Learning from the past, assessing the present, discerning the future

a comprehensive evaluation of restoration success in alpine environment using ecosystem-, community-, and population-level studies

Thesis for the degree of Philosophiae Doctor (ph.d.)

Jan Sulavik

Natural History Museum
Faculty of Mathematics and Natural Sciences
University of Oslo
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Abstract
Global biodiversity decline and environmental deterioration require an increased focus on restoration reflected by United Nations declaring years 2021–2030 a Decade on Ecosystem Restoration. The scientific basis for restoration is restoration ecology, which, however, is still a young and developing science. Evaluation of restoration success is a key research topic of restoration ecology, and reliable methods for assessment and prediction of restoration outcomes are sought by both ecologists and practitioners. A reliable evaluation requires identification of relevant indicators of restoration success. Another key research topic is functioning of restored ecosystems, recently linked to species’ functional traits. However, the functional trait research has concentrated mainly on vascular plants, while traits of bryophytes and lichens, organism groups functionally important in many ecosystems including alpine, have been much less studied. Similarly, population-level studies of restoration success are also less common than community- and ecosystem-level studies. Population dynamics of foundation species may, however, influence restoration outcomes as one or few foundation species often shape and define ecosystems. In addition, population-level studies may be useful in assessing historical contingency that is another key research topic in restoration ecology.

In this thesis, I present restoration evaluation through studies at population, community, and ecosystem levels, examining the past, present, and future of restored alpine spoil heaps. Paper I presents a new method for assessment and prediction of restoration outcomes, the ordination regression-based approach (ORBA). In Paper II, ORBA is used together with other biotic and abiotic indicators to assess restoration success at alpine spoil heaps. Paper III presents a trait-based evaluation of restoration success at alpine spoil heaps using functional traits of vascular plants, bryophytes, and lichens, employing ORBA in assessment of joint functional trait composition. In Paper IV, population spatial and age structure of crowberry (*Emetrum nigrum* ssp. *hermaphroditum*), a foundation species, is used to assess abiotic and biotic factors of crowberry establishment at an alpine spoil heap.

ORBA is a flexible framework providing a relevant indicator of restoration success, successional distance, which can be calculated and modelled based on both species and functional trait compositional data. Our results suggest that successional changes at restored sites are in general non-linear and asymptotic models are more appropriate for prediction of future restoration outcomes than linear models. Moreover, restoration assessments based on species composition and functional traits complement each other, as well as assessments based on abiotic soil indicators. We found that crowberry establishment was influenced by the distance to seed sources and by intraspecific facilitation. We demonstrate the use of a “snapshot” of population spatial and age structure to hindcast spatially explicit population dynamics of foundation species and identify important factors of establishment.
The results and discussion presented in this thesis highlight the advantages of a comprehensive, holistic approach to restoration evaluation. Assessments of restoration success through species and functional trait composition, facilitated by ORBA, through abiotic soil indicators, and through spatially explicit population dynamics of foundation species, facilitated by recent developments in precise mapping and point pattern analyses, can advance restoration ecology and strengthen its role as a reliable scientific basis for the global restoration endeavour.
List of papers
Following published articles and an unpublished original manuscript are presented in this thesis:


Supplementary materials for all published articles are available online at the websites of the respective journals. For author contributions, see Papers I–IV.
Introduction

The biosphere is facing unprecedented anthropogenic pressure resulting in extensive declines at all levels of biodiversity, from genetic to ecosystem diversity (Diaz et al. 2019). With less than a quarter of the terrestrial surface remaining without significant anthropogenic disturbance (Watson et al. 2016), restoration of degraded ecosystems is fundamental for safeguarding biodiversity, alongside conservation of undisturbed ecosystems (Brudvig 2011; CBD 2016). The importance of restoration has been acknowledged in multiple international agreements in the recent years (Suding et al. 2015), among others by Convention on Biological Diversity (CBD) Strategic Plan for Biodiversity 2011–2020 (Aichi targets 14 and 15; Navarro et al. 2017) and United Nations’ (UN) 2030 Agenda (Sustainable Development Goals; Herrick et al. 2019). Most recently, UN declared 2021–2030 a Decade on Ecosystem Restoration (UN Environment 2019).

How is restoration defined? UN uses the following definition in the declaration of Decade on Ecosystem Restoration: “a process of reversing the degradation of ecosystems, such as landscapes, lakes and oceans to regain their ecological functionality; in other words, to improve the productivity and capacity of ecosystems to meet the needs of society” (UN Environment 2019). With such a broad definition, there is an implicit need for a reliable scientific basis to specify key terms, principles, and standards. The scientific basis for restoration is restoration ecology, a young and developing science (Hobbs 2018). Society for Ecological Restoration (SER) plays a central role in the development in the field. SER has recently published an updated set of international principles and standards for restoration (Gann et al. 2019), building upon an earlier edition (McDonald et al. 2016). Adoption of these principles and standards has, however, not been undisputed (e.g. Gann et al. 2018; Higgs et al. 2018a; Higgs et al. 2018b). While an open discussion and different opinions contribute to the advancement of restoration ecology (Hobbs 2018), they also indicate that more knowledge is needed to improve the scientific basis for restoration practice.

Several key research topics and knowledge gaps have been identified for restoration ecology in the 21st century (e.g. Brudvig 2011; Perring et al. 2015; Suding 2011). To define evaluation criteria for restoration is an apparent, yet elusive task, intrinsically connected with setting of goals and definition of success, as well as with selection of appropriate reference ecosystems (Prach et al. 2019). How to set restoration goals that are simultaneously realistic and effective has early been identified as a key research topic for restoration ecology (Hobbs 2007). How to define and measure restoration success has been identified as one of the priority questions in landscape restoration in Europe (Ockendon et al. 2018). Both setting of goals and definition of success depend on a reference model for restoration, based on an appropriate reference ecosystem (Gann et al. 2019). Assuming that the appropriate reference is identified, Prach et al. (2019) proposed a framework starting with general
goals translated into specific and measurable targets that should guide selection of appropriate indicators of success. Despite slight differences in terminology, a similar framework was adopted in the SER international principles and standards for restoration (Gann et al. 2019). To provide measurable targets and indicators of success responds to the needs of restoration practitioners (Ockendon et al. 2018), but also to the calls for a more evidence-based restoration ecology (Cooke et al. 2019; Suding 2011).

Generally, an indicator in ecology is “a component or a measure of environmentally relevant phenomena used to depict or evaluate environmental conditions or changes or to set environmental goals” (Heink & Kowarik 2010). Specifically, ecological indicators in restoration are “variables that are measured to assess changes in the physical (e.g. turbidity units), chemical (e.g. nutrient concentration), or biotic (e.g. species abundance) ecosystem attributes as guided by the reference model” (Gann et al. 2019). Evaluation of restoration success through indicators has developed considerably in the recent decades. The first comprehensive review of restoration success evaluation assessing the status around the beginning of the 21st century (Ruiz-Jaen & Mitchell Aide 2005) reported few empirical studies, using mainly few and simple indicators (e.g. species richness, in terrestrial ecosystems predominantly of vascular plants). According to the follow-up review (Wortley et al. 2013), both the number of empirical studies evaluating restoration success and the number and complexity of used indicators (e.g. species composition: diversity and abundance) have increased substantially in the following years. However, only less than a half of the studies in the latter review compared the restored ecosystem with an undisturbed reference ecosystem (Wortley et al. 2013). To promote more widespread use of reference ecosystems recommended by Gann et al. (2019), it is necessary to identify indicators of restoration success that are both representative for ecosystem state and easily measured (cf. Dale & Beyeler 2001) for both restored and reference sites.

Regular monitoring of appropriate indicators provides data for modelling of recovery trajectories of the restored sites that can be used for prediction of future restoration outcomes (Prach et al. 2019). Prediction has early been identified as a key research topic for restoration ecology (Brudvig 2011). Transformation of restoration ecology into a predictive science remains crucial for increased achievement of restoration goals (Brudvig 2017) and success of the UN Decade on Ecosystem Restoration (Brudvig & Catano 2021). There are several challenges associated with prediction in restoration ecology. A major challenge is the issue of variation in restoration: restoration outcomes may vary in comparison with the reference and with other outcomes in spite of using similar restoration methods (Brudvig et al. 2017). Another challenge is the global climate change: changing climate impacts definition of appropriate references and targets for restoration (Harris et al. 2006) as well as it increases the uncertainty of outcomes that has to be included in the predictions (Brudvig &
Catano 2021). To deliver useful and informative predictions of restoration outcomes, it is essential to develop prediction methods that consider variation in the restored and reference ecosystems, allow for flexible definition of restoration targets, and account for the uncertainty (Choi 2007).

Concerning variation and prediction of restoration outcomes, different relevant indicators of success are not equally variable: Brudvig et al. (2017) proposed a hierarchy of predictability with functional diversity being a less variable — and more predictable — indicator than species composition. This relates to another key research topic for restoration ecology, functioning of restored ecosystems. In the recent decades, there has been an increased focus on ecosystem functioning in restoration ecology (e.g. Brudvig 2011; Choi 2007; Kollmann et al. 2016; Shackelford et al. 2013), on definition of functional goals (Perring et al. 2015) and targets (Laughlin 2014) for restoration. Indeed, this topic has in the context of global environmental and climate change pervaded ecology in general, and to assess the links between functional traits of organisms and ecosystem functioning has even been defined as “the Holy Grail” of ecology (Funk et al. 2017; Lavorel & Garnier 2002; Suding & Goldstein 2008). Functional trait is a “morphological, physiological or phenological feature measurable at the individual level which impacts fitness indirectly via its effects on growth, reproduction and survival” (Violle et al. 2007). Functional trait research has in the recent decades advanced understanding of ecosystem functioning in restoration (Carlucci et al. 2020; Kollmann et al. 2016) and general ecological contexts (Funk et al. 2017).

However, many knowledge gaps regarding ecosystem functioning and functional traits remain unfilled in restoration ecology. Vascular plants and their functional traits have been used predominantly in assessments of ecosystem functioning in restored terrestrial ecosystems (Carlucci et al. 2020; Kollmann et al. 2016). Even though plants certainly deserve attention in restoration (Brudvig 2011) since vegetation structure largely defines terrestrial ecosystems (Prach et al. 2019), other organism groups may also have important functions and should be evaluated for assessments of ecosystem functioning (Kollmann et al. 2016). For example, bryophytes and lichens are essential components in many high-elevation and high-latitude ecosystems (Asplund & Wardle 2017; Cornelissen et al. 2007). Bryophytes and lichens possess traits fundamental for the functioning of these ecosystems, yet distinct from the traits of vascular plants (St. Martin & Mallik 2017). Compared with vascular plants, functional trait research in bryophytes and lichens is in its infancy, but has advanced considerably in recent years (St. Martin & Mallik 2017). Inclusion of multiple important organism groups in analyses may provide a more comprehensive assessment of ecosystem functioning (Gann et al. 2019), but also improve evaluation of restoration success (Ruiz-Jaen & Mitchell Aide 2005) and prediction of restoration outcomes (cf. Carlucci et al. 2020). To include multiple organism groups in
functional trait-based restoration evaluation, it is necessary to develop methods that can handle and analyse distinct sets of functional traits in a common framework (cf. St. Martin & Mallik 2017).

