compositional change during restoration

In 1998, at the start of restoration, prominent taxa of intact blanket bogs such as dwarf shrubs *Calluna vulgaris*, *Erica tetralix*, and lichens were frequent in all MTCs (Figure 2; Appendix S2: Table S1). Subsequently, in all MTCs, *C. vulgaris* declined considerably from year 0 to year 13 but then increased, from year 13 to year 24. In contrast, the graminoids *Eriophorum angustifolium* (Figure 2) and *Eriophorum vaginatum* were initially concentrated in the Furrow microform but later became approximately equally distributed among microforms. Considering the commonest species of peat mosses, *Sphagnum* spp. (Figure 2), *Sphagnum cuspidatum*, and *Sphagnum capillifolium* tended to be most abundant in furrows and original surfaces, respectively, with some decline later in the study; meanwhile, *Sphagnum subnitens* was rarer but increased later in the study across all microforms. *Sphagnum* spp. were generally rare in Ridge microforms. Differences between Enhanced and Standard treatments appeared modest.

Taxa that were found in the restoration area but infrequent or lacking in the reference area showed a wide spectrum of temporal patterns. The endpoints of this spectrum comprised conifer seedlings of *P. sitchensis* and *P. contorta* which were largely found in early years, and the grass *Deschampsia flexuosa* (Figure 2) which increased over the study period to become one of the most prominent species in most restored treatments. Between these extremes, the grass *Agrostis* spp. and the mosses *Dicranum*/*Campylopus* spp. tended to decline in the restoration area during the study. Meanwhile, the mosses *Hylocomium splendens* and *Pleurozium schreberi* (Figure 2), the grass *Molinia caerulea* and the moss *Polytrichum* spp. increased across all treatments.

Gradients in species composition

The ordination results revealed that the complex spatial and temporal variation in species composition in the study area was structured along three interpretable compositional gradients.

GNMDS axis 1 separated reference from treatment QTCs (Figure 3). At the start of restoration, all MTCs except Furrow Enhanced (note, however, this was prior to Enhanced treatment) differed significantly from the reference along GNMDS axis 1 (Appendix S2: Table S2). Thereafter, QTCs from all six MTCs increasingly trended toward lower scores on this axis, that is, away from the reference, until the last period, 13–24 years after restoration. At that point, this trend was halted with a slight reversal, that is, displacement toward the reference, for the Standard treatment (Figure 3; Appendix S2: Table S5). No consistent temporal ordering of treatments was observed along GNMDS axis 1. The reference vegetation showed only minor temporal change.

Considering GNMDS axis 1 at the individual plot level, this also showed relative stability across time points (Figure 4). The most striking pattern was found for the Original microform (Figure 4; Appendix S2: Figures S1–S3), for which the plot centroids made up three distinct groups. The sloping plots 5, 8, and 9 scored low on the axis, and the flatter plots 3, 6, and 7 scored high, and the other plots were intermediate (Figure 4). Among the remaining microforms, the more sloping plots, that is, 5, 8, and 9, were differentiated from all other plots concerning their GNMDS 1 centroids. In contrast, the other six plots made up one big cluster (Figure 4). The more sloping plots (5, 8, and 9) also showed greater dynamics, trending more markedly away from reference conditions early in the study, then back toward the reference later.

The relative species optima along GNMDS axis 1 (Figure 5) formed two groups that were separated by a distinct gap. Species with optima to the left of the gap were rare in reference QTCs and much more frequent in restoration QTCs. The converse was true for species with optima to the right of the gap (Figure 5; Appendix S2: Table S1). The contrast in abundance between restoration and reference QTCs increased from this gap, outward toward the two gradient extremes. Thus, the forbs and graminoids with the lowest axis 1 optima, *Juncus effusus*, *Agrostis* spp., and *Galium saxatile*, were largely characteristic of the restoration area rather than the reference. The species with the highest optima, *Racomitrium lanuginosum*, *Trichophorum cespitosum*, and *Sphagnum tenellum* showed an opposite pattern. GNMDS axis 1 thus reflected a gradient from species with low values that were rare in blanket bogs but frequent in restoration areas, to species with higher values that were most typical of intact blanket bogs.

GNMDS axis 2 tended to separate the three microforms in the order Ridge (low scores)–Original–Furrow (high scores) (Figures 3 and 4). This implied that higher scores reflected wetter conditions. At the start of restoration, Ridge and Original microforms differed significantly from the reference along this axis (Appendix S2: Table S3). Over time, the centroids of all treatments consistently shifted toward higher GNMDS 2 scores, indicating increased wetness, with Ridge experiencing significantly higher rates of change compared to Furrow (Appendix S2: Table S6). The centroids of Original and Ridge QTCs reached the level of reference scores along GNMDS 2 in

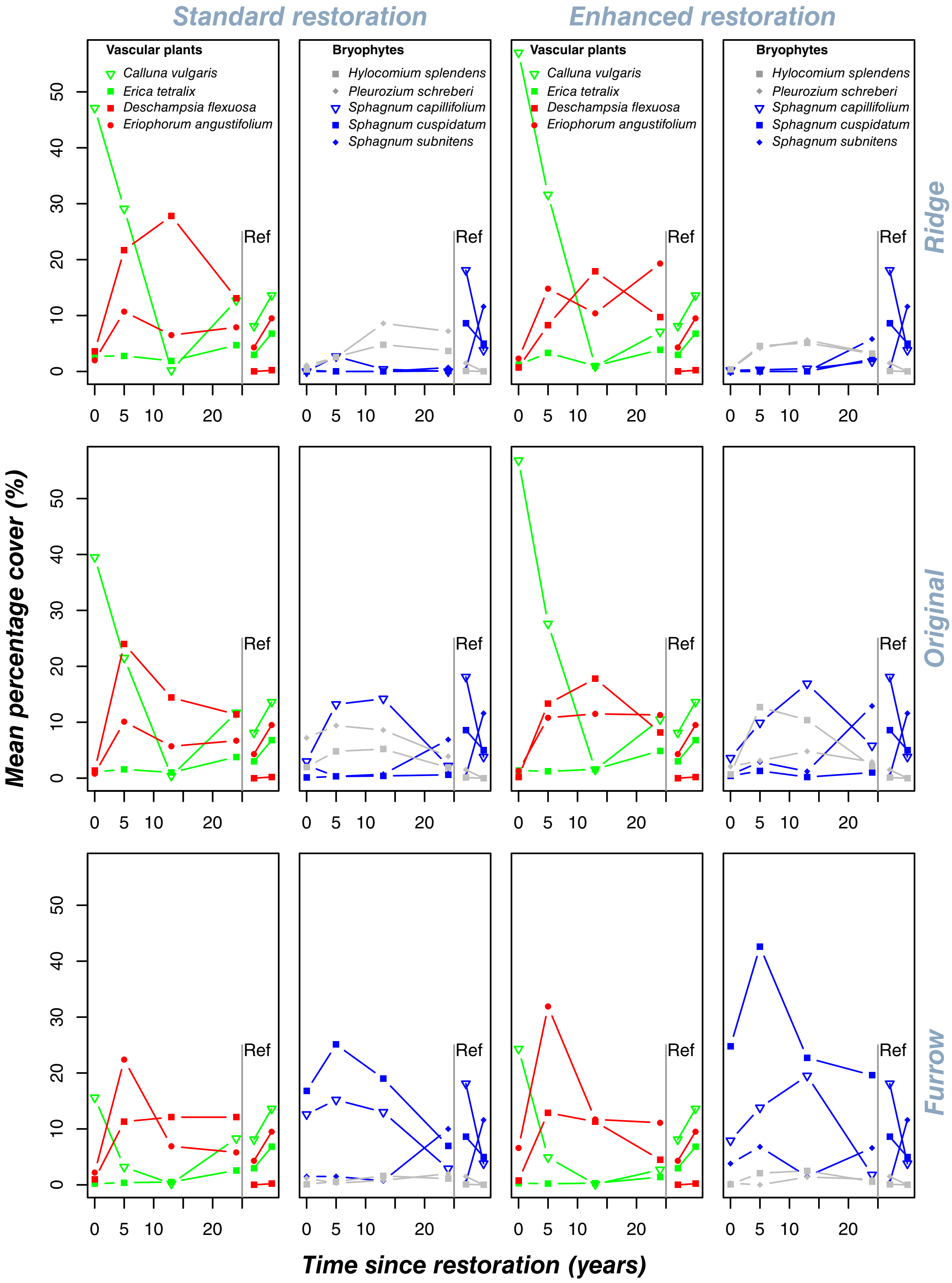

FIGURE 2 The changes in mean percentage cover over the years since restoration for a selection of the most common species in the six microform-treatment combinations. The cover changes in the reference quadrats (Ref) between 13 and 17 and 24 years since restoration are shown on the right-hand side of each figure.