Evaluation of restoration success and prediction of restoration outcomes rely on regular monitoring of restored sites, which, however, has not been a common practice in the past decades (Brudvig 2011). At the same time, historical contingency has been recognized as one of the key research topics in restoration ecology (Brudvig 2011). Lack of regular monitoring entails that past indicator values and key processes influencing the present and future restoration outcomes may not have been investigated in real time. Is knowledge about the past development at restored sites thus lost forever? Not necessarily. Hindcasting of site-scale indicators at ecosystem and community levels may be rather challenging (but see Maire et al. 2015) due to their inherent variability (cf. Brudvig et al. 2017). However, it may be feasible to assess key past processes at the restored sites, for example plant establishment or interactions (McCallum et al. 2018), through patterns at the population level (cf. Velázquez et al. 2016). Population-level patterns can significantly influence restoration outcomes because the vegetation structure of many terrestrial ecosystems is determined by one or few dominant, foundation species (Ellison 2019). Relevance of population-level studies for evaluation of restoration success has been acknowledged early (Montalvo et al. 1997), but such studies remain uncommon in restoration ecology (Harzé et al. 2018).

Paucity of population-level studies in restoration ecology can be linked to generally limited resources for monitoring of restored sites favouring readily measurable indicators (Brudvig 2011; Prach et al. 2019). This may in many cases preclude detailed multiannual demographic studies usually employed in ecology to assess population dynamics, because such studies require considerable time and effort (Harzé et al. 2018). To avoid the extensive requirements of demographic studies and still gather useful information about population dynamics of foundation species, “hidden information” about population-level processes can be extracted from spatial patterns (Wiegand et al. 2003) as these act as an “ecological archive” (Velázquez et al. 2016). In the recent decades, there has been an increased interest in the links between spatial patterns and processes in ecology (Velázquez et al. 2016) and a considerable development in statistical methods and tools for analysis of spatial patterns (Baddeley et al. 2015). Nevertheless, spatial structure remains among the least studied population attributes in the relatively few population-level studies in the restoration context (Harzé et al. 2018). To gain access to the “ecological archive” that spatial patterns present for studying key past processes and dynamics in foundation species populations at the restored sites, it is essential to explore the extensive toolbox for analysis of spatial patterns (cf. Baddeley et al. 2015) and adapt it for the restoration context.
Various research topics outlined throughout this Introduction are connected by the overarching theme of restoration evaluation. To improve the scientific basis for restoration practice, restoration ecology should provide reliable knowledge about probable past, present state, and possible future of the restored sites, and preferably the reference sites as well. This is particularly important for restoration of alpine ecosystems, where ecosystem recovery and biological processes are slow and effects of misguided management may linger for decades (Rydgren et al. 2013). Ecosystem functioning in alpine ecosystems is significantly influenced by bryophytes and lichens (St. Martin & Mallik 2017), as well as by foundation species of vascular plants such as shrubs (Cáceres et al. 2014). To comprehensively evaluate restoration in alpine ecosystems, it is therefore advantageous to conduct studies at ecosystem, community, and population levels.

Restoration ecology as a young and developing science may not yet possess methods and tools for answering all the relevant questions of restoration practice, but it might not be necessary to “reinvent the wheel” either. There is a considerable potential for greater integration of theoretical ecology in restoration (Török & Helm 2017), as well as for increased connectivity between different subfields of applied ecology (Staples et al. 2019) and ecology in general. As much as restoration ecology can profit from theoretical concepts, methods, and tools developed in other ecological subfields, can restoration also provide valuable feedback for ecological theory (Török & Helm 2017) and methods and tools, for example for prediction, relevant beyond restoration context (Brudvig 2017).

Aims and structure of the thesis
The main aim of this thesis is to explore and develop methods for a comprehensive restoration evaluation, examining the past, present, and future of the restored sites, particularly in alpine environment. This main aim is approached through four studies conducted at ecosystem, community, and population levels, addressing different specific research questions, and constituting the four papers presented in this thesis (Figure 1):

In Paper I, we present the ordination regression-based approach (ORBA) which uses data on species composition collected at multiple time-points at restored and reference sites. ORBA provides an indicator of the present state at the restored sites and predictions of time to recovery based on flexible recovery thresholds. ORBA is further used in Papers II–III as a tool for evaluation and prediction of restoration outcomes. Note that Paper I is the only paper in this thesis not analysing data from alpine spoil heaps, but from a boreal forest site.
In Paper II, we study dynamics of multiple uni- and multivariate indicators of restoration success at four alpine spoil heaps and in their immediate undisturbed surroundings acting as a reference. By using ORBA for the first time in the restoration context, we aim to compare relevance and usefulness of ORBA results with other biotic and abiotic indicators for restoration evaluation and prediction of time to recovery.

In Paper III, we conduct a functional trait-based evaluation of restoration success at the same alpine spoil heap sites as in Paper II, using functional traits of vascular plants, bryophytes, and lichens. Apart from studying changes in community-weighted means of traits (CWM), commonly used trait-based indicators, we also explore whether ORBA can be used to assess dynamics of joint functional trait composition of multiple organism groups.

In Paper IV, we study a population of crowberry (*Empetrum nigrum* ssp. *hermaphroditum*), a foundation species of dwarf shrub, at one of the four alpine spoil heaps studied in Papers II–III. By analyses of crowberry spatial patterns and age structure, we explore past population dynamics, abiotic and biotic factors of establishment.

Figure 1: An overview of the Papers presented in this thesis. Paper I presents a new method for assessment of compositional dynamics, the ordination regression-based approach (ORBA), which is further used in Papers II–III for evaluation of present state (at the time-point of the study) and prediction of future restoration outcomes. Paper IV presents a hindcast, or reconstruction, of past population dynamics based on spatial patterns and age structure, while Papers I–III use data from past monitoring.

**Methods: an overview**

This is a general overview of methods used in the four presented Papers, for details see Methods sections in Papers I–IV. All study sites were in southern Norway (Figure 2). All studies were conducted
within the RELEASE project (Renewable Energy Projects: Local Impacts and Sustainability; Norwegian Research Council grant number 238281).

Figure 2: An overview of the study sites, their positions within Norway (inset map 1), and detail of positions of alpine spoil heap sites (inset map 2). In Paper I, we used data from an experimentally disturbed boreal forest site in Østmarka Nature Reserve. In Papers II–IV, we used data from alpine spoil heap sites: four in Papers II–III (Fossane, Kleådalen, Øydalen and Svartavatn spoil heaps and their undisturbed surroundings) and one in Paper IV (Fossane spoil heap).

In Paper I, we described and explored the ordination regression-based approach (ORBA). Testing and exemplification of ORBA required detailed data on species composition collected at multiple time-points over a period adequate for assessment of compositional dynamics. Since detailed data from long-term monitoring are relatively uncommon for restored sites (cf. Brudvig 2011), we used data from an experimentally disturbed boreal forest site in Østmarka Nature Reserve (Rydgren et al. 2004). These data were in several aspects optimal for the purpose: 1) the dataset contained species composition data collected in the same study plots with high temporal resolution over a considerable period (censuses in 1994–2003, 2005 and 2011), 2) design of the original study contained a gradient of disturbance severity which enabled testing of ORBA for a variety of possible restoration scenarios, and 3) the dataset contained an appropriate, static reference (species composition in study plots recorded prior to disturbance in 1993), which allowed for assessment and modelling of successional distances.
In Papers II–IV, we focused on restored alpine spoil heaps (Figure 3), large (22000–41000 m²) mounds of surplus rock material from hydropower tunnels established between 1974 and 1984, all seeded with a commercial grass mixture and fertilised. The four spoil heaps studied in this thesis were in the early 1990s a part of a larger botanical-ecological evaluation study of hydropower spoil heaps in southern Norway (Skjerdal & Odland 1995). In 2008, the spoil heaps were revisited, and permanently marked plots for vegetation sampling were established at the spoil heaps as well as in their undisturbed surroundings acting as a reference (Rydgren et al. 2011). Studies by Skjerdal and Odland (1995) and Rydgren et al. (2011) provided valuable data on past biotic (total cover of vascular plants, bryophytes and lichens, species richness and composition) and abiotic properties (soil organic matter and pH). In 2015, we resampled the species composition in the permanently marked plots and collected soil samples for measurements of soil organic matter and pH.

Figure 3: An illustration of the alpine spoil heap sites. a) Fossane (spoil heap in the bottom right part of the picture). b) Kleådalen (spoil heap in the centre of the picture). See also Figure 1 in Paper II.

For evaluation of uni- and multivariate abiotic and biotic indicators of restoration success at the alpine spoil heaps (Paper II), we used data from the early 1990s, 2008, and 2015. Thanks to the data collected at three time-points, we could conveniently account for eventual non-linear responses in modelling of future restoration outcomes. The approximately two decades between the first and the third census provided a sufficient time span for assessment of compositional and environmental dynamics. Inclusion of the surroundings in the 2008- and 2015-censuses allowed for use of ORBA with a dynamic reference. Even though the surroundings were not sampled in the 1990s, it was justified to use the data on surroundings from the 2008-census as a proxy for surroundings in the 1990s due to the minimal changes in the surroundings between 2008 and 2015. We assessed how the successional distance between restored and reference sites (ORBA-derived multivariate biotic indicator) and the univariate indicators (biotic: species richness and total cover; abiotic: soil organic matter and pH) changed over time and modelled their future dynamics.
For functional trait-based evaluation of restoration success at the alpine spoil heaps (Paper III), we used the same data on species composition as in Paper II together with database and literature data on functional traits. To balance the distinct traits of vascular plants, bryophytes, and lichens, we simplified the categories of categorical traits and centred and standardised continuous traits. To solve the challenge of dealing with both categorical and continuous functional traits in the assembly of joint functional trait composition dataset, we converted the continuous traits into categorical (cf. van Son et al. 2013) prior to multiplication of trait values by species abundance. We thus obtained a dataset with the same structure and units (trait-category abundance, a “common currency”) for all organism groups, traits, and plot-by-census combinations, which could be analysed by ORBA. Apart from assessment and modelling of successional distances, we used the ordination results also to extract trait-category optima along the successional gradient to study changes in categorical traits. To study changes in continuous traits, we calculated community-weighted means of traits (CWM), accounting for species abundance (cf. Garnier et al. 2004)

Figure 4: An illustration of a) crowberry (Empetrum nigrum ssp. hermaphroditum), and b) crowberry mapping and sampling. See also Figure 1 in Paper IV.

Assessments of crowberry population dynamics, abiotic and biotic factors of establishment (Paper IV) required data on the relationship between size and age in crowberry (Figure 4 a), and data on population spatial and size structure. For this study, we chose the Fossane spoil heap, one of the four spoil heaps studied in Papers II–III, because a preliminary survey suggested low prevalence of clonal reproduction in crowberry and simple identification of individual plants necessary for a population-level study. In 2015, we collected crowberry individuals for age determination and subsequent allometric modelling, and in 2016, we measured and mapped all crowberry individuals in three 5 m wide transects traversing the spoil heap edge-to-edge (Fig. 4 b). The resulting “snapshot” of population spatial and (modelled) age structure allowed for a hindcast of past population dynamics and interactions between crowberry individuals (biotic factor) during population establishment. It also
allowed for analyses of the effect of distance to seed sources in the surroundings (abiotic factor) on the establishment.

Results and discussion: a synthesis
The ordination regression-based approach (ORBA; Paper I) is a flexible tool for evaluation of the present state and prediction of future outcomes at restored sites. ORBA can be used to calculate and predict successional distances between restored and reference sites based on species composition (Paper II) as well as on functional trait composition (Paper III). It also enables simultaneous inclusion of multiple relevant organism groups, such as vascular plants, bryophytes, and lichens. We explored use of both static reference (sampled only once; Paper I) and dynamic reference (sampled multiple times simultaneously with restored sites; Papers II–III), with the latter being a preferred solution in the restoration context (cf. Gann et al. 2019). In combination with multiple parallel ordinations (MPO; van Son & Halvorsen 2014), ORBA enables a robust assessment of the successional gradient in the compositional data to ensure reliable calculation of successional distances. Nested sampling design and multiple study sites can be accounted for in ORBA by using mixed-effects models (Bates et al. 2015) in the regression step. Uncertainty of predictions can be quantified by calculation of confidence intervals for the models. ORBA offers considerable flexibility in selection of recovery thresholds, that is, target successional distance reflecting the compositional similarity between the restored and reference sites: either a pre-defined fixed threshold or a statistical threshold based on the variation in the reference composition. We explored both pre-defined fixed thresholds (Papers I–II) and statistical thresholds: +1 SD off centroid of reference plot scores (Papers I–II) and mean absolute deviation (MAD) of reference plots around their centroid (Paper III); for details, see Future directions.

Rates of compositional change during succession at the experimentally disturbed boreal forest site (Paper I) and at the restored alpine spoil heap sites (Papers II–III) decreased over time. Given that a non-linear decrease was observed across a gradient of experimental disturbance severity (Paper I) as well as at real-world restored sites (Papers II–III), our results suggest that non-linear, asymptotic models are generally more appropriate for modelling of future successional distance at restoration sites than linear models. Linear models may be useful for assessment of shorter periods of compositional change but have consistently predicted unrealistically short time to recovery at our study sites (Papers I–II).

In comparison of different indicators of restoration success at the alpine spoil heaps (Paper II), total cover and species richness of bryophytes and lichens reached reference levels within several decades, while ORBA-derived successional distance based on the species composition and univariate
abiotic indicators (soil organic matter and pH) suggested longer time to recovery. Rates of change of total cover and species richness of vascular plants varied between the studied heaps, but generally suggested shorter time to recovery. The multivariate biotic indicator (ORBA-derived successional distance) and univariate abiotic indicators (soil organic matter and pH) addressed fundamental properties of restored ecosystems – species composition (Shackelford et al. 2013) and soil conditions (Muñoz-Rojas 2018) – and showed monotonic patterns, which facilitated modelling and prediction of future outcomes. On the other hand, univariate biotic indicators (total cover and species richness) had larger uncertainties in model estimates (including multiple non-significant models), showed non-monotonic patterns, and ignored the presence of species not representative for the reference, such as pioneer and seeded non-native grass species. Our results show that species composition and soil conditions are highly relevant for assessments of restoration success, and ORBA-derived successional distance is a convenient indicator useful both for evaluation of the present state as well as for prediction of species compositional recovery.

Trait-based evaluation of restoration success at the alpine spoil heaps (Paper III) clarified its functional aspects and complemented Paper II. Changes in single traits showed multiple functional shifts across all studied organism groups during succession, such as the shift from wind-dispersed propagules to vegetative (clonal) reproduction or the shift from prostrate to more upright growth forms indicative of more closed vegetation. The importance of propagule influx from the surroundings to the spoil heaps was indicated by increasing similarity in dispersal-related traits over time. Analyses of joint functional composition by ORBA provided a slightly different view than Paper II: faster recovery of functional trait composition in comparison with species composition and one spoil heap (Kleådalen) reaching recovery threshold by the 2015-census. In addition, the spoil heap with the slowest rate of species compositional recovery (Svartavatn) had the second fastest rate of functional compositional recovery. Our results show how trait-based evaluation of restoration success can complement species composition-based evaluation and how they together may provide answers to a variety of questions concerning compositional and functional recovery of restored sites (cf. Engst et al. 2016).

By analyses of the “snapshot” of crowberry spatial and age structure (Paper IV), we explored population dynamics, abiotic, and biotic factors of establishment. Crowberry established successfully at the studied alpine spoil heap (Fossane) and we observed the highest individual densities close to the spoil-heap edges, indicating the effect of distance to seed sources in the surroundings on establishment. The clustered spatial pattern indicated dominance of positive interactions (facilitation) between crowberry individuals (cf. Kikvidze et al. 2005), showing at present no signs of germination inhibition known from other species interacting with crowberry (González et al. 2014). Gradual evolution and amplification of the clustered pattern revealed by analyses of spatial patterns of
consecutive age-based cohorts of recruits suggested that facilitation is an important biotic factor of the crowberry establishment. Our results show how the “snapshot” approach can be used for a population-level study of foundation species at restored sites with lower time and resource demands than multiannual demographic studies. A combination of estimation of the age structure by allometric modelling, precise mapping of plant individuals by survey-grade equipment, and analyses of spatial patterns by accessible open-source tools (Baddeley et al. 2015) can be used to access the “ecological archive” represented by the population spatial and size structure.

Future directions

ORBA is a new method, used so far only in Papers I–III and by Auestad et al. (2020). Encouraging results notwithstanding, its general relevance for restoration evaluation must be further tested in a variety of restoration settings and ecosystems. Reliance on open-source tools and R programming language may be both its strength and its weakness: implementation of ORBA through R makes the approach transparent, streamlined, and flexible (and cheap, as far as the software is concerned). On the other hand, the steep learning curve of R may be discouraging for potential ORBA users not familiar with R. We tried to alleviate this potential problem by the open-source publication of a readily-available set of auxiliary R functions for ORBA (Sulavik 2018), a “protopackage” that may evolve into a full R package in the future.

Choice of thresholds is crucial for time-to-recovery predictions of restored sites by ORBA. The implicit question posed is: how similar (to the reference) is similar enough? Statistical thresholds based on SD or mean absolute deviation (MAD) of reference ordination scores reflect the natural variation in the reference and are therefore “natural” choices for further investigation. Each of the statistical thresholds explored in this thesis has its merits: SD is a commonly used measure of variation in ecology, which makes SD-based recovery threshold intuitive for many potential ORBA users, facilitating comparisons of time-to-recovery predictions across different sites and studies. MAD is a less common measure of variation in ecology, maybe with exception of functional ecology (Laliberte & Legendre 2010; Pakeman & Oksanen 2014), which makes it a less intuitive choice. Arguments for use of MAD as a recovery threshold are related to the rationale behind ORBA: the regression step models successional distance between average restored and reference plots (or centroids of restored and reference plot scores). By defining the recovery threshold as MAD around the reference centroid, the recovery is reached when an average restored plot (centroid of the restored plot scores, represented by the model fit) is as similar to the reference centroid as an average reference plot, that is, their successional
distance is equal to MAD. This definition of recovery threshold has theoretical merits; however, further studies are necessary to assess its usefulness in practice.

Ordination methods are based on the reduction of multidimensionality in compositional datasets and extraction of axes representing complex environmental gradients (Økland 1990). The successional gradient was represented by the first ordination axes in Papers I–III and we calculated successional distances along the first axis – in other words, in a one-dimensional way. However, also higher-order axes may be included in the restoration evaluation by ORBA in the future, given that they are satisfactorily interpreted (cf. Økland 1990). By inclusion of the second and the third ordination axes in the recovery assessments, compositional data could be studied as two- and three-dimensional structures instead of in terms of one-dimensional successional distances. This would open up multiple exciting possibilities, for example to use concepts from computational geometry such as convex hulls, which are already in use in functional ecology (Laliberte & Legendre 2010; Podani 2009), to quantify compositional overlaps between restored and reference sites. Another concept potentially relevant for two- and three-dimensional assessments of restoration success is the n-dimensional hypervolume (Blonder et al. 2014), already in use in functional ecology and niche modelling (Blonder 2018).

Ideas about using functional traits in assessments of restoration success are not new, however, the functional trait research has generally been skewed towards vascular plants. We demonstrate that in many ecosystems such as alpine, inclusion of multiple organism groups in the assessments is a more comprehensive approach, facilitated by ORBA. The distance-based framework for measurement of functional diversity from multiple traits (Laliberte & Legendre 2010), already in use in restoration ecology (e.g. Laughlin et al. 2017), is ordination-based and allows for inclusion of multiple organism groups. Are we trying to “reinvent the wheel” by proposing ORBA for multi-trait, multi-organism assessments of restoration success? In my opinion, no. The framework of Laliberte and Legendre (2010) has many strengths and is easily implemented through their R package ‘FD’. Yet in the present R implementation, the framework relies on a single ordination method (principal coordinates analysis, PCoA) and ordination and calculation of ordination-based functional diversity indices take place within a “black box” of a single R function. This simplifies and streamlines analyses for the users, which, however, are uninformed about the actual ordination results and possible distortion axes (cf. Økland 1999) reducing relevance of the calculated indices. The “second opinion” is also lacking due to solely using PCoA in the ordination step instead of multiple parallel ordinations (MPO; van Son & Halvorsen 2014). Using the stepwise, transparent principles of ORBA, the calculation of functional diversity indices by the distance-based framework of Laliberte and Legendre (2010) could be performed after the ordination step. The regression step and predictions of time to recovery would be independent of an eventual “functional diversity” step. Future studies combining the distance-based framework and
ORBA may further improve the trait-based evaluation of restoration success, building upon the strengths of both approaches.