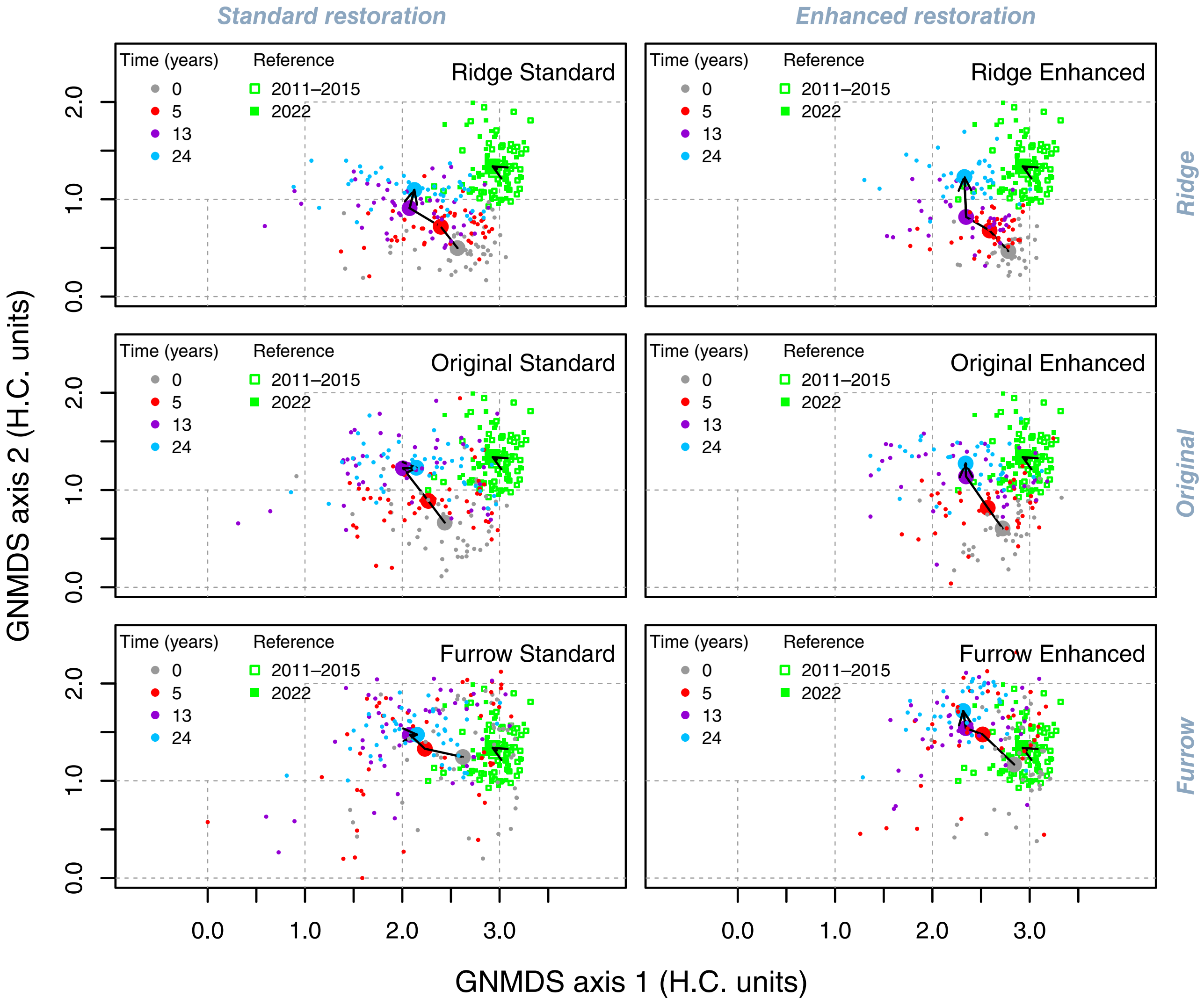

FIGURE 3 Quadrat level data and displacement vectors in global nonmetric multidimensional scaling (GNMDS) ordination space (gradient lengths 3.33 and 2.32 H.C. units for axes 1 and 2, respectively), joining centroids (large dots) for combinations of microform (Ridge, Original, and Furrow), treatment (Standard or Enhanced), and year since restoration (0, 5, 13, and 24 years). Positions of the 1062 quadrat × time combinations (QTCs) are shown by small symbols. The reference quadrat data (QTCs and centroids) is also shown in all graphs; its vector is very short, indicating little change in reference vegetation.

5–13 and 24 years, respectively (Figure 3), implying that recovery had been achieved, by this measure. Displacement patterns in the last period (13–24 years) differed between treatments for the Furrow and Ridge microforms: while Furrow Enhanced moved out of the range spanned by reference QTCs, to significantly higher (i.e., wetter) scores, Ridge Standard had still not fully caught up with reference scores after 24 years (Figure 3). Contrasting with the dynamics of the restoration area, the reference vegetation showed only minor change.

At the level of individual plots (Figure 4), the temporal displacement patterns along GNMDS axis 2 did not differ strongly, except for the more sloping plots 5, 8, and 9 for Furrow, which had lower (drier) GNMDS 2 scores in early years (Figure 4; Appendix S2: Figures S1–S3).

Species with optima near the low-score (dry) end of GNMDS axis 2 were either absent from intact blanket bog in our reference areas (*J. effusus* and seedlings of *P. sitchensis* and *P. contorta*) or typical of drier microsites (*C. vulgaris* and *Hypnum* spp.). In contrast, all *Sphagnum* species had optima near the high-score (wet) end of GNMDS axis 2 (Figure 5). This also supports the interpretation that GNMDS axis 2 reflected variation from less to more hydrophilous vegetation, and hence from drier to wetter microsites.

Along GNMDS axis 3, all microforms except Original had significantly lower scores than the reference at the start of restoration (Appendix S2: Figure S4 and Table S4). Moreover, all MTCs showed the same displacement patterns over time (Appendix S2: Table S7): weak

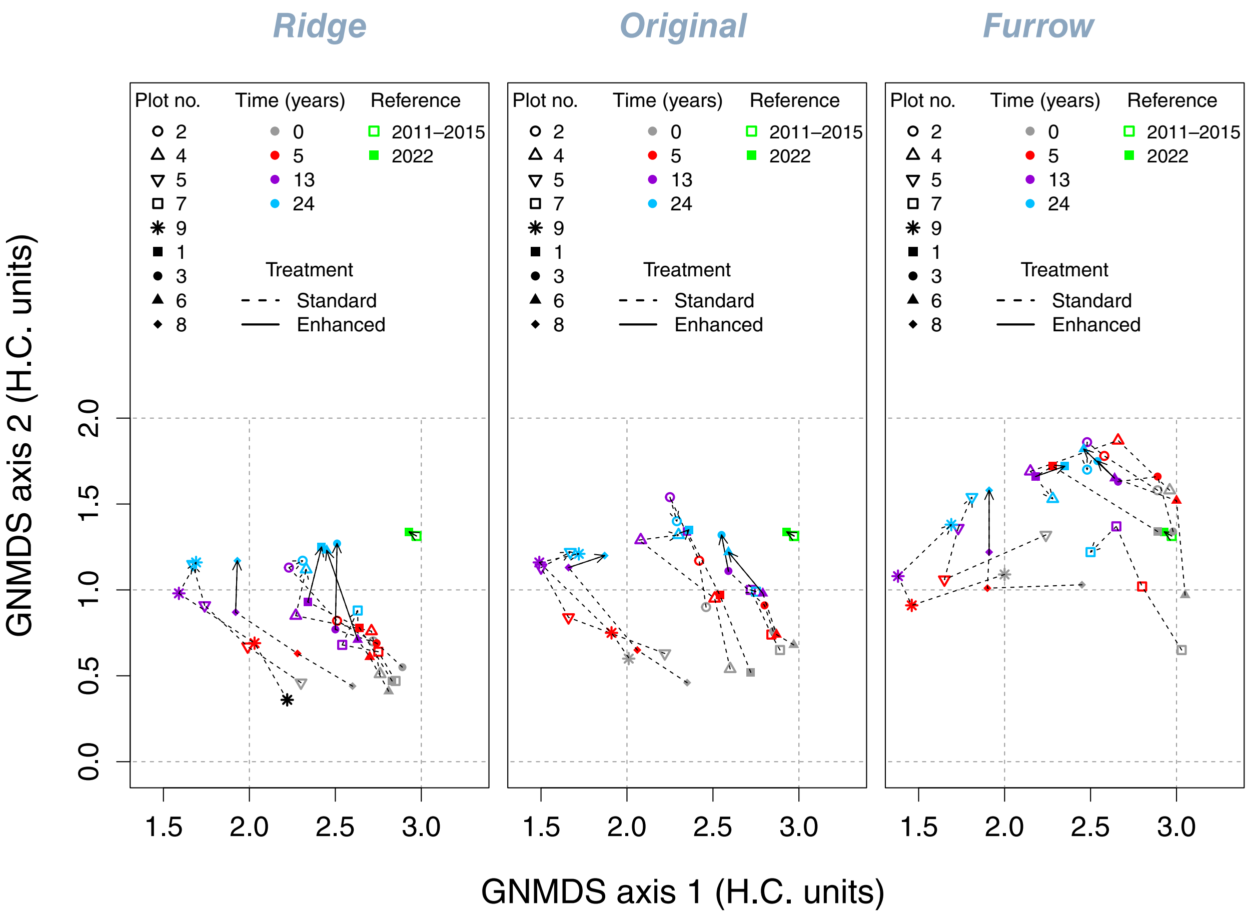

FIGURE 4 Whole-plot level displacement vectors in global nonmetric multidimensional scaling (GNMDS) ordination space (axes 1 and 2) joining centroids for combinations of microform (Ridge, Original, and Furrow), plot (1–9) and year since restoration (0, 5, 13, and 24 years). Plots 1, 3, 6, and 8 were subjected to Enhanced treatment after year 13. The reference is the same in all graphs.

displacements away from the reference QTCs in the first two periods (0–5, and 5–13 years) and then significant displacement toward the reference later (13–24 years). On this axis, the reference vegetation (as indicated by its centroid) did not change over time. Except for the low scores of graminoids *J. effusus* and *Agrostis* spp., little segregation of species optima was observed along GNMDS axis 3 (Appendix S2: Figure S5). The different ordering of microform centroids along GNMDS axis 3 (Furrow–Ridge–Original) compared to GNMDS axis 2 (Furrow–Original–Ridge) and the larger spread of optima for species not typical of bogs (low GNMDS 1 scores) suggested that GNMDS 3 expressed differences in the temporal dynamics of species, that were unrelated to hydrological conditions (which were instead expressed on GNMDS axis 2).

Time to recovery

The patterns of displacement from the reference in each of the three-dimensional GNMDS ordination axes (Figures 6 and 7; Appendix S2: Figure S6) can be characterized as initial divergence followed by slight convergence (axes 1 and 3) or simply convergence (axis 2). Combining all these into the three-dimensional ordination space (Figure 8), the average successional distance to the reference peaked around 5–13 years after restoration and thereafter decreased considerably, reaching a minimum at the most recent survey, 24 years after restoration began. The strongest decreases in successional distance in the last period were observed for the Furrow Standard and the Ridge Enhanced; the smallest decrease was observed for Furrow Enhanced.