Trait-based evaluation of restoration success requires data on multiple functional traits. Given the usually limited resources available for restoration monitoring, direct measurement of traits at the restored sites is in most cases unrealistic. Database data should be sufficient if available, as differences between species dominate the trait variation in ecosystems with strong environmental gradients (Auger & Shipley 2013), which applies to many restored sites. However, trait variation within species should be accounted for (cf. Siefert et al. 2015), at least on a regional scale. TRY has in the recent years become a leading open-access trait database for vascular plants (Fraser 2020) with regional datasets covering a span of environmental and climatic conditions. Regional trait datasets should be sufficient to address the intraspecific trait variation for the purpose of restoration evaluation. Reflecting the skewed focus towards vascular plants in functional ecology, functional traits of bryophytes and lichens are so far rather sparsely covered by the trait databases. For bryophytes, several regional databases are currently available, for example BRYOATT for Britain and Ireland (Hill et al. 2007), BRYOTRAIT-AZO for Azores (Henriques et al. 2017), or BryForTrait for Central Europe (Bernhardt-Römermann et al. 2018), while a global database is currently lacking. For lichens, several regional and one global database (LIASlight; Rambold et al. 2014) are currently available (for review, see Ellis et al. 2021). However, LIASlight is in the present form rather user-unfriendly. Until user-friendly, open-access “databases of databases” similar to TRY (cf. Fraser 2020) become available also for bryophytes and lichens, multiple literary and database sources of traits data will probably remain necessary for trait-based evaluation of restoration success in ecosystems where these organism groups play important functional roles.

Apart from assessments of compositional and functional recovery, population-level studies of foundation species at the restored sites may also elucidate important factors of plant establishment and restoration success. As we demonstrate, a combination of population age structure obtained through allometric models and spatial pattern can be used to hindcast spatially explicit population dynamics even with a single “snapshot”. This may be highly relevant for restoration evaluation at sites with no or little data from past monitoring but may also complement community- and ecosystem-based evaluations at sites with sufficient data about the past. Individual ages necessary for allometric modelling can be obtained for all perennial plants (Schweingruber & Poschlod 2005), hence for most foundation species at restored sites. More studies are needed to improve allometric modelling, especially to identify the best readily measurable predictors of individual age as well as the best practices for building of allometric models.
Assessments of population spatial patterns require high-precision data on individual positions. Such data are becoming increasingly available through survey-grade mapping equipment that reduces the workload considerably, although still demanding quite a lot of time and resources. A major boost for spatially explicit population studies in restoration ecology is likely to come with increased use of remote sensing methods for environmental monitoring, especially unmanned aerial systems (Manfreda et al. 2018). Remote sensing methods are already in use in restoration monitoring (Reif & Theel 2017), and their further development and improvement of spatial resolution will significantly enhance data availability, quality, and scale, and simultaneously reduce time and costs associated with population-level studies. However, even the best possible data are useless without proper analysis methods. Luckily, such methods are probably available already – or at least soon will be. Methods of point pattern analysis based on decades of continuous development, summarised in the comprehensive state-of-the-art book of Baddeley et al. (2015), and implemented in the frequently updated R package ‘spatstat’, can provide answers to most ecological questions related to spatial patterns (cf. Illian & Burslem 2017). However, this scientific field is vast and many opportunities remain underexplored and underused at present (Velázquez et al. 2016). Further research is needed to identify the best methods and approaches to point pattern analysis in the restoration context. Particularly promising are the point process models (Illian & Burslem 2017; Renner et al. 2015) that have potential to directly link patterns to processes (Velázquez et al. 2016) and inform not only about the present and the past but also about the future of the restored sites.

Concluding remarks

To face the challenges resulting from the current levels of environmental degradation and fulfil the ambitious goals of the UN Decade on Ecological Restoration, restoration ecology must become a more evidence-based (Cooke et al. 2019; Young & Schwartz 2019) and predictive (Brudvig 2017) science. To successfully restore ecosystems, it is necessary to identify – and operationalise – relevant indicators of restoration success (Prach et al. 2019) and implement principles and standards of ecological restoration in practice (Gann et al. 2019). Reflecting these needs, this thesis focused on restoration evaluation through species composition, abiotic indicators, functional traits, and population dynamics of foundation species. I assert that a holistic approach to restoration evaluation can advance restoration ecology, and I hope this thesis presents a humble yet relevant contribution to the global restoration endeavour.
Abbreviations

CBD    Convention on Biological Diversity
CWM    Community-weighted means of traits
MAD    Mean absolute deviation
MPO    Multiple parallel ordinations
ORBA   Ordination regression-based approach
PCoA   Principal coordinates analysis
SD     Standard deviation
SER    Society for Ecological Restoration
UN     United Nations
References


Cooke, S. J., Bennett, J. R., & Jones, H. P. 2019. We have a long way to go if we want to realize the promise of the "Decade on Ecosystem Restoration". *Conservation Science and Practice*, 1(12), e129. https://doi.org/10.1111/csp2.129


McCallum, K. P., Lowe, A. J., Breed, M. F., & Paton, D. C. 2018. Spatially designed revegetation—why the spatial arrangement of plants should be as important to revegetation as they are to natural systems. Restoration Ecology, 26(3), 446-455. https://doi.org/10.1111/rec.12690


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Advancing restoration ecology: A new approach to predict time to recovery.


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Advancing restoration ecology: A new approach to predict time to recovery

Knut Rydgren1 | Rune Halvorsen2 | Joachim P. Töpper3 | Inger Auestad4
Liv Norunn Hamre1 | Eelke Jongejan4 | Jan Sulavik1,2

Abstract
1. Species composition is a vital attribute of any ecosystem. Accordingly, ecological restoration often has the original, or "natural," species composition as its target. However, we still lack adequate methods for predicting the expected time to compositional recovery in restoration studies.
2. We describe and explore a new, ordination regression-based approach (ORBA) for predicting time to recovery that allows both linear and asymptotic (logarithmic) relationships of compositional change with time. The approach uses distances between restored plots and reference plots along the successional gradient, represented by a vector in ordination space, to predict time to recovery. Thus, the approach rests on three requirements: (a) the general form of the relationship between compositional change and time must be known; (b) a sufficiently strong successional gradient must be present and adequately represented in a species compositional dataset; and (c) a restoration target must be specified. We tested the approach using data from a boreal old-growth forest that was followed for 18 years after experimental disturbance. Data from the first 9 years after disturbance were used to develop models, the subsequent 9 years for validation.
3. Rates of compositional recovery in the example dataset followed the general pattern of decrease with time since disturbance. Accordingly, linear models were too optimistic about the time to recovery, whereas the asymptotic models provided more precise predictions.
4. Synthesis and applications. Our results demonstrate that the new approach opens for reliable prediction of recovery rates and time to recovery using species compositional data. Moreover, it allows us to assess whether recovery proceeds in the desired direction and to quantitatively compare restoration speed, and hence effectiveness, between alternative management options.

Keywords
ordination, prediction, recovery, reference, restoration ecology, species composition, successional gradient, time to recovery
1 | INTRODUCTION

In a world of progressive ecosystem degradation, the discipline of restoration ecology has become ever more important and now plays a significant role in sustainable development efforts across the globe (Brudvig, 2011; Perring et al., 2015; Roberts, Stone, & Sugden, 2009; Suding, 2011). It is, however, still a young science and as such in need of methodological improvements (Brudvig, 2017; Laughlin, 2014; Urban, 2006) to more effectively inform management (Suding, 2011). For restoration ecology to become a predictive science (Brudvig, 2017; Brudvig et al., 2017), there is an urgent need to develop appropriate methods for predicting time to recovery after disturbance that is until specific restoration goals are achieved.

Metrics commonly used to evaluate restoration success (SER, 2004) can be ordered in four categories from general to specific by the ecosystem properties they address (Brudvig et al., 2017): (a) physical structure; (b) diversity that is richness and evenness measures that do not take species’ identity into account; (c) functional and phylogenetic diversity that is measures for which species may be functionally redundant of one another; and (d) species (taxonomic) composition. While their information content increases from the general to the specific metrics, the precision of predictions that can be made from them is expected to decrease (Brudvig et al., 2017). Accordingly, several authors have argued that large and unpredictable variation in species composition among restoration sites makes composition-based metrics less useful for measuring restoration success than the more general metrics (Brudvig et al., 2017; Laughlin et al., 2017). Others have argued that species composition is a fundamental attribute of restored ecosystems (Clewell & Aronson, 2013; Reid, 2015), and that the rate and direction of vegetation change (succession) are fundamental properties that must be considered when restoration success is evaluated (Urban, 2006). Furthermore, monitoring of compositional change during restoration and prediction of time to recovery may actually guide the restoration process (Zedler & Callaway, 1999). Such prediction is particularly valuable in harsh environments where restoration may take decades or even centuries (Harper & Kershaw, 1996; Jorgenson, Ver Hoef, & Jorgenson, 2010; Rydgren, Halvorsen, Odland, & Skjerdal, 2011). Several authors therefore regard data on species composition as particularly informative for evaluation of restoration success (Heslinga & Grese, 2010; Matthews, Spyreas, & Endress, 2009; Reid, 2015; Waldén & Lindborg, 2016).

Previous approaches have used floristic dissimilarity measures to predict time to recovery after disturbances (Curran, Hellweg, & Beck, 2014; Prach et al., 2016; Woodcock, McDonald, & Pywell, 2011) or multivariate methods such as constrained and unconstrained ordination (Rydgren et al., 2011; Sarmiento, Llambi, Escalona, & Marquez, 2003) with the implicit assumption that successions are linear, namely, that the rate of plant compositional change with time is constant. Floristic dissimilarities have proved unsuitable for this purpose because of the three basic problems associated with use of compositional dissimilarity as a proxy for distance along an ecological gradient (Gauch, 1973; Økland, 1986, 1990): (a) the internal association problem that is small ecological distances cannot be separated from ecological replicates by floristic dissimilarity; (b) the indetermination problem that is the ecological distance between observations with no species in common cannot be deduced from their species composition, and (c) the nonlinearity problem, that is, the presence of a general, nonlinear relationship between ecological distance and floristic dissimilarity. Constrained ordination might seem a plausible alternative for summarising compositional change in response to one, given, variable (here: time since disturbance). However, constrained ordination is also inappropriate for this purpose, because it expresses only linear responses of variables (or specific transformations of these) on ordination axes (ter Braak, 1986), and therefore fail to reflect nonlinear relationships.