The six MTCs differed considerably in time-to-recovery predictions, with more than a twofold difference between the lowest and highest values. These ranged between 47–99 and 122–283 years for the “Relaxed” and “Strict” criteria, respectively (Figure 8). The rank order of time-to-recovery predictions for the six MTCs followed almost the same pattern for the two recovery criteria. Overall, the shortest time to recovery was consistently predicted for Ridge Enhanced followed by Furrow Standard. The two

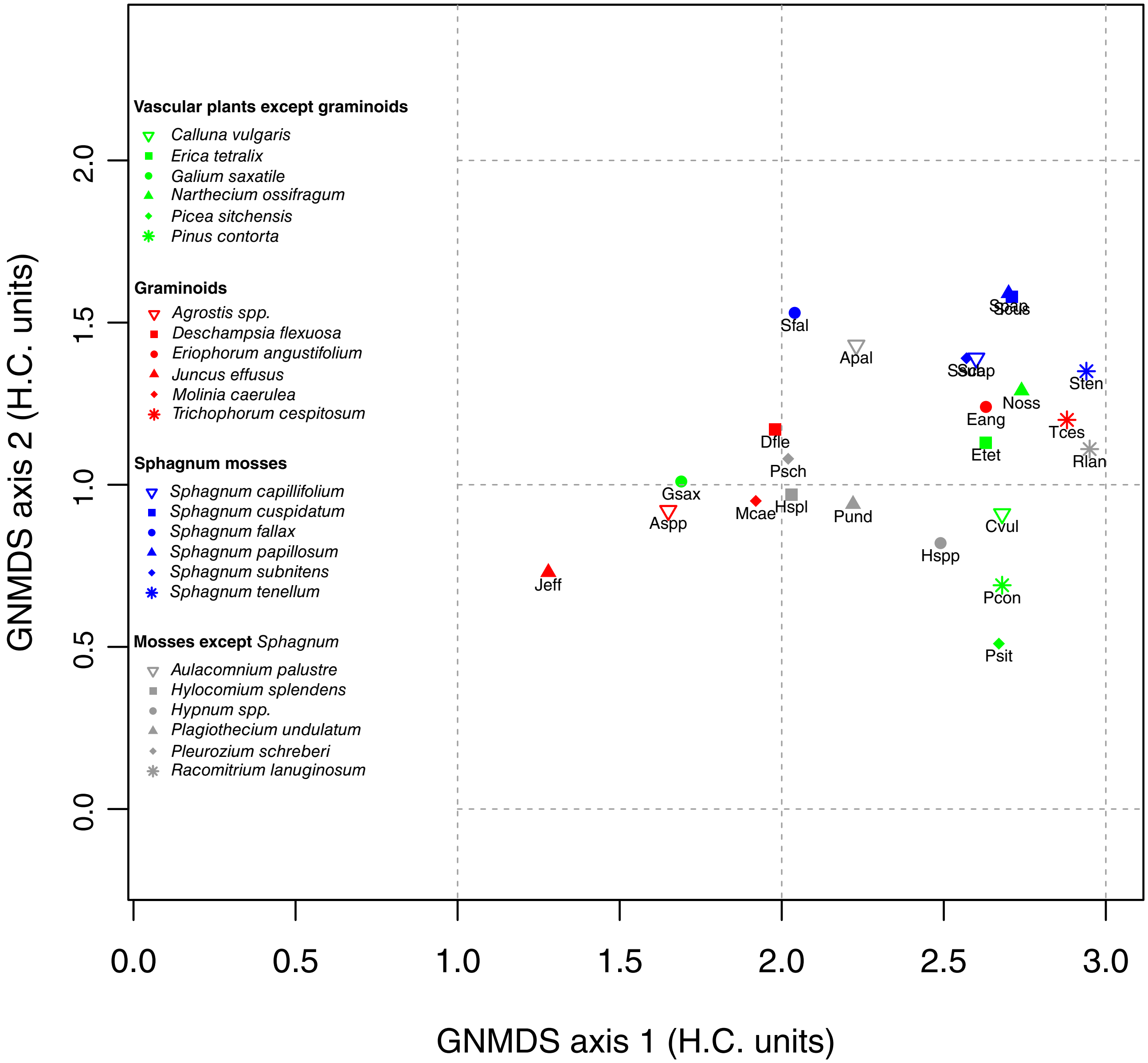

FIGURE 5 Relative species optima for a selection of the most common species in the global nonmetric multidimensional scaling (GNMDS) ordination space, axes 1 and 2, calculated as weighted averages of quadrat × time combination (QTC) scores using species abundances as weights. The words below the species optima symbols are abbreviated species names. Note that the relative species optima and QTC scores of Figure 3 are expressed on different scales.

Furrow treatments differed markedly. Furrow Enhanced always had the longest predicted time to recovery. The Original treatments had similar predictions, irrespective of whether Standard or Enhanced restoration methods were used. Surprisingly, the results did not always show a positive effect of Enhanced restoration: for Ridges, the Enhanced treatment was predicted to lead to faster recovery, but for Furrows, the converse was true (Figure 8).

At the plot level, the median of the time-to-recovery predictions for each microform, based on successional distance in the last period (13–24 years) in the ordination (Table 2) is similar to predictions at the MTC level. However, there were large differences between the plots (Table 2): the more sloping plots 5, 8, and 9 generally had the longest predicted time to recovery. These plots' median predictions (over the three microforms) ranged between 99–148 and 255–392 for the "Relaxed" and "Strict" criteria, respectively (Table 2). The other plots had median predictions around half these values, in the range 43–59 and 110–175 for the "Relaxed" and "Strict" criteria, respectively.

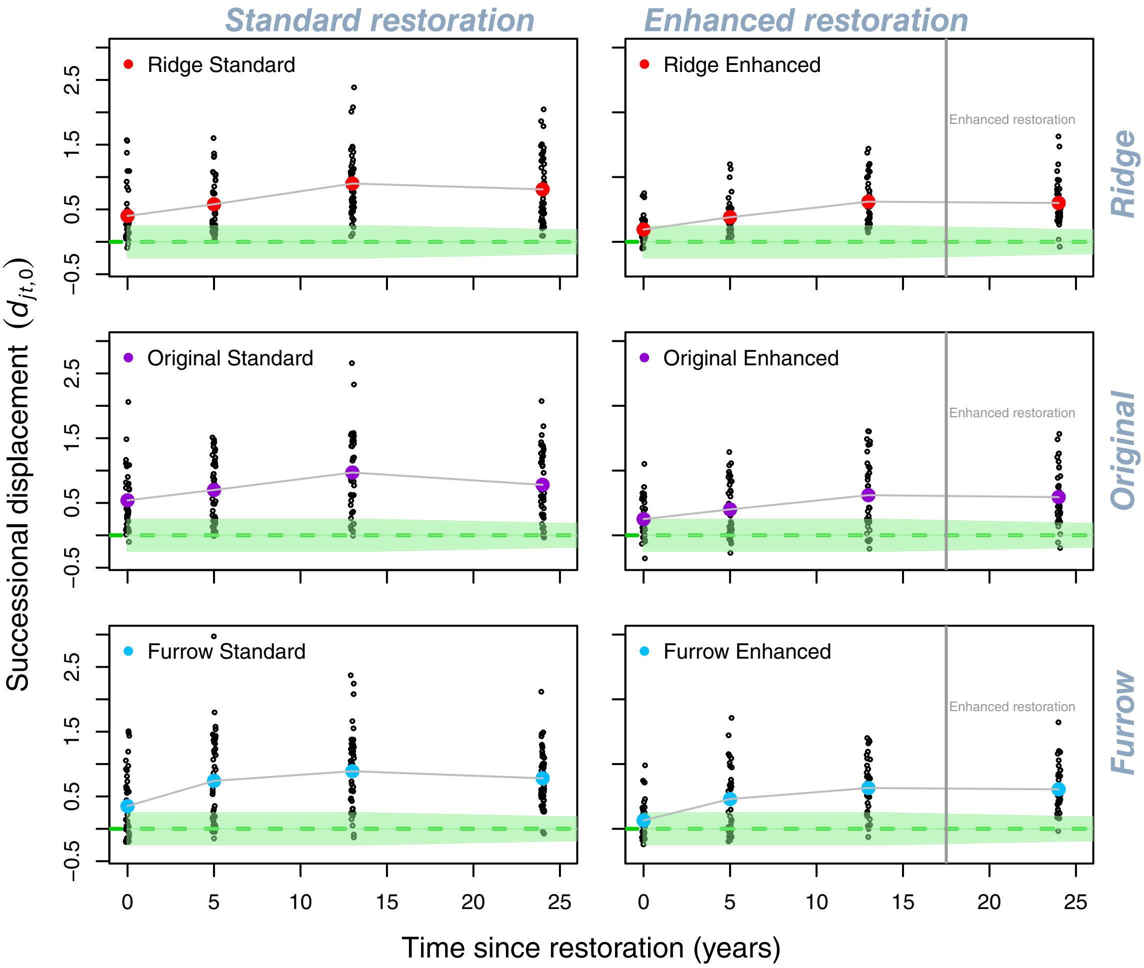

FIGURE 6 Global nonmetric multidimensional scaling (GNMDS) axis 1: Successional displacement for each quadrat-by-time combination (QTC). These are plotted as slightly jittered points across time for the six microform-treatment combinations (MTCs). The red, violet, and blue-colored points joined by trendlines show mean successional displacement at each time point for the different MTCs. The green-dotted horizontal line represents the centroid of reference QTC scores along the successional gradient with +1 SD indicated by light green shading. SD was 0.24 for the first three time points and 0.18 for 2022. The gray vertical line shows the time point at which the Enhanced treatment was carried out.

DISCUSSION

Our results show that the recovery of plant species composition in forest-to-bog restoration sites at Talaheel initially followed a trajectory away from comparable intact bog (reference) vegetation for approximately a decade. Later, a reversal of this trajectory started to take place. This supports our first hypothesis, that after initially diverging from the reference, the trajectory of species composition of all MTCs will eventually converge back toward the reference conditions of an intact bog. Furthermore, without additional restoration measures, time-to-recovery predictions suggest that 50–100, or 120–285, years will be needed to fully restore blanket bog vegetation at this site, using the "Relaxed" or "Strict" recovery criteria, respectively. Our second hypothesis, that the Enhanced treatment, applied 17.5 years after restoration began, would reduce the predicted time to recovery, is, apparently, not supported during this study period. The Enhanced treatment does indeed reduce predicted time to recovery in the Ridge microform; however, the opposite appears to be the case for the Furrow microform, perhaps because this latter microform trended toward even wetter conditions than those found in our reference areas (see below). Similarly, our third hypothesis is also not supported, that is, that the predicted time to recovery is longer in Ridge than in the other microforms. Instead, we found, for the Standard treatment, no difference between microforms. Meanwhile, for the Enhanced treatment, surprisingly, Ridges had lower predicted recovery times than Original and Furrow microforms.

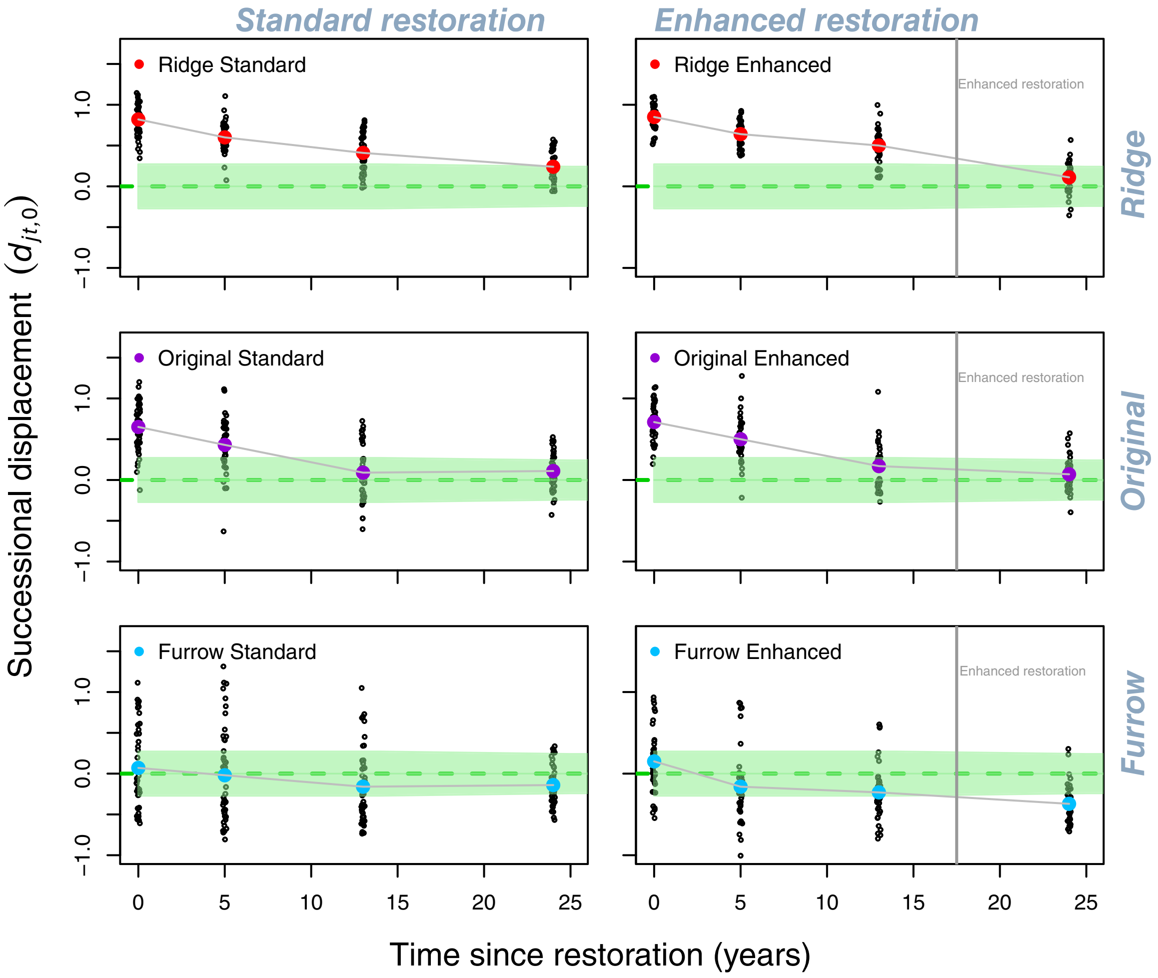

FIGURE 7 As Figure 6, for global nonmetric multidimensional scaling (GNMDS) axis 2 except that the SD was 0.27 for the first three time points and 0.24 for 2022 (note that the GNMDS axis 2 scores were inverted for visualization purposes, compared to Figure 3).

Time to recovery of blanket bogs at Talaheel (H1)

The initial phase of restoration, which ends when the difference from intact blanket bog peaks, is primarily characterized by increasing abundance and/or frequency of plants typical of non-wetland and/or nutrient-enriched conditions such as *G. saxatile*, *Agrostis* spp., *D. flexuosa*, *M. caerulea*, and *J. effusus*. This reflects the legacy and long-term response to the drastic environmental changes resulting from the attempt to convert the bog to a production forest by deep plowing, fencing to reduce grazing, tree planting, and fertilization. These measures impact all four fundamental requirements of plants: soil nutrient concentrations are increased, and soil moisture, incoming radiation, and, hence, temperatures at ground level are all reduced (e.g., Anderson et al., 2016; Gaffney et al., 2018; Howson et al., 2023; Waddington et al., 2015). In contrast, intact blanket bogs are characterized by low nutrient concentrations and a high and stable water table. Hence, they are typified by specifically adapted vascular plants like sedges and ericaceous shrubs and a bottom layer (mosses and lichens) dominated by *Sphagnum* species (Sottocornola et al., 2009; Tallis, 1998; Wheeler & Proctor, 2000). The restoration plots on steepest slopes (5, 8, and 9) were conspicuous in their consistent differentiation from the flatter sites, notably with higher covers of *D. flexuosa* and *M. caerulea*. While this may reflect initial compositional differences, it is more likely that these plots were more heavily impacted by drainage, afforestation, fertilization, and/or deforestation and were hence more difficult to rewet.

There are several reasons why the effect of 13–15 years of conifer plantation on a blanket bog could take far longer to reverse. Plowing prior to tree planting immediately lowers the water table. Thereafter, the growing trees increase evapotranspiration and rainfall interception, contributing further to drying out the peat (Farrick & Price, 2009; Payne & Jessop, 2018), also causing compaction (Sloan et al., 2019). The developing presence of a tree canopy radically impacts light, temperature, and moisture

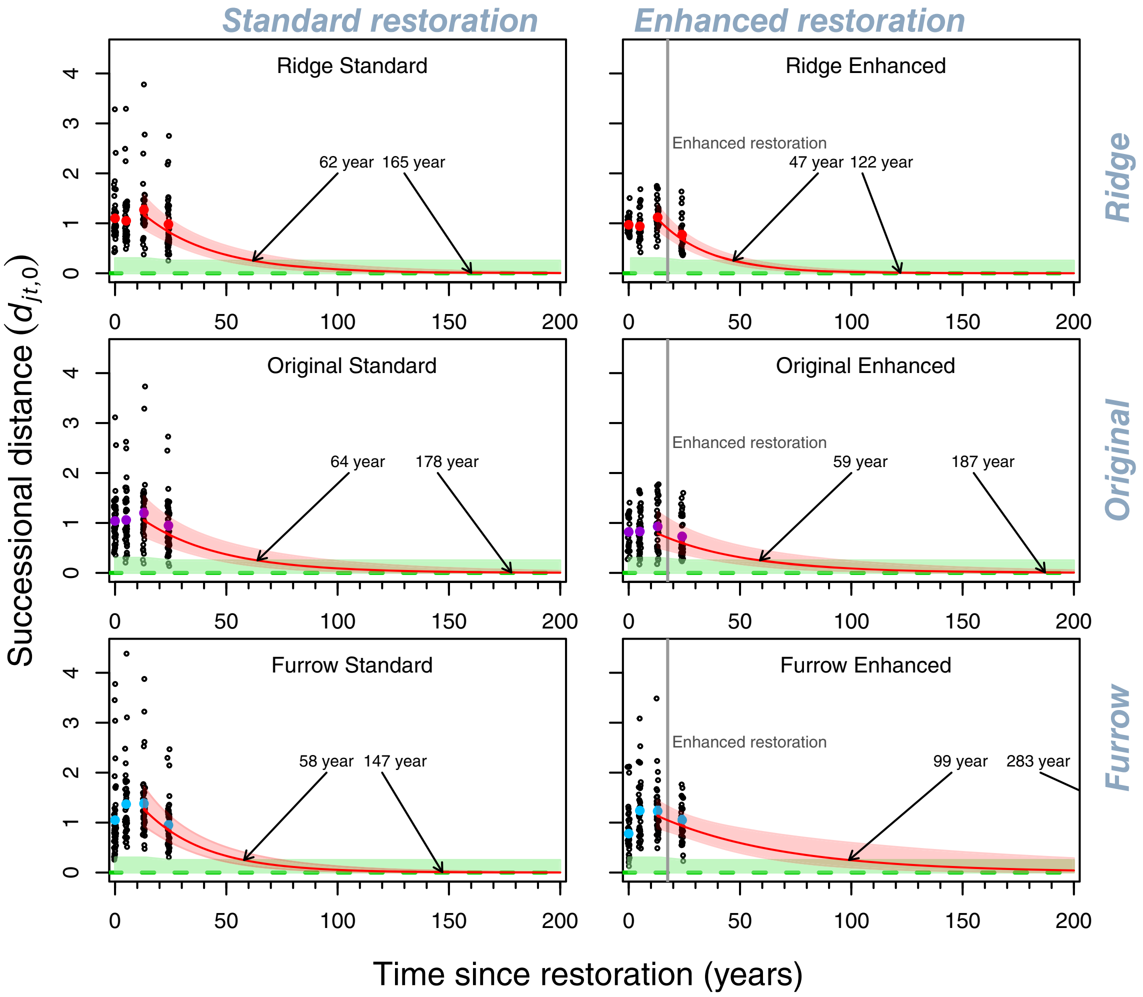

FIGURE 8 Time to species compositional recovery after restoration as predicted by ordination-regression-based approach (ORBA). Time estimates are given using a "Relaxed" and a "Strict" recovery criterion, these being the smallest and largest value, respectively, as indicated by arrows. The slightly jittered points represent successional distances for each quadrat × time combination (QTC), calculated for the three-dimensional global nonmetric multidimensional scaling (GNMDS) ordination space. The colored points show the mean successional distance at each time point. Fitted asymptotic models with 95% CIs are shown by red lines and red shading, respectively. All models were significant at p level <0.001, except Furrow Enhanced with $p = 0.002$. The green dashed horizontal line and light green shading (successional distance = 0) show the centroid of reference QTCs +1 SD (standard deviation of the distance between reference QTCs and their centroid). The SD differed slightly between years 0, 5, and 13 (SD = 0.302) (based on the 2011–2015 survey) and year 24 (SD = 0.252) (based on the 2022 survey). The gray vertical line at year 17.5 shows the time point when the Enhanced treatment was carried out.

at ground level. The application of fertilizer when trees were planted (Hancock et al., 2018) contributes to long-lasting species compositional legacies by enhancing decomposition and mineralization (Ojanen & Minkkinen, 2019). This in turn further increases N and P and reduces cation concentrations in the peat (Holden et al., 2004; Sundström et al., 2000). The legacy of the fertilization may be prolonged when felled trees are rolled into furrows rather than removed, because nutrients retained in the deposited biomass are slowly released (Konings et al., 2019). This is also illustrated by the legacy effect of excess N in pore and surface waters in forest-to-bog sites being restored toward blanket bog (Gaffney et al., 2018).