Unconstrained ordination methods, on the other hand, summarise compositional gradients regardless of these gradients’ relationship with time or other explanatory variables. Therefore, it could potentially also summarise compositional change along successional gradients. But for these methods to provide robust predictions for time to recovery, five issues need to be addressed: (a) To ascertain that potentially distorted axes are not used for predictions for time to recovery, they must be identified by applying more than one ordination method to the same dataset (van Son & Halvorsen, 2014). (b) Compositional change along a specific successional gradient must be identifiable as a vector in ordination space, for example, the gradient must be strong (see Philippu, Dixon, & Taylor, 1998). This is, however, almost always the case after major disturbances. (c) A reference that the restored sites can be compared to must be established. Since nature is not static, this reference should be dynamic, allowing change with time, rather than fixed to a historic, ideal time point (Choi, 2004; Hiers et al., 2012). (d) Compositional differences as given by distances in the ordination space must be modelled as a function of time. This is not straightforward, as shown in the few existing, ordination-based restoration studies (e.g., Jacquet & Prodon, 2009; Rydgren et al., 2011; Sarmiento et al., 2003). (e) Linear models will fail to account for decrease in successional rates with time (Rydgren, Halvorsen, Töpper, & Njå, 2014). Therefore, an alternative approach for predicting time to recovery based on a nonlinear model must be developed.

The aim of this paper is to describe a novel ordination regression-based approach (ORBA) for predicting time to recovery in restoration studies. The approach includes guidelines for how to select a reference for the restoration target, how to choose an appropriate functional relationship between species composition at different time points and the reference to use in modelling, and how to choose time-to-recovery predictors. We demonstrate the approach for linear and asymptotic (logarithmic) relationships between species compositional change and time, using an 18-year-long dataset recovery after experimental disturbance in an old-growth boreal forest.

2 | THEORY: A NOVEL APPROACH TO PREDICT TIME TO RECOVERY

Our approach—ordination regression-based approach (ORBA)—to predict time to recovery consists of the following components: (a) availability of species composition data, recorded in plots that were established after, or ideally prior to, disturbances, and that have been reanalysed on later occasions; (b) an adequate reference for the targeted species composition (successful restoration); (c) a proxy
for the successional gradient obtained by ordination; (d) a regression model which relates “compositional distance” from restored plots, analysed at a given time point, to the temporal gradient; and (e) a predictor for time to recovery. Here, we will describe the analytic methods that constitute the approach, as well as data requirements.

2.1 | Input data

The basic data requirement is one matrix $\mathbf{M}$ with $n$ observation units (the restoration plots), established at a time point $t_j$ and re-analysed with respect to the species composition $s$ times after disturbance ($j = 1, ..., n$; time points $t = 1, ..., s$, corresponding to recordings of species made $v_i$ years after disturbance). The matrix $\mathbf{M}$ thus contains $n\times s$ columns, one for each restoration plot $\times$ time $(\mathbf{R} \times \mathbf{T})$ combination $j$. Furthermore, one matrix $\mathbf{Q}$ of $u$ ($k = 1, ..., u$) observation units for the reference is required. The reference may be static that is it consists of plots analysed with respect to species composition at one time point. However, ideally a dynamic reference should be used, consisting of $u$ undisturbed plots analysed at all or some time points $t$. The static reference may consist of the restoration plots, analysed before disturbance, of plots from the undisturbed surroundings, analysed at any time point, or, in principle, any other species composition $\mathbf{Q}$ that represents the restoration target. With a static reference, the matrix $\mathbf{Q}$ contains $u$ columns, one for each reference plot, while a full dynamic reference matrix $\mathbf{Q}$ contains $u \times s$ columns. In the following, the approach is outlined for a static reference but it can easily be adapted to a dynamic reference.

The combined data matrix $\mathbf{MQ}$, with $n\times s + u$ recordings of the species composition, is subjected to ordination, preferably by two or more ordination methods in parallel, for identification of major gradients in species composition. The ordination(s) are subsequently checked for artefacts and interpreted ecologically by standard methods (Ökland, 1990; van Son & Halvorsen, 2014). Plot scores $x_i$ along an interpreted ordination axis or another vector in the ordination space that represents the successional gradient are used as input for time-to-recovery prediction. The successional gradient vector is orientated in the direction from the disturbed plots to the restoration reference.

2.2 | Regression time to recovery (TR)

For each restoration plot $\times$ time $(\mathbf{R} \times \mathbf{T})$ combination $jt$, the successional distance $d_{jt}$, that is the distance along the successional gradient, from the position $x_o$ of the reference to $x_t$, is calculated (Figure 1a; see Appendix S1 for computer code):

$$d_{jt} = x_o - x_t$$

(1)

The position $x_o$ may be the centroid of observations in $\mathbf{Q}$. Thereafter, model $d_{jt}$ as a function of $v_i$, the time since disturbance (years), using an appropriate statistical modelling method. Methods derived from general linear models (GLM; Venables & Ripley, 2002) are obvious choices, and may be used with an untransformed or a logarithmically transformed response variable (Figure 1b). Two models are particularly relevant: (i) The linear response model $M_i$—obtained as a linear model with untransformed response variable (Figure 1b). According to $M_i$, the composition of restoration plots changes at a constant rate so that these plots first approach the reference, then reach recovery ($d_{jt} = 0$) and thereafter depart from the reference again ($d_{jt} < 0$). (ii) The asymptotic model $M_A$—obtained as a linear model with logarithmically transformed response variable (Figure 1b). Predictions from $M_A$ approach $d_{jt} = 0$ asymptotically. Temporal and spatial pseudoreplication due to repeated recording of species composition in permanent plots and nested sampling can be accounted for by general linear mixed-effects models (GLMM; Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

Time-to-recovery predictors $\mathbf{TR}_i$ and $\mathbf{TR}_A$—time to recovery predicted by use of the linear response model $M_i$ and the asymptotic model $M_A$, respectively—are obtained by a two-step procedure: (a) Define a threshold value for the successional distance $d_{jt}$ at which restoration is regarded as successful. (b) The predictor $\mathbf{TR}$ is the value of $v_i$, the predicted number of years since disturbance which, according to the model in question, corresponds to $d_{jt}$. Threshold values may be defined in at least three different ways: (a) The reference itself that is successional distance $d_{jt} = 0$ (Figure 1a). (b) A fixed successional distance $c$ from the threshold, that is, $d_{jt} = c$. (c) A “statistical threshold” obtained as a parameter that characterises the statistical distribution of reference plot scores along the successional gradient, for example, the standard deviation, the mean absolute difference from the mean, or quantities. With the exception that the zero threshold does not make sense for asymptotic models, predictors and models can be combined freely. The fixed successional distance is most relevant for the asymptotic model, in particular for a low value of $c$ for comparison with linear models using $d_{jt} = 0$. We therefore concentrate on four combinations of model (L—linear and A—asymptotic) and predictor (0—the reference, c—a fixed distance, and $s$—a statistical threshold) which will be referred to as $\mathbf{TR}_0$, $\mathbf{TR}_L$, and $\mathbf{TR}_A$, respectively. The use of statistical thresholds will facilitate cross-system and cross-study comparisons. One plausible choice of statistical criterion is +1 SD off the centroid of reference plot scores along the successional gradient, which we will refer to as the “+1 SD criterion” (Figure 1b), and denote $\mathbf{TR}_{A+1}$. One plausible choice of fixed successional distance $c$ is 0.01 from the threshold, which we will denote $\mathbf{TR}_{A+0.01}$.

3 | WORKED EXAMPLE

3.1 | The dataset

To exemplify and explore the proposed approach, we used a dataset that originates from an 18 years experimental disturbance study in a boreal old-growth forest in south-eastern Norway (Rydgren, Ökland, & Hestmark, 2004). The dataset comprises records of the species composition of 80 permanently marked plots, each 0.25 m². A nested sampling design was used, with 10
subjectively placed blocks (5 × 10 m each), each with eight randomly placed plots. The plots were established in 1993 prior to experimental disturbance and thereafter revisited yearly from 1994 until 2003, in 2005, and in 2011, after 18 years of recovery. Three plots in each block served as controls while five were subjected to selective soil removal treatments, T1 (removal of vegetation), T2 (removal of vegetation and the litter layer), T3 (removal of vegetation, the litter, and the mor soil layers), T4 and T5 (removal of vegetation, organic, and bleached soil layers; with T4 bordering intact vegetation on two sides, whereas T5 had a minimum distance of 0.5 m to intact vegetation). Treatments T1–T5 thus made up a disturbance severity gradient (Rydgren et al., 2004). Species’ abundances were recorded as frequency in 16 equal-sized subplots. The combined boreal forest matrix MQS consisted of 69 taxa (20 vascular plants, 44 bryophytes, and 5 lichens) recorded for 1,031 plot × time combinations (80 plots × 13 time points; nine treatment plots in 1994 were devoid of species and omitted from further analyses). The boreal forest dataset exemplifies a near ideal dataset for restoration studies: relatively rapid recovery (Rydgren et al., 2004) and good temporal replication that covers most of the period from disturbance to recovery.

3.2 Statistical analyses
We extracted the gradient structure of the species compositional data matrix MQS by parallel use of detrended correspondence analysis (DCA; Hill & Gauch, 1980) and global nonmetric multidimensional scaling (GNMDS; Minchin, 1987) as implemented in the vegan package version 2.3-3 (Oksanen et al., 2016), see Appendix S2 for specification details. We calculated pairwise Kendall’s rank correlation coefficients r between pairs of ordination axes to ensure that only axes representing true compositional gradients were used for further interpretation (Økland, 1996; van Son & Halvorsen, 2014; see Appendix S2 for details). The first DCA and GNMDS axes had |r| > 0.7 and both were confidently interpreted as

![Graphical illustration of the rationale behind the new approach for predicting time to recovery, exemplified by a dataset with restoration plots analysed at three different time points using a static reference with the centroid as large green circle.](image-url)
the successional gradient in response to disturbance. The DCA and the three-dimensional GNMDS solutions, orientated with reference plots at the high-score end, were used to represent the successional gradient and, hence, for prediction of time to recovery. R version 3.2.2 was used for all statistical analyses (R Development Core Team 2016).

We modelled successional distance $d_{p,t}$ as a function of years after disturbance $v_t$ using general linear mixed-effects modelling (GLMM) implemented in the R packages lme4 (Bates, Mächler, Bolker, & Walker, 2015) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2016). We parameterised models for the example dataset by using data for the first 9 years after disturbance, $t = 1, \ldots, 9$. For one plot, the value $d_{p,0} = 0.000$ (obtained for T1 disturbance in year $t = 9$) was replaced by $d_{p,0} = 0.001$ to allow a logarithmic transformation. We evaluated the models visually by using data for 10, 12, and 18 years after disturbance, and calculated the difference between predicted and observed values for the last observation (18 years after disturbance).