The three main axes in our GNMDS ordination analysis of the plant species composition reflect different aspects of environmental and temporal change. Axis 2 is related to increases in hydrophilous species and clearly shows that reestablishment of the water table close to the peat surface—a prerequisite for successful restoration—is achieved by both restoration treatments within 24 years. Thus, restoring the hydrology is the first phase in a forest-to-bog restoration (after tree felling). Axis 3 is related to mid-successional increases in species that are rare in intact bogs. The main vegetation gradient expressed by axis 1 is characterized by a slow recovery of the species composition. Due to legacies inherited from

TABLE 2 Predicted time to species compositional recovery (TR) for different plots, microforms, and recovery criteria.

		Ridge		Original		Furrow		Median	
Treatment	**Plot no.**	**TR (relaxed)**	**TR (strict)**	**TR (relaxed)**	**TR (strict)**	**TR (relaxed)**	**TR (strict)**	**TR (relaxed)**	**TR (strict)**
Standard	2	**55**	**172**	56	183	**47**	**131**	55	172
Standard	4	**45**	**114**	**43**	**110**	**42**	**99**	43	110
Standard	5	252	704	**148**	**392**	**97**	**250**	148	392
Standard	7	**40**	**96**	44	138	**51**	**145**	44	138
Standard	9	113	291	**100**	**255**	80	186	100	255
Enhanced	1	**37**	**92**	53	175	**72**	**210**	53	175
Enhanced	3	**36**	**90**	60	264	**59**	**170**	59	170
Enhanced	6	**53**	**144**	**45**	**152**	762	2380	53	152
Enhanced	8	**99**	**269**	**78**	**193**	129	337	99	269

Note: The table shows estimates for each plot (1–9) × Treatment (Standard or Enhanced) × microform (Ridge, Original, or Furrow) combination, measured in years, as obtained from an ordination-regression-based approach (ORBA) models. TR (Relaxed) is the time to recovery (TR; years since restoration) for an asymptotic model at predicted successional distance +1 SD off the centroid of reference plot scores, and TR (Strict) is TR at distance 0.01 off the centroid of reference plot scores. All ORBA models are based on data from the two last time points, that is, 13 and 22 years since restoration. Each plot had nine observations for each time point. Values in boldface indicate significant models ($p < 0.05$), that is, successional distance decreases significantly over time.

non-native conifer afforestation, including changes in peat properties and increased nutrient loads, the second phase in peatland restoration—the gradual replacement of species that are not present in intact bogs with typical mire species—proceeds slowly (e.g., Jauhiainen et al., 2002; Kokkonen et al., 2019; Kyrkjeeide et al., 2024). Moreover, the steeper parts of the landscape are more challenging to restore, even if only ~3–4° (Hancock et al., 2018). Thus, restorations including more sloping areas may require repeated management interventions or more time to recover, while relatively flat degraded peatlands may represent a "low-hanging fruit" where lower effort restoration could deliver large gains quickly.

Successional rates are influenced by a combination of abiotic and biotic factors such as dispersal, establishment, and interspecific interactions (Anderson, 2007). Thus, restoration of local conditions alone may not be sufficient for restoring species composition (Matthews, Peralta, et al., 2009). The establishment and prolonged persistence after afforestation of graminoids that are either absent or very sparse in nearby intact blanket bogs (e.g., *Agrostis* spp., *D. flexuosa*, and *M. caerulea*) and the difficulties that many typical mire species seem to meet during restoration (e.g., *Eric. tetralix*, *Drosera* species, and *Narthecium ossifragum*) are major reasons for the slow recovery of the damaged blanket bog at Talaheel. The long-term presence of graminoids suggests that certain areas within such restoration sites tend to retain nutrient levels above those of intact bogs. Species such as *M. caerulea* take advantage of increased nitrogen levels (Limpens et al., 2003), and its dense sward may suppress *Sphagnum* through light deprivation and litterfall (Pilkington et al., 2021).

The time-to-recovery predictions obtained here using ORBA indicate that full species compositional recovery is proceeding slowly with the restoration techniques that have been applied, but the trajectories are now trending toward reference conditions, implying that a species composition resembling intact bog vegetation will ultimately be achieved. This contrasts with the more uncertain outcomes of restoring more nutrient-rich fens in Europe, which are often affected by helophytization (Kreyling et al., 2021). However, predictions for a distant future are always uncertain. The recovery process may accelerate, take longer, or diverge from the intended target, for example, due to external drivers such as climate warming (Andersen et al., 2024; Moore, 2002; Swindles et al., 2019; Weltzin et al., 2003), nutrient enrichment (Konings et al., 2019), atmospheric pollution (Levy et al., 2019; Noble et al., 2018), or Enhanced restoration management (Allan et al., 2024).

The effect of the Enhanced restoration treatment (H2)

Our second hypothesis was apparently not supported. The Enhanced restoration with its additional dams along the furrows, established seven growing seasons before the last vegetation survey, did not accelerate the recovery of the species composition in all three microforms compared to their Standard restoration counterparts, at least not during the current study period. The Ridge microform—previously identified as the most challenging microform to restore (Hancock et al., 2018)—did, however, respond to the Enhanced treatment. This microform showed significantly increased rates of change in species composition (displacement along GNMDS axis 2, which we considered to be related to depth to the water table). Accordingly, there were reduced time-to-recovery predictions for this microform, compared to the Standard restoration. Most likely, this was a combined effect of further raising the water table due both to additional dams and slight re-profiling of the peat surface, which flattened the ridges, bringing their surfaces closer to the water table.

In contrast, the Furrow Enhanced MTC showed the highest time-to-recovery predictions among all MTCs. Our results indicate that this microform exhibited a species composition that diverged from and appeared even more hydrophilous than the reference. Most likely, this reflects the formation of multiple small pools in the furrows, due to the creation of these additional dams. In general, dams were located at some distance from the quadrats, but on flatter terrain, water backing up from the dams would inundate some of the quadrats and create very high water table conditions, different from the typical reference bog controls used in this study. Concentrations of many small pools ("pool systems") are characteristic features of flat or nearly flat blanket bogs (Belyea & Lancaster, 2002; Boatman, 1983; Lindsay et al., 1988) but were absent from our reference data, which were collected on gently sloping peatlands (averaging around ~2°) to match the terrain of the restoration area. The ex-forestry restoration area in turn reflected the fact that forestry tended to be established in gently sloping areas, being impossible in the very wettest—flattest—parts of the bog. The Original Enhanced MTC was also affected by the raised water table as shown by the stronger reduction of the successional distance (steeper slope) than its Standard counterpart. Accordingly, the longer recovery times predicted for the Furrow Enhanced MTC may result from lack of correspondingly wet sites in the reference data. This pinpoints the importance of ensuring that the reference data cover the entire breadth of relevant environmental variation.

Our results show that unless targeted management actions are taken, the legacies of previous ditching, afforestation, and artificial microtopography may remain for a long time. Importantly, the techniques and machinery used in the restoration of formerly afforested blanket bogs in Scotland have evolved since the start of such restoration work at Talaheel in 1998 (Hancock et al., 2018). Felling and leaving conifers in furrows is no longer practiced. Instead, timber, and where possible, brash, is extracted, and furrow blocking and/or various surface re-profiling techniques have become standard practice (Gaffney et al., 2022; NatureScot, 2024). Re-profiling, which markedly reduces artificial post-forestry microtopography, has become widely used for blanket bog restoration in Forsinard Flows Reserve and the wider Flow Country over the last 10–15 years. The techniques have evolved further to include the use of more specialized equipment, completely removing the ridges and infilling the furrows. A further recent development reuses the furrow vegetation (which would otherwise have been buried by ridge re-profiling) to re-turf bare peat areas created by the re-profiling management. All these changes in restoration measures are expected to result in higher successional rates and markedly shorter times to species compositional recovery.

Variation between microforms (H3)

Our third hypothesis was not supported. Surprisingly, the predicted time to recovery was not longer for Ridge than for the two other microforms. Indeed, the shortest time-to-recovery predictions among all MTCs were found for the Ridge Enhanced. A plausible explanation for this is that the ground water table had been raised to a level allowing reestablishment of mire species, after the ridges had been flattened out. Once again this demonstrates the challenges, and a solution, for restoring a more natural hydrology when the peat surface had been profoundly changed by plowing. Furthermore, the patterns observed for Ridge Enhanced add to previous indications that preparation of restoration sites (Grand-Clement et al., 2015) using modern techniques like surface re-profiling reduces the time to recovery by better restoring more natural microtopographic relief and surface position in relation to the ground water table. Supporting this idea, in the Flow Country, satellite data suggest that areas under restoration by the older (here termed Standard) restoration techniques tend to have higher water table depth fluctuations than areas restored by newer restoration techniques, including surface smoothing (Toca et al., 2023).

ORBA in a broader perspective

Restoration ecology requires methodological improvements (Brudvig, 2017; Urban, 2006). Better predictions of recovery times for key attributes such as species composition are particularly needed (Gann et al., 2019). ORBA may fill this methodological gap, estimating timescales involved in species compositional recovery. When multivariate techniques are used to summarize successional patterns, for example, during restoration of ecosystems, the first ordination axis often captures the compositional change during succession (Auestad et al., 2020; Matthews & Spyreas, 2010; Rydgren et al., 2020). Our study reveals that the restoration of a blanket bog at Talaheel led to a more complex successional pattern, unfolding across three ordination dimensions.

The time-to-recovery predictions from ORBA (Rydgren et al., 2019) depend on dataset properties (Auestad et al., 2020) such as thematic and geographic resolution and data quality. We based our recovery predictions on two time points only; more time points would improve these predictions (Rydgren et al., 2019). The time-to-recovery predictions would likely have become shorter if our reference data had distinguished between microforms, the key gradient in bogs that accounts for most of the variation in species composition (Økland, 1990a; Rydin et al., 1999). On the other hand, a better taxonomic resolution, that is, fewer frequent taxa determined to genera or broader groups such as lichens and liverworts, may have the opposite effect on time-to-recovery predictions. Observer errors, such as misidentification and overlooking of species (Milberg et al., 2008; Morrison, 2016), will also impact the predictions but with an unpredictable outcome. These issues should be considered when designing long-term restoration monitoring programs, provided they can be addressed at a reasonable cost, because they add precision to the guidance provided by analytic tools like ORBA.

ORBA uses clear goals for species compositional recovery, and our "Strict" criterion specifies (for the plant community) the highest standards of full recovery of Gann et al. (2019). We recommend using ORBA with two threshold criteria for recovery—"Strict" and "Relaxed," as we have done here (see *Methods*). The "Relaxed" criterion is most relevant when ecosystems are severely degraded or where recovery of some functionality may take precedence over complete species recovery. Although the choice of threshold criterion is arbitrary, the use of common, standard criteria facilitates comparison across studies. With enough data, ORBA can be applied at different spatial scales. In the present study, we revealed that plots belonging to more sloping areas had the largest restoration challenges, and we also pinpointed large restoration challenges in specific parts of the landscape, that is, the Furrow microforms in plot 6. Such information at a relatively early stage can be valuable for adapting the management for peatland recovery at specific sites.

Our time-to-recovery predictions for Talaheel may seem long, particularly using the "Strict" criterion, but we know little about the timescales involved in species compositional recovery after restoration of peatlands and other ecosystems. A large review of fen peatlands showed that, after many decades, even the most successful long-term restorations still only resulted in a pale shadow of the natural systems they hoped to recreate (Kreyling et al., 2021). Similar observations have been made for restorations of other ecosystems (Mori & Isbell, 2024) implying high "recovery debt" (Moreno-Mateos et al., 2017). The few studies done so far, which use ORBA with an asymptotic model and "Strict" criteria, predict a range of times to species compositional recovery to that of remnant more natural habitats. Examples include 46–143 years after removal of alpine roads (Evju et al., 2023), 91–1030 years for boreal and alpine spoil heaps (Auestad et al., 2020; Rydgren et al., 2020), 100–200 years for subalpine forest (Kreyling, 2025), and 130 years for developed habitats in Tokyo, Japan (Iwachido et al., 2023). While ORBA is now established as an approach that can inform the effectiveness of restoration (Elo et al., 2024), which focuses on one of the most important attributes of ecosystems—the species composition (Clewell & Aronson, 2013), and from early phases in the restoration process, the method still needs to be tested on more data sets. In particular, tests are needed on long-term data with many repeated surveys performed throughout the restoration process, with later surveys allowing earlier predictions to be evaluated.

ORBA sets clear goals for species compositional restoration—one of the key attributes of an ecosystem (Gann et al., 2019), but there may be other restoration targets, and some of them can begin to accrue much earlier in the restoration journey. For example, at our Talaheel restoration site, after just 16 years of restoration, the area became a net sink for greenhouse gases (Hambley et al., 2019). Another example, from a very different ecosystem, is the significant nature conservation benefits that tropical secondary forests can provide, even if their vegetation differs substantially from that of intact, primary reference conditions (Chazdon et al., 2009). With pristine sites becoming increasingly rare, these considerations highlight the potential value of protecting and restoring impacted sites.

CONCLUSIONS

Peatland restoration has been conducted for almost four decades (Rochefort & Andersen, 2017), but we still lack precise knowledge about the timescales at which plant species compositional recovery takes place; our study helps to redress this balance. Our results, analyzing plant species compositional data from the restoration of afforested blanket bogs in northern Scotland, suggest that decadal or even centennial timescales (under the strictest criteria) may be required for the complete restoration of plant species composition. There is no quick fix or rapid solution to complete forest-to-bog restoration because of the legacies left from the forestry; both innovation and patience are needed, most notably because the species replacement process is slow. On the other hand, there is increasing empirical evidence demonstrating that peatland restoration, including forest-to-bog, has other immediate benefits, including the reduction in greenhouse gas emissions, increased resilience to wildfires, improved water quality in receiving watercourses and biodiversity benefits—as some specialist species do indeed return readily and quickly, across a range of taxa. Restoration practices should be continuously improved in parallel with monitoring and research, learning from outcomes and adapting management accordingly (Gann et al., 2019), such as is being done in Talaheel (Hancock et al., 2018; this study). The biodiversity and climate crises have brought a renewed focus on peatlands, with their essential carbon stores and climate regulation function (Günther et al., 2020), their specialist flora and fauna (Guilfoyle et al., 2025), and their rich cultural values (Byg et al., 2017; Heindorf et al., 2024); for all these reasons, peatland restoration is more important than ever.

AUTHOR CONTRIBUTIONS

Neil Cowie designed and set up the original field surveys and repeat data collection in 1998, 2003 and 2011. Mark H. Hancock and Robert D. Hughes collated the data, which was collected by a range of their colleagues over the years; see Hancock et al. (2018). Alice Martin-Walker organized the most recent (2022) repeat field survey, collated, and supplied those data. Knut Rydgren analyzed the data and led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Rydgren et al., 2025) are available on Zenodo at https://doi.org/10.5281/zenodo.17160429.

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REFERENCES

Alderson, D. M., M. G. Evans, E. L. Shuttleworth, M. Pilkington, T. Spencer, J. Walker, and T. E. H. Allott. 2019. "Trajectories of Ecosystem Change in Restored Blanket Peatlands." *Science of the Total Environment* 665: 785–796.

Allan, J. M., M. Guêné-Nanchen, L. Rochefort, D. J. T. Douglas, and J. C. Axmacher. 2024. "Meta-Analysis Reveals that Enhanced Practices Accelerate Vegetation Recovery during Peatland Restoration." *Restoration Ecology* 32: e14015.

Andersen, R., C. Farrell, M. Graf, F. Muller, E. Calvar, P. Frankard, S. Caporn, and P. Anderson. 2017. "An Overview of the Progress and Challenges of Peatland Restoration in Western Europe." *Restoration Ecology* 25: 271–282.

Andersen, R., P. Fernandez-Garcia, A. Martin-Walker, D. Klein, C. Marshall, D. J. Large, R. Hughes, and M. H. Hancock. 2024. "Blanket Bog Vegetation Response to Wildfire and Drainage Suggests Resilience to Low Severity, Infrequent Burning." *Fire Ecology* 20: 26.

Anderson, K. J. 2007. "Temporal Patterns in Rates of Community Change during Succession." *American Naturalist* 169: 780–793.

Anderson, R., and A. Peace. 2017. "Ten-Year Results of a Comparison of Methods for Restoring Afforested Blanket Bog." *Mires and Peat* 19: 6.

Anderson, R., H. Vasander, N. Geddes, A. Laine, A. Tolvanen, A. O'Sullivan, and K. Aapala. 2016. "Afforested and Forestry-Drained Peatland Restoration." In *Ecological Reviews*, edited by A. Bonn, H. Joosten, M. Evans, R. Stoneman, and T. Allott, 213–233. Cambridge: Cambridge University Press.

Auestad, I., K. Rydgren, and R. Halvorsen. 2020. "Dataset Properties Affect the Performance of the Ordination Regression-Based Approach (ORBA) in Predicting Time to Recovery." *Ecological Engineering* 152: 105875.

Bacon, K. L., A. J. Baird, A. Blundell, M.-A. Bourgault, P. J. Chapman, G. Dargie, G. P. Dooling, et al. 2017. "Questioning Ten Common Assumptions about Peatlands." *Mires and Peat* 19: 12.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Belyea, L. R., and J. Lancaster. 2002. "Inferring Landscape Dynamics of Bog Pools from Scaling Relationships and Spatial Patterns." *Journal of Ecology* 90: 223–234.

Bertuol-Garcia, D., E. Ladouceur, L. A. Brudvig, D. C. Laughlin, S. M. Munson, M. F. Curran, K. W. Davies, L. N. Svejcar, and N. Shackelford. 2023. "Testing the Hierarchy of Predictability in Grassland Restoration across a Gradient of Environmental Severity." *Ecological Applications* 33: e2922.

Boatman, D. J. 1983. “The Silver Flowe National Reserve, Galloway, Scotland.” *Journal of Biogeography* 10: 163–274.

Borkenhagen, A., D. J. Cooper, M. House, and D. H. Vitt. 2024. “Establishing Peat-Forming Plant Communities: A Comparison of Wetland Reclamation Methods in Alberta’s Oil Sands Region.” *Ecological Applications* 34: e2929.

Brudvig, L. A. 2017. “Toward Prediction in the Restoration of Biodiversity.” *Journal of Applied Ecology* 54: 1013–17.

Byg, A., J. Martin-Ortega, K. Glenk, and P. Novo. 2017. “Conservation in the Face of Ambivalent Public Perceptions – the Case of Peatlands as ‘the Good, the Bad and the Ugly’.” *Biological Conservation* 206: 181–89.

Castillo, D., D. Kaplan, and J. Mossa. 2016. “A Synthesis of Stream Restoration Efforts in Florida (USA).” *River Research and Applications* 32: 1555–65.