We used the species composition of restoration plots in 1993, before experimental disturbance, as a static reference in the analyses. Alternatively, we could have used control plots, which were mostly not significantly displaced along the successional gradient from 1993 to 2011 (Table S1). We fitted a linear model and an asymptotic model to all combinations of five response variables, one for each of treatments T1–T5 and two ordination methods to obtain time-to-recovery predictions $TR_e$ and $TR_a$. For each of the 20 combinations of model type, treatment and ordination, we first obtained a model using data for all 9 years, thereafter successively left out observations for $t = 1$, then $t = 2$ and so on, to obtain the model with the best fit to the data based on the $t$ value. The rationale behind this was to avoid the influence of the first chaotic years after disturbance (Rydgren et al., 2004) since they provide poor estimators of time to recovery. The model with the best fit was used to predict time to recovery. In the few cases of negative or zero successional distances (see Figure S1), for which $\ln(d_{p,0})$ was undefined, they were not included in the asymptotic models.

We modelled temporal and spatial stochasticity in species compositional change by parameterising random effects for each time point and block. The random block effect applied to control plots only since the disturbance treatments were not replicated within blocks. We tested if control plots were displaced along the successional gradient during the study period, using a backward elimination procedure with likelihood ratio tests (Hastie, Tibshirani, & Friedman, 2009) to obtain minimal adequate models.

### 4 | RESULTS

Restoration trajectories along the first ordination axes (Figure 2, Table S2) were roughly similar for all treatments: the distance to the reference $d_{p,0}$ increased (for 2 years with GNMDS and 3–6 years with DCA), before starting to decrease gradually. The maximum single-plot $d_{p,t}$ values were 3.79 SD units and 3.22 H.C. (half-change) units, as obtained by DCA and GNMDS, respectively. This indicated that the most severe treatment (T5) affected some plots so severely that, after disturbance, shared almost no species with the reference. From the time of maximum dissimilarity with the reference, yearly successional rates decreased with increasing $t$ (Figure 2).

Eighteen years after disturbance, the two least severe treatments (T1 and T2) had reached recovery according to the “+1 SD criterion,” that is with $d_{p,t}$ values within +1 SD off the centroid of reference plot along the successional gradient (Figure 3).

The linear and asymptotic models $M_\text{L}$ and $M_\text{A}$ of successional distance $d_{p,t}$ as a function of years after disturbance $v_t$ for combinations of ordination method and treatment, were closely similar for the years used to parameterise the models. However, with increasing time since disturbance, predictions from the two models became increasingly different (Figure 3, Figure S1). Using field observations 18 years after disturbance as a reference, the linear model clearly underpredicted successional distance in all cases except two (T3 and T5) with DCA ordination (Figure S1; Table 1). Predictions from the asymptotic
model accorded generally well with observations, with no tendency for systematic under- or overprediction of successional distances after 18 years of recovery (Table 1). Generally, predictions from the asymptotic GNMDS-based models fitted the data better than predictions from DCA-based models (Table 1).

For the linear $M_L$ models, the 10 TR$_{10}$ predictions for time to full recovery (5 treatments x 2 ordination methods) ranged between 13 and 29 years, whereas the 10 TR$_{1:1}$ predictions gave 2-4 years shorter time to recovery. Comparison of DCA-based and GNMDS-based predictions indicated that the former gave equal or higher values than the latter (Figure 3; Figure S1). For the asymptotic $M_A$ models, the TR$_{A<0.01}$ and TR$_{A<0.1}$ predictions ranged between 28-100 and 11-43 years, respectively. With the exception of T4, time to recovery increased with increasing disturbance severity (Figure 3; Figure S1).

Our results suggest the compositional change over time is a nonlinear process as successional rates gradually decrease over time (Foster & Tilman, 2000; Lepš, 1987; Myster & Pickett, 1994). We show that such nonlinearity can be described precisely as a linear function of log-transformed compositional distances (in ecological space) from the expected successional end point. Linear models of untransformed distances, on the other hand, can only describe successional rates over very short time periods, since they overpredict successional rates in the longer run and hence strongly underpredict time to recovery. In the following, we discuss basic methodological issues relating to prediction of time to recovery in restoration ecological studies.

![Figure 3](image_url) The example dataset: Best linear (black lines) and asymptotic models (red lines) for successional distance (distance along the successional gradient represented by the first global nonmetric multidimensional scaling (GNMDS) ordination axis) as a function of time since disturbance, with 95% confidence intervals indicated by grey and red shading, respectively. Both the linear and asymptotic models were parameterised using the first 9 years of data after disturbance, shown by open, black circles. Red dots represent the mean values for each year for the first 9 years. Blue dots indicate observations 10, 12, and 18 years after disturbance. Green shading indicates the recovery reference, that is, the centroid of reference plot scores along the successional gradient $+1$ standard deviation. T1—removal of vegetation; T2—removal of vegetation and the litter layer; T3—removal of vegetation, the litter, and the mor soil layers; T4—removal of vegetation, organic, and bleached soil layers bordering intact vegetation on two sides; T5—removal of vegetation, organic, and bleached soil layers with a minimum distance of 0.5 m to intact vegetation.

<table>
<thead>
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<th>Treatment</th>
<th>DCA</th>
<th>GNMDS</th>
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<td>T5</td>
<td>-0.05</td>
<td>-0.10</td>
</tr>
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</table>
5.1 | The functional relationship of succession models and time-to-recovery predictors

Our worked example shows that successful predictions of time to recovery strongly depend on appropriate specification of the functional relationship of successional distance to time since disturbance. The boreal forest data presents five cases of very close fit to a nonlinear relationship between compositional distance and time. The fact that the same functional relationship seems to apply over a considerable span of disturbance severities, suggests that this functional relationship may apply to successions after disturbance more generally. Until general validity of this functional relationship is proven, a priori specification of models for use in time-to-recovery prediction should be informed by knowledge of the studied system and expert judgements.

When the datasets include just two time points only a linear function is possible to fit (Rydgren et al., 2011). However, when successional rates decrease over time, as typically found in primary successions (Robbins & Matthews, 2010; Rydgren et al., 2014; Whittaker, 1989), predictors based upon a linear model will under-predict time to recovery strongly and should therefore be avoided if the data allows it. Our results unequivocally point to TR$_2$ predictors that are based on an asymptotic model (M$_3$), as best choices. The minimum data requirement for M$_3$ models is a time series of at least three temporal recordings. An additional danger of obtaining mis-specified models from sparse data appears when compositional dissimilarity from the restoration target increase shortly after disturbance (Auestad, Rydgren, & Auestad, 2016; Kirmer, Rydgren, & Tischew, 2018). In successions, random variation in species composition between years may override a weak temporal trend. Thus, datasets used for time-to-recovery prediction should cover a temporal interval of sufficient length to describe the succession adequately. Another prerequisite for using the proposed approach (ORBA) for time-to-recovery prediction is that the imprint of the successional gradient on the species composition is strong enough to be recognised as a vector in ordination space. This requirement was satisfied in our example dataset, and likely also in other restoration projects where disturbances have been severe. Typically, a strong successional gradient emerges as the main axis when postdisturbance revegetation data after severe disturbance are subjected to ordination (Alday, Marrs, & Martinez-Ruiz, 2011; Fagan, Pywell, Bullock, & Marrs, 2008; Matthews & Spyreas, 2010). In cases where the successional gradient appears on several ordination axes (i.e., as a vector that does not run parallel with one ordination axis), the vector of best fit to the time-after-disturbance variable should be used to estimate successional distance (see Rydgren et al., 2014). As the asymptotic approach handles decreasing successional rates over time, the modelled succession levels off and asymptotically approaches a limit, which is in accordance with assumptions of convergent succession. In the linear approach, the modelled succession principally goes on forever, which is why we consider the linear model as a generally inappropriate descriptor of the recovery process. This parallels the use of linear species response models for extraction of compositional gradients in ordination, which results in spurious ordination axes (Økland, 1990). We therefore caution against uncritical use of linear models for ecological data that describe single species’ or species compositional responses to environmental gradients.

5.2 | Choice of reference for the restoration target

Selection of a suitable reference is crucial in time-to-recovery prediction from species compositional data, as in all restoration projects. Optimally designed field experiments provide suitable candidates for the reference, preferably the species compositions of control plots or predisturbance plots. If control plots show small compositional change during the experiment (as in our example data), predisturbance restoration plots represent an optimal choice of reference. When reference plots are located in exactly the same positions as restoration plots, effects of local environmental factors are efficiently ruled out. If, however, control plots undergo systematic changes in species composition during the restoration process, for example, due to climate change (Hobbs & Cramer, 2008; Timpane-Padgham, Beechie, & Klingler, 2017), use of control plots analysed at a latest possible time point should be considered. But since restoration projects seldom are planned experiments (see McKay, Christian, Harrison, & Rice, 2005; Rydgren, Hagen, Rosef, Pedersen, & Aradottir, 2017) restoration targets may be difficult to define precisely in terms of species composition. An important point is that the variation along major environmental gradients (and hence species composition) among reference plots must match the restoration plots for the two datasets to be comparable (Rydgren et al., 2011). Unclear restoration targets therefore necessarily translate into difficulties in defining a reference for predicting time to recovery. We recommend choosing the reference by taking all available knowledge on the species composition of the restoration site and the successional process into account. Moreover, we recommend using a dynamic reference (Hiers, Jackson, Hobbs, Bernhardt, & Valentine, 2016; Hiers et al., 2012; Kirkman et al., 2013; Rydgren et al., 2011) based upon species composition of reference plots analysed simultaneously with restored plots, to handle changes in undisturbed control plots due to, for example, climate change (Prach & Walker, 2011).

Selection of a threshold for "successful" recovery to be used in time-to-recovery prediction also requires careful consideration. The choice of threshold value for acceptable recovery should be made after careful consideration of the goal of each restoration project. We used the centroid of the reference points ±1 SD, but this particular solution needs further testing with other datasets before it can be generally recommended as a default value.

5.3 | The role of time-to-recovery prediction in restoration ecology

Development of methods for prediction of time to recovery based on the species composition, a fundamental ecosystem attribute (Clewell
& Aronson, 2013), will be a boon to restoration ecology (Urban, 2006). Species composition data may appear variable and less predictable than other ecosystem properties (Brudvig et al., 2017; Laughlin et al., 2017), but our example nevertheless demonstrates its value for assessing the outcome of restoration and, more generally, its usefulness in predictive restoration science (Brudvig et al., 2017). Better methods for prediction of time to recovery may shift the perspective in restoration ecology, from a narrow focus on whether restoration goals are reached or not, to insights that may guide the entire restoration process. We need to assess different restoration measures, predict the time-scales involved in the recovery process, and propose knowledge-based management recommendations on, for example, additional restoration measures. Knowing that ecological restoration may require decades or even centuries (Harper & Kershaw, 1996; Jorgenson et al., 2010; Prach, Fajmon, Jongepierová, & Rehounková, 2015), availability of reliable methods for prediction of time to recovery will significantly advance restoration ecology.