CBD. 2022. *Kunming-Montreal Global Biodiversity Framework*. CBD/COP/DEC/15/4. Montreal: Convention on Biological Diversity. 14 p. https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf.

Chapman, S. J., J. Bell, D. Donnelly, and A. Lilly. 2009. “Carbon Stocks in Scottish Peatlands.” *Soil Use and Management* 25: 105–112.

Charman, D. J. 1994. “Late Glacial and Holocene Vegetation History of the Flow Country, Northern Scotland.” *New Phytologist* 127: 155–168.

Chazdon, R. L., C. A. Peres, D. Dent, D. Sheil, A. E. Lugo, D. Lamb, N. E. Stork, and S. E. Miller. 2009. “The Potential for Species Conservation in Tropical Secondary Forests.” *Conservation Biology* 23: 1406–17.

Clapham, A. R., T. G. Tutin, and D. M. Moore. 1987. *Flora of the British Isles*, 3rd ed. Cambridge: Cambridge University Press.

Clewell, A. F., and J. Aronson. 2013. *Ecological Restoration: Principles, Values, and Structure of an Emerging Profession*, 2nd ed. Washington, DC: Island Press.

Crawley, M. J. 2013. *The R book*, 2nd ed. Chichester: Wiley.

Díaz, S., J. Settele, E. S. Brondizio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, et al. 2019. “Pervasive Human-Driven Decline of Life on Earth Points to the Need for Transformative Change.” *Science* 366: eaax3100.

Elo, M., S. Kareksela, O. Ovaskainen, N. Abrego, J. Niku, S. Taskinen, K. Aapala, and J. S. Kotiaho. 2024. “Restoration of Forestry-Drained Boreal Peatland Ecosystems Can Effectively Stop and Reverse Ecosystem Degradation.” *Communications Earth & Environment* 5: 680.

Evju, M., D. Hagen, S. L. Olsen, and A. C. Mehlhoop. 2023. “Recovery of Vegetation on Former Alpine Roads: How Long Does it Take?” *Nordic Journal of Botany* 2023: e03984.

Farrell, C. A., J. Aronson, G. C. Daily, L. Hein, C. Obst, P. Woodworth, and J. C. Stout. 2022. “Natural Capital Approaches: Shifting the UN Decade on Ecosystem Restoration from Aspiration to Reality.” *Restoration Ecology* 30: e13613.

Farrick, K. K., and J. S. Price. 2009. “Ericaceous Shrubs on Abandoned Block-Cut Peatlands: Implications for Soil Water Availability and *Sphagnum* Restoration.” *Ecohydrology* 2: 530–540.

Gaffney, P. P. J., M. H. Hancock, M. A. Taggart, and R. Andersen. 2018. “Measuring Restoration Progress Using Pore- and Surface-Water Chemistry across a Chronosequence of Formerly Afforested Blanket Bogs.” *Journal of Environmental Management* 219: 239–251.

Gaffney, P. P. J., M. H. Hancock, M. A. Taggart, and R. Andersen. 2022. “Restoration of Afforested Peatland: Effects on Pore- and Surface-Water Quality in Relation to Differing Harvesting Methods.” *Ecological Engineering* 177: 106567.

Gann, G. D., T. McDonald, B. Walder, J. Aronson, C. R. Nelson, J. Jonson, J. G. Hallett, et al. 2019. “International Principles and Standards for the Practice of Ecological Restoration. Second Edition.” *Restoration Ecology* 27: S3–S46.

Gewin, V. 2020. “Bringing Back the Bogs.” *Nature* 578: 204–8.

González, E., and L. Rochefort. 2014. “Drivers of Success in 53 Cutover Bogs Restored by a Moss Layer Transfer Technique.” *Ecological Engineering* 68: 279–290.

González, E., L. Rochefort, S. Boudreau, S. Hugron, and M. Poulin. 2013. “Can Indicator Species Predict Restoration Outcomes Early in the Monitoring Process? A Case Study with Peatlands.” *Ecological Indicators* 32: 232–38.

Grand-Clement, E., K. Anderson, D. Smith, M. Angus, D. J. Luscombe, N. Gatis, L. S. Bray, and R. E. Brazier. 2015. “New Approaches to the Restoration of Shallow Marginal Peatlands.” *Journal of Environmental Management* 161: 417–430.

Guilfoyle, C., J. Lusby, E. de Eyto, H. T. Lally, and C. T. Graha. 2025. “Avian Communities Show Distinct Responses to Forest-to-Bog Restoration.” *Journal of Environmental Management* 373: 123763.

Günther, A., A. Barthelmes, V. Huth, H. Joosten, G. Jurasinski, F. Koebsch, and J. Couwenberg. 2020. “Prompt Rewetting of Drained Peatlands Reduces Climate Warming despite Methane Emissions.” *Nature Communications* 11: 1644.

Haapalehto, T. O., H. Vasander, S. Jauhiainen, T. Tahvanainen, and J. S. Kotiaho. 2011. “The Effects of Peatland Restoration on Water-Table Depth, Elemental Concentrations, and Vegetation: 10 Years of Changes.” *Restoration Ecology* 19: 587–598.

Hambley, G., R. Andersen, P. Levy, M. Saunders, N. R. Cowie, Y. A. Teh, and T. C. Hill. 2019. “Net Ecosystem Exchange from Two Formerly Afforested Peatlands Undergoing Restoration in the Flow Country of Northern Scotland.” *Mires and Peat* 23: 5.

Hancock, M. H., D. Klein, R. Andersen, and N. R. Cowie. 2018. “Vegetation Response to Restoration Management of a Blanket Bog Damaged by Drainage and Afforestation.” *Applied Vegetation Science* 21: 167–178.

Heindorf, C., S. Schüler, and T. Plieninger. 2024. “Poetic Inquiry to Explore the Relational Values of a Transforming Peat Landscape.” *People and Nature* 6: 1189–1205.

Hill, M. O., and H. G. Gauch, Jr. 1980. “Detrended Correspondence Analysis: An Improved Ordination Technique.” *Vegetatio* 42: 47–58.

Holden, J., P. J. Chapman, and J. C. Labadz. 2004. “Artificial Drainage of Peatlands: Hydrological and Hydrochemical Process and Wetland Restoration.” *Progress in Physical Geography* 28: 95–123.

Howson, T., P. J. Chapman, N. Shah, R. Anderson, and J. Holden. 2021. “The Effect of Forest-to-Bog Restoration on the Hydrological Functioning of Raised and Blanket Bogs.” *Ecohydrology* 14: e2334.

Howson, T. R., P. J. Chapman, J. Holden, N. Shah, and R. Anderson. 2023. “A Comparison of Peat Properties in Intact, Afforested and Restored Raised and Blanket Bogs.” *Soil Use and Management* 39: 104–121.

Iwachido, Y., K. Uchida, and T. Sasaki. 2023. “Artificial Developed Habitats Can Sustain Plant Communities Similar to Remnant

Ecosystems in the Tokyo Megacity." *Urban Forestry & Urban Greening* 83: 127899.

Jauhiainen, S., R. Laiho, and H. Vasander. 2002. "Ecohydrological and Vegetational Changes in a Restored Bog and Fen." *Annales Botanici Fennici* 39: 185–199.

Joosten, H., I. Szallies, and C. Tegetmeyer. 2016. *The Flow Country (Scotland) as a Blanket Bog Landscape – A Global Evaluation*. Greifswald: Greifswald Mire Centre and IMCG.

Jorgenson, J. C., J. M. Ver Hoef, and M. T. Jorgenson. 2010. "Long-Term Recovery Patterns of Arctic Tundra after Winter Seismic Exploration." *Ecological Applications* 20: 205–221.

Kokkonen, N. A. K., A. M. Laine, J. Laine, H. Vasander, K. Kurki, J. Gong, and E.-S. Tuittila. 2019. "Responses of Peatland Vegetation to 15-Year Water Level Drawdown as Mediated by Fertility Level." *Journal of Vegetation Science* 30: 1206–16.

Konings, W., K. G. Boyd, and R. Andersen. 2019. "Comparison of Plant Traits of Sedges, Shrubs and *Sphagnum* Mosses between Sites Undergoing Forest-to-Bog Restoration and near-Natural Open Blanket Bog: A Pilot Study." *Mires and Peat* 23: 7.

Kreyling, J. 2025. "Space-for-Time Substitution Misleads Projections of Plant Community and Stand-Structure Development after Disturbance in a Slow-Growing Environment." *Journal of Ecology* 113: 68–80.

Kreyling, J., F. Tanneberger, F. Jansen, S. van der Linden, C. Aggenbach, V. Blüml, J. Couwenberg, et al. 2021. "Rewetting Does Not Return Drained Fen Peatlands to their Old Selves." *Nature Communications* 12: 5693.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2016. "lmerTest. Tests in Linear Mixed Effects Models." Package Version 2.0-32. The R Foundation for Statistical Computing. https://cran.r-project.org/web/packages/lmerTest/index.html.

Kyrkjeeide, M. O., M. Jokerud, A. C. Mehlhoop, L. M. F. Lunde, M. Fandrem, and A. Lyngstad. 2024. "Peatland Restoration in Norway – Evaluation of Ongoing Monitoring and Identification of Plant Indicators of Restoration Success." *Nordic Journal of Botany* 2024: e03988.

Levy, P., N. van Dijk, A. Gray, M. Sutton, M. Jones, S. Leeson, N. Dise, I. Leith, and L. Sheppard. 2019. "Response of a Peat Bog Vegetation Community to Long-Term Experimental Addition of Nitrogen." *Journal of Ecology* 107: 1167–86.

Limpens, J., F. Berendse, and H. Klees. 2003. "N Deposition Affects N Availability in Interstitial Water, Growth of *Sphagnum* and Invasion of Vascular Plants in Bog Vegetation." *New Phytologist* 157: 339–347.

Lindsay, R. A., D. J. Charman, E. Everingham, R. M. O'Reilly, M. A. Palmer, T. A. Rowell, and D. A. Stroud. 1988. *The Flow Country: The Peatlands of Caithness and Sutherland*. Peterborough: Nature Conservancy Council.

Lindsay, R. A., and J. Clough. 2017. "United Kingdom." In *Mires and Peatlands of Europe: Status, Distribution and Conservation*, edited by H. Joosten, F. Tanneberger, and A. Moen, 705–720. Stuttgart: Schweizerbart.