This paper describes and provides the first applications of new approach (ORBA) for time-to-recovery prediction, intended for use in restoration ecological studies. More studies are needed to get a full overview of the circumstances that influence the performance of the proposed predictors, for example, the quality and quantity of data required to obtain reliable predictions. Nevertheless, our results clearly indicate that predictors based upon asymptotic models for successional distance should be preferred over predictions based on linear models whenever adequate data are available.

ACKNOWLEDGEMENTS

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AUTHORS’ CONTRIBUTIONS

K.R., R.H., J.P.T., and J.S. contributed to the ideas in this manuscript. K.R. analysed the data; K.R. and R.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Author order is alphabetical after the third author.

DATA ACCESSIBILITY

R script and data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.vr93sj5 (Rydgren et al., 2018).

ORCID

Knut Rydgren http://orcid.org/0000-0001-8910-2465
Rune Halvorsen http://orcid.org/0000-0002-6859-7726

Joachim P. Töpper http://orcid.org/0000-0002-6996-7223
Inger Auestad http://orcid.org/0000-0001-6321-0433
Liv Norunn Hamre http://orcid.org/0000-0002-9033-4260
Eelke Jongejans http://orcid.org/0000-0003-1148-7419
Jan Sulavik http://orcid.org/0000-0001-9562-2854

REFERENCES


**SUPPORTING INFORMATION**

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

PAPER II

Rydgren, K., Auestad, I., Halvorsen, R., Hamre, L.N., Jongejans, E., Töpper, J.P., Sulavik, J.

2020.

Assessing restoration success by predicting time to recovery—But by which metric?


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Assessing restoration success by predicting time to recovery—But by which metric?

Knut Rydgren1 | Inger Auestad1 | Rune Halvorsen2 | Liv Norunn Hamre1 | Eelke Jongejans3 | Joachim P. Töpper4 | Jan Sulavik1,2

Abstract

1. Restoration of degraded ecosystems may take decades or even centuries. Accordingly, information about the current direction and speed of recovery provided by methods for predicting time to recovery may give important feedback to restoration schemes. While predictions of time to recovery have so far been based mostly upon change in species richness and other univariate predictors, the novel ordination-regression based approach (ORBA) affords a multivariate approach based upon species compositional change.

2. We used species composition data from four alpine spoil heaps in western Norway, recorded at three time points, to predict time to recovery using ORBA. This approach uses distances between restored plots and reference plots along a successional gradient, represented by a vector in ordination space, to model linear or asymptotic relationships of compositional change as a function of time. Results from ORBA were compared with results from models of more generic univariate attributes, that is total cover, species richness and properties of the physical environment as functions of time.

3. ORBA predictions of time to species compositional recovery varied from less than 60 years with linear models to 115–212 years with asymptotic models. The long estimated time to recovery suggests that the restoration schemes adopted for these spoil heaps are likely to be suboptimal.

4. Much shorter time to recovery was predicted from some of the more generic univariate attributes, that is species richness and total cover, than from species composition. Given the current rates of recovery, most spoil heaps will reach reference levels for total cover and species richness within 50 years, whereas predictions indicate that 67–111 years are needed to restore levels of soil organic matter and pH.

5. Synthesis and applications. Species composition and soil conditions provide information of generally higher relevance for evaluation of ecosystem recovery processes than the most commonly used metric to assess restoration success, species richness. Species richness is decoupled from species compositional recovery, and likely to be a generally poor measure of restoration success. We therefore
encourage further improvement of methods like the ordination-regression based approach that use species compositional data to predict time to recovery.

KEYWORDS
ORBA, Ordination-Regression Based Approach, restoration ecology, soil conditions, species composition, species richness, spoil heaps, time to recovery

1 | INTRODUCTION

Prediction play a minor role in most branches of ecology (Houlahan, McKinney, Anderson, & McGill, 2017), partly because of the complexity of ecosystems (Byers, 2018). However, to respond to the rapid changes in climate and ecosystems due to human activities (Ceballos et al., 2015), ecology needs to become more predictive (Evans, Norris, & Benton, 2012). This also applies to restoration ecology (Brudvig, 2017), since predictions of, for example time to recovery, are directly relevant for evaluation of progress in ecological restoration (Urban, 2006). Until recently, restoration ecology has lacked proper methods to predict time to recovery for informed evaluation of restoration success. The novel ordination regression based approach (ORBA; Rydgren, Halvorsen, et al., 2019b) facilitates prediction of time to recovery through modelling either linear or asymptotic trajectories of compositional change over time. In particular, the asymptotic model appears promising since it accounts for declining successional rates, a common characteristics of successions (Anderson, 2007; Rydgren, Økland, & Hestmark, 2004). Reliable predictions of time to species compositional recovery are relevant for assessing success in restoration because species composition constitutes one of the most important attributes of ecosystems, summarizing the outcomes of all important ecological processes (cf. Clewell & Aronson, 2013).

Although species composition may provide indications of a much wider range of ecosystem properties than aggregated, more generic properties of vegetation such as total cover and species richness, the latter are much more often used to assess restoration success (Ruiz-Jaén & Aide, 2005; Waldén & Lindborg, 2016). Which metrics to use is still vigorously debated (Abella, Schetter, & Walters, 2018; Brudvig et al., 2017; Durigan & Suganuma, 2015; Reid, 2015). In general, we expect species composition to recover more slowly than total cover and species richness. Predictions of restoration success is therefore expected to depend on the metrics considered (cf. Crouzeilles et al., 2016). Still, the view that simpler measures (cover, richness) may be appropriate as proxies for more complex properties such as species composition is not uncommon (Brancalion & Holl, 2016; Suganuma & Durigan, 2015). A closer examination of the idea that simpler measures can approximate species composition for assessing restoration success by predicting time to recovery, is therefore needed.

Soil conditions may play an important role in successful restoration of species composition (Piqueray et al., 2011; Rydgren, Halvorsen, Auestad, & Hamre, 2013). Because abiotic and biotic ecosystem components mutually influence each other, both have to be taken into account in restoration of ecosystems. In harsh environments, such as alpine environments where the majority of hydropower spoil heaps are found, soil processes are slow (Kidd, Strever, & Jorgenson, 2006). Accordingly, alpine spoil heaps have low levels of soil organic matter even after eight decades (Rydgren et al., 2013), and slower recovery of soil properties than of univariate biotic ecosystem properties such as species richness and total cover is therefore expected.

In this study, we use ORBA with both linear and asymptotic models to analyse data from three censuses of species composition and environmental conditions of alpine spoil heaps and their undisturbed surroundings, over a period of 24 years, 7–41 years after the initial disturbance, to predict time to recovery of species composition. ORBA results are compared with parallel analyses of time-to-recovery predictions for selected properties of the physical environment, total cover and species richness. The studied spoil heaps consist of surplus rock material resulting from tunnel construction for hydropower plants. In alpine areas, such spoil heaps pose serious restoration challenges due to the harsh environment (Rydgren et al., 2013). Previously, full species compositional recovery of the four alpine spoil heaps addressed in the present study was predicted to be achieved in less than 50 years (Rydgren, Halvorsen, Øødland, & Skjerdal, 2011). However, the analyses of Rydgren et al. (2011) were based upon time-to-recovery predictions derived from a linear model of compositional change over time between two time-points. The resulting predictions are likely to be over-optimistic as constant successional rates are unrealistic (Rydgren et al., 2011). The present study is based on three censuses. Since we expect successional rates to decrease with time, we hypothesize that (a) species compositional recovery will be slower than indicated by Rydgren et al. (2011) (hypothesis 1) and we further expect (b) species compositional recovery to be slower than the recovery of functionally less specific properties such as total cover or species richness (hypothesis 2). Finally, we expect (c) that recovery of the physical environment will be slower than recovery of total cover and species richness (hypothesis 3).

2 | MATERIALS AND METHODS

2.1 | Field sites

We studied four low alpine spoil heaps in western Norway, situated from 1,000 to 1,360 m a.s.l., within an extent of 30 km (Figure 1, see Figure S1, all of which were also included in a previous study (Rydgren et al., 2011). The climate is relatively wet and cold with
annual precipitation in the range 1,500–1,900 mm and mean July temperatures of 6.6–8.8°C for the period 1971–2000 (NVE, 2018).

The spoil heaps were constructed between 1974 and 1984, and vary in size from 2.7 to 4.1 ha. They consist of blasted rocks, except Kleåalen which consists of finer-grained substrate (Rydgren et al., 2011). The spoil heaps are made up by bedrock material similar to that of their surroundings, mainly consisting of gneisses, granites, phyllite and other metamorphosed rocks (Skjerdal & Odland, 1995).

Shortly after construction, compound fertilizer was added to all spoil heaps, followed by seeding with commercial seed mixtures annually for at least 3 years (Skjerdal & Odland, 1995). Additional fertilization and seeding also took place later years (see Appendix S1 for details). All spoil heaps have been sporadically grazed by sheep since construction.

2.2 | Sampling design and data collection

Data on the physical environment (soil organic matter and pH), total cover (vascular plants, and bryophytes and lichens), species richness (vascular plants, bryophytes and lichens), and species composition were collected at all sites in the early 1990s (Skjerdal, 1993; Skjerdal & Odland, 1995), in 2008 (Rydgren et al., 2011) and in 2015. In the early 1990s (1991 in Svaratsvatn, Fossane and Kleåalen and 1994 in Øyalen), 10–20 non-permanent sample plots (0.5 × 0.5 m each) were placed on each spoil heap by stratified random sampling (64 plots in total), using a baseline approach (Skjerdal, 1993). In 2008, we selectively placed 8 blocks per spoil heap (5 blocks on the heap and 3 in their undisturbed surroundings), each 5 × 10 m. Within each block, three permanent sample plots (0.5 × 0.5 m) were placed at random, with the extra condition that plots had to be separated by at least 1 m (Rydgren et al., 2011). All permanent plots were re-analysed in 2015 except one block at the Kleåalen spoil heap, which was lost due to deposition of rock material. The resulting dataset comprised 253 sample plots with 239 recorded taxa (107 vascular plants, 86 bryophytes and 46 lichens; see Appendix S2 for nomenclature).

The species composition of the plots was recorded in July–September at the three sampling occasions. We divided each plot into 16 equally sized subplots and recorded the abundance of vascular plants, bryophytes and lichens as the frequency in 16 subplots. We
also visually estimated the total percentage cover of vascular plants, bryophytes and lichens in each plot. Species richness variables (the number of species of vascular plants, bryophytes and lichens respectively) for each plot were derived from species composition data.