Matthews, J. W., A. L. Peralta, A. Soni, P. Baldwin, A. D. Kent, and A. G. Endress. 2009. "Local and Landscape Correlates of Non-Native Species Invasion in Restored Wetlands." *Ecography* 32: 1031–39.

Matthews, J. W., and G. Spyreas. 2010. "Convergence and Divergence in Plant Community Trajectories as a Framework for Monitoring Wetland Restoration Progress." *Journal of Applied Ecology* 47: 1128–36.

Matthews, J. W., G. Spyreas, and A. G. Endress. 2009. "Trajectories of Vegetation-Based Indicators Used to Assess Wetland Restoration Progress." *Ecological Applications* 19: 2093–2107.

Met_Office. 2023. "UK Climate Averages." Kinbrace (Highland). https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-climate-averages/gfm5qbgxz.

Milberg, P., J. Bergstedt, J. Fridman, G. Odell, and L. Westerberg. 2008. "Observer Bias and Random Variation in Vegetation Monitoring Data." *Journal of Vegetation Science* 19: 633–644.

Minchin, P. R. 1987. "An Evaluation of the Relative Robustness of Techniques for Ecological Ordination." *Vegetatio* 69: 89–107.

Moore, P. D. 2002. "The Future of Cool Temperate Bogs." *Environmental Conservation* 29: 3–20.

Moreno-Mateos, D., E. B. Barbier, P. C. Jones, H. P. Jones, J. Aronson, J. A. López-López, M. L. McCrackin, P. Meli, D. Montoya, and J. M. Rey Benayas. 2017. "Anthropogenic Ecosystem Disturbance and the Recovery Debt." *Nature Communications* 8: 14163.

Mori, A. S., and F. Isbell. 2024. "Untangling the Threads of Conservation: A Closer Look at Restoration and Preservation." *Journal of Applied Ecology* 61: 215–222.

Morrison, L. W. 2016. "Observer Error in Vegetatin Surveys: A Review." *Journal of Plant Ecology* 9: 367–379.

Myster, R. W., and S. T. A. Pickett. 1994. "A Comparison of Rate of Succession over 18 Yr in 10 Contrasting Old Fields." *Ecology* 75: 387–392.

NatureScot. 2024. "Peatland ACTION – Technical Compendium. Peatland ACTION Sharing Good Practice for Peatland Restoration Techniques." NatureScot. Scotlands Nature Agency. https://www.nature.scot/doc/peatland-action-technical-compendium.

Noble, A., S. M. Palmer, D. J. Glaves, A. Crowle, L. E. Brown, and J. Holden. 2018. "Prescribed Burning, Atmospheric Pollution and Grazing Effects on Peatland Vegetation Composition." *Journal of Applied Ecology* 55: 559–569.

Ojanen, P., and K. Minkkinen. 2019. "The Dependence of Net Soil CO_2 Emissions on Water Table Depth in Boreal Peatlands Drained for Forestry." *Mires and Peat* 24: 27.

Økland, R. H. 1990a. "A Phytoecological Study of the Mire Northern Kisselbergmosen, SE Norway. II. Identification of Gradients by Detrended (Canonical) Correspondence Analysis." *Nordic Journal of Botany* 10: 79–108.

Økland, R. H. 1990b. "Vegetation Ecology: Theory, Methods and Applications with Reference to Fennoscandia." *Sommerfeltia* 1: 1–233.

Økland, R. H. 1999. "On the Variation Explained by Ordination and Constrained Ordination Axes." *Journal of Vegetation Science* 10: 131–36.

Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, et al. 2022. "vegan: Community Ecology." Package Version 2.6-2. The R Foundation for Statistical Computing. http://cran.r-project.org.

Payne, R. J., and W. Jessop. 2018. "Community-Identified Key Research Questions for the Future of UK Afforested Peatlands." *Mires and Peat* 21: 22.

Pilkington, M., J. Walker, C. Fry, P. Eades, R. Meade, N. Pollett, T. Rogers, et al. 2021. "Diversification of *Molinia* Dominated

Blanket Bogs Using *Sphagnum* Propagules." *Ecological Solutions and Evidence* 2: e12113.

R Development Core Team. 2023. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rochefort, L., and R. Andersen. 2017. "Global Peatland Restoration after 30 Years: Where Are We in this Mossy World?" *Restoration Ecology* 25: 269–270.

Ruiz-Jaén, M. C., and T. M. Aide. 2005. "Restoration Success: How Is it Being Measured?" *Restoration Ecology* 13: 569–577.

Rydgren, K. 1993. "Herb-Rich Spruce Forests in W Nordland, N Norway: An Ecological and Methodological Study." *Nordic Journal of Botany* 13: 667–690.

Rydgren, K., R. Andersen, R. Halvorsen, M. H. Hancock, R. D. Hughes, A. Martin-Walker, J. P. Töpper, and N. Cowie. 2025. "Restoration of Formerly Afforested Blanket Bog: Estimating Time for Vegetation Recovery." Dataset. Zenodo. https://doi.org/10.5281/zenodo.17160429.

Rydgren, K., I. Auestad, R. Halvorsen, L. N. Hamre, E. Jongejans, J. P. Töpper, and J. Sulavik. 2020. "Assessing Restoration Success by Predicting Time to Recovery—But by which Metric?" *Journal of Applied Ecology* 57: 390–401.

Rydgren, K., R. Halvorsen, J. P. Töpper, I. Auestad, L. N. Hamre, E. Jongejans, and J. Sulavik. 2019. "Advancing Restoration Ecology: A New Approach to Predict Time to Recovery." *Journal of Applied Ecology* 56: 225–234.

Rydgren, K., R. H. Økland, and G. Hestmark. 2004. "Disturbance Severity and Community Resilience in a Boreal Forest." *Ecology* 85: 1906–15.

Rydin, H., H. Sjörs, and M. Löfroth. 1999. "Mires." *Acta Phytogeographica Suecica* 84: 91–112.

Searle, M., S. B. Cornish, A. Heard, J. H. Charles, and J. Branch. 2019. "Structure of the Northern Moine Thrust Zone, Loch Eriboll, Scottish Caledonides." *Tectonophysics* 752: 35–51.

Sloan, T. J., R. J. Payne, A. R. Anderson, P. Gilbert, D. Mauquoy, A. J. Newton, and R. Andersen. 2019. "Ground Surface Subsidence in an Afforested Peatland Fifty Years after Drainage and Planting." *Mires and Peat* 23: 6.

Smith, A. J. E. 2004. *The Moss Flora of Britain and Ireland*, 2nd ed. Cambridge: Cambridge University Press.

Sottocornola, M., A. Laine, G. Kiely, K. A. Byrne, and E.-S. Tuittila. 2009. "Vegetation and Environmental Variation in an Atlantic Blanket Bog in South-Western Ireland." *Plant Ecology* 203: 69–81.

Suding, K. N. 2011. "Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead." *Annual Review of Ecology, Evolution, and Systematics* 42: 465–487.

Sundström, E., T. Magnusson, and B. Hånell. 2000. "Nutrient Conditions in Drained Peatlands along a North-South Climatic Gradient in Sweden." *Forest Ecology and Management* 126: 149–161.

Swindles, G. T., P. J. Morris, D. J. Mullan, R. J. Payne, T. P. Roland, M. J. Amesbury, M. Lamentowicz, et al. 2019. "Widespread Drying of European Peatlands in Recent Centuries." *Nature Geoscience* 12: 922–28.

Tallis, J. H. 1998. "Growth and Degradation of British and Irish Blanket Mires." *Environmental Reviews* 6: 81–122.

Tanneberger, F., A. Moen, A. Barthelmes, E. Lewis, L. Miles, A. Sirin, C. Tegetmeyer, and H. Joosten. 2021. "Mires in Europe – Regional Diversity, Condition and Protection." *Diversity* 13: 381.

Toca, L., R. R. E. Artz, C. Smart, T. Quaife, K. Morrison, A. Gimona, R. Hughes, M. H. Hancock, and D. Klein. 2023. "Potential for Peatland Water Table Depth Monitoring Using Sentinel-1 SAR Backscatter: Case Study of Forsinard Flows, Scotland, UK." *Remote Sensing* 15: 1900.

Urban, D. L. 2006. "A Modeling Framework for Restoration Ecology." In *Foundations of Restoration Ecology*, edited by D. A. Falk, M. A. Palmer, and J. B. Zedler, 238–256. Washington, DC: Island Press.

van Son, T. C., and R. Halvorsen. 2014. "Multiple Parallel Ordination and Data Manipulation: The Importance of Weighting Species Abundance Data." *Sommerfeltia* 37: 1–37.

Vasander, H., E.-S. Tuittila, E. Lode, L. Lundin, M. Ilomets, T. Sallantaus, R. Heikkilä, M.-L. Pitkänen, and J. Laine. 2003. "Status and Restoration of Peatlands in Northern Europe." *Wetlands Ecology and Management* 11: 51–63.

Waddington, J. M., P. J. Morris, N. Kettridge, G. Granath, D. K. Thompson, and P. A. Moore. 2015. "Hydrological Feedbacks in Northern Peatlands." *Ecohydrology* 8: 113–127.

Waldén, E., and R. Lindborg. 2016. "Long Term Positive Effect of Grassland Restoration on Plant Diversity – Success or Not?" *PLoS One* 11: e0155836.

Warren, C. 2000. "'Birds, Bogs and Forestry Revisited': The Significance of the Flow Country Controversy." *Scottish Geographical Journal* 116: 315–337.

Weltzin, J. F., S. D. Bridgham, J. Pastor, J. Chen, and C. Harth. 2003. "Potential Effects of Warming and Drying on Peatland Plant Community Composition." *Global Change Biology* 9: 141–151.

Wheeler, B. D., and M. C. F. Proctor. 2000. "Ecological Gradients, Subdivisions and Terminology of North-West European Mires." *Journal of Ecology* 88: 187–203.

Wilkie, N. M., and P. W. Mayhew. 2003. "The Management and Restoration of Damaged Blanket Bog in the North of Scotland." *Botanical Journal of Scotland* 55: 125–133.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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