Soil samples were collected from the upper 5 cm soil layer at the three sampling occasions, and analysed for soil organic matter in % and pH (see Appendix S3 for details).

### 2.3 Data analyses

All statistical analyses were performed in R versions 3.2.2 or 3.5.3 (R Development Core Team, 2019).

We used ORBA to predict time to species compositional recovery (Rydgren, Halvorsen, et al., 2019b). This entailed first extracting the gradient structure of a species compositional dataset by parallel use of detrended correspondence analysis (DCA; Hill & Gauch, 1980) and global non-metric multidimensional scaling (GNMDS; Minchin, 1987) as implemented in the vegan package version 2.3.3 (Oksanen et al., 2016), see Appendix S4 for specification details. Axis1 of all ordinations revealed a successional gradient of species composition, running from spoil-heap plots analysed in the 1990s via plots analysed in 2008 and in 2015, to plots from the surroundings (Figure 2: Table S1). Second, we calculated successional distance (d_{ij}) along these gradients, that is the distance between a restoration plot and its reference, using the mean position of plots from the surroundings at a given time point as our dynamic reference. Since 2008 was the first year plots from the surroundings were censused, we used the 2008 plots as references also for plots from the 1990s, implicitly assuming that the reference vegetation was as stable between these years as it was between 2008 and 2015 (Table S1).

Finally, we modelled successional distance as a function of time since disturbance with generalized linear mixed models (GLMMs; Bates, Mächler, Bolker, & Walker, 2015) with identity-link and Gaussian error distribution, by fitting two types of responses, a linear relationship (M_1), and a log-linear, asymptotic relationship (M_2). From the models we derived three different time-to-recovery predictions for each spoil heap: TR_{L_0} (linear model; restoration target: predicted successional distance = 0), TR_{A_m} (asymptotic model; restoration target: predicted successional distance = +1 S.D. off the centroid of reference plot scores) and TR_{AH-0.01} (asymptotic model; restoration target: predicted successional distance = 0.01).

We modelled the physical environmental variables and the biotic variables as functions of time since disturbance (year of spoil-heap construction). Soil organic matter, vascular plant cover and bryophyte and lichen cover were expressed as percentages, that is as strictly bounded but non-binomial data. We therefore logit-transformed these variables (Warton & Hui, 2011) before modelling them with identity-link and Gaussian errors. The species richness variables were modelled with log-link and Poisson errors, whereas pH was modelled with identity link and Gaussian errors. Finally, we used the models to predict the number of years before reference levels (mean values in the undisturbed surroundings) are reached.

All models were parameterized using the R package LME4, version 1.1.21 (Bates et al., 2015), accounting for repeated measurements and the spatially nested sampling structure by specifying plot nested within site with block as random effects in the models. The fact that the spoil-heap plots were not set up in a block design in the censuses of the 1990s was handled by allocating the 1990s plots randomly to blocks to fit the structure of the model. For the species richness variables the mixed-effects models did not converge, even when the random effect was reduced to only consist of sites. The preliminary estimates from these models showed that the random effects hardly contained any variation. Therefore, we used generalized linear models without random effects for the species richness variables. Time to recovery estimates from these models therefore have to be interpreted more conservatively.

### 3 RESULTS

#### 3.1 Species compositional change during restoration

The first axis of the DCA and GNMDS ordinations represented the restoration successional gradient (Table S1), showing similar displacement patterns for plots from all four sites over time in direction of the reference plots (Figure 2). The compositional turnover along the first axes, that is their gradient lengths, were 5.34 standard deviation (S.D) units for DCA and 2.93 half change (H.C) units for GNMDS, respectively, indicating that considerable shifts in species composition took place during restoration succession at all spoil heaps.

In the early phase, the species composition of all spoil heaps was dominated by pioneer species like Bryum spp., which decreased rapidly over time both in frequency and abundance (Table S2). Other pioneer species, like Ceratodon purpureus, experienced a slower population decline, and some, exemplified by Sagina saginoides, maintained relatively stable populations. Some species, for example Sanionia uncinata, that were common in the surroundings, established early on the spoil heaps and increased further to frequencies higher than in the surroundings. Empertrum nigrum, which with the exception of the seeded grasses was the most frequent vascular plant species on the spoil heaps in 2015, also established early on the spoil heaps and increased considerably over time until approaching frequencies equal to those of the surroundings.

Most species that were common in the surroundings established slowly on the spoil heaps and were still infrequent there in 2015, for example ericaceous species such as Vaccinium myrtillus, V. uliginosus and V. vitis-idaea, forbs such as Bistorta vivipara and Hieracium alpinum, graminoids such as Anthoxanthum odoratum, Avenella flexuosa and Carex bigelowii, and bryophytes such as Hylococum splendens and Barbilophozia floerkei. Lichens established slowly as well, but several lichen species that were common in the surroundings occurred regularly on the spoil heaps in 2015, for example Cetraria islandica agg., Cladonia arbuscula, C. gracilis, C. rangiferina, C. squamosa agg. and Stereocaulon spp.
Time-to-recovery predictions for the spoil heaps, obtained by ORBA, were between 43 and 60 years for linear models (TR$_{1,1}$) and in the ranges 41–105 and 115–212 years for the asymptotic models TR$_{A>1}$ and TR$_{A>0.01}$, respectively (Figure 3; Table 1). Generally, longer time-to-recovery predictions were obtained by use of successional distances obtained from DCA than from GNMDS ordination, but the differences between ordination methods were generally small (two of the predictions based upon TR$_{A>0.01}$ excepted). The shortest and longest predictions were most often obtained for the Kleåålen and Svartavatn spoil heaps respectively (Table 1).

3.2 | Dynamics of total cover

Patterns of change in vascular plant cover over time differed considerably among the four spoil heaps (Figure 4). Significant increase over time was observed only at Kleåålen and Svartavatn where reference levels were predicted to be reached in 43 and 55 years after disturbance respectively (Table 2).

The cover of bryophytes and lichens increased rapidly after disturbance at all spoil heaps and had reached reference levels at all sites in 2015, 31–37 years after disturbance (Figure 4, Table 2). Particularly rapid recovery of bryophyte and lichen cover was observed at Kleåålen, where the reference level was reached already at the first census in 1991, 10 years after disturbance.

3.3 | Dynamics of species richness

The number of vascular plants (species richness) increased significantly over time at all spoil heaps except Øydalen (Figure 5). Predictions from the significant models indicated that the reference levels would be reached in 36–58 years after disturbance in these spoil heaps (Table 2). The number of bryophyte species increased more rapidly than vascular plant species numbers and reached reference levels at the second census, 13–28 years after disturbance (Figure 5). The number of lichen species followed the same pattern as bryophytes; reference levels were reached at the second or third census (Figure 5).

3.4 | Dynamics of the physical environment

Soil organic matter increased significantly over time at all four spoil heaps (Figure 6), but was still far below reference levels at
FIGURE 3  Models for successional distance [distance along the successional gradient represented by the first DCA axis (upper panel) and the first global non-metric multidimensional scaling (GNMDS) axis (lower panel)] as a function of time since disturbance, obtained separately for each of the four spoil heaps by ordination-regression based approach (ORBA). The fitted linear models are represented by black lines, asymptotic models by red lines. The 95% confidence intervals are indicated by grey and red shading respectively. The green dotted horizontal line represents the centroid of reference plot scores along the successional gradient in 2015 with +1 standard deviation indicated by light green shading.

TABLE 1  Predicted time to species compositional recovery, measured in years, as obtained from three different ordination-regression based approach (ORBA) models: TR_{L0} (linear model; restoration target: predicted successional distance = 0), TR_{A + 1} (asymptotic model; restoration target: predicted successional distance = +1 SD off the centroid of reference plot scores) and TR_{A + 0.01} (asymptotic model; restoration target: predicted successional distance = 0.01)

<table>
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<th>Site</th>
<th>DCA</th>
<th>GNMDS</th>
</tr>
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<tr>
<td></td>
<td>TR_{L0}</td>
<td>TR_{A+1}</td>
</tr>
<tr>
<td>Fossane</td>
<td>46</td>
<td>85</td>
</tr>
<tr>
<td>Kleådalen</td>
<td>51</td>
<td>41</td>
</tr>
<tr>
<td>Øydalen</td>
<td>60</td>
<td>105</td>
</tr>
<tr>
<td>Svartavatn</td>
<td>56</td>
<td>89</td>
</tr>
</tbody>
</table>

Note: Successional distance, the response variable in the models, was calculated from results of DCA and GNMDS ordinations.

all sites in 2015, 31–41 years after disturbance. For most sites c. 100 years was predicted to be required after disturbance before reference levels are reached (Table 2). Shortly after disturbance, pH was much higher at the spoil heaps than in their surroundings but, with the exception of the Svartavatn spoil heap, decreased significantly over time (Figure 6). For these three spoil heaps pH was predicted to reach reference levels 67–92 years after disturbance.

4 | DISCUSSION

4.1 | Time to recovery estimation using ORBA

Our results show that successional rates in the four studied spoil heaps decline over time, a common characteristic of successions (Chang et al., 2019; Foster & Tilman, 2000; del Moral, Saura, & Emenegger,
FIGURE 4 Models for the cover of vascular plants (upper panel) and bryophytes and lichens (lower panel) as functions of time since disturbance, obtained separately for each of the four spoil heaps. Model predictions are represented by black lines; continuous lines indicate significant ($p < .05$), whereas dotted lines indicate nonsignificant models. Grey shaded areas indicate 95% confidence intervals. The green dotted horizontal line represents the mean values for plots from the spoil heap’s surroundings in 2015, with ±0.5 standard deviation indicated by light green shading.

TABLE 2 Predicted time (in years) to the reference level (mean values for plots from the undisturbed surroundings) after disturbance (the year each spoil heap was constructed), measured in years, as obtained from LMM or GLM (for species richness) models, for the physical environment, total cover and species richness variables

<table>
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<tr>
<th>Site</th>
<th>Cover of vascular plants</th>
<th>Cover of bryophytes and lichens</th>
<th>Number of vascular plants</th>
<th>Number of bryophytes</th>
<th>Number of lichens</th>
<th>Soil organic matter</th>
<th>pH</th>
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<td>58</td>
<td>13</td>
<td>NA</td>
<td>111</td>
<td>87</td>
</tr>
<tr>
<td>Kleådalen</td>
<td>43</td>
<td>n.s.</td>
<td>36</td>
<td>n.s.</td>
<td>22</td>
<td>61</td>
<td>92</td>
</tr>
<tr>
<td>Øydalen</td>
<td>n.s.</td>
<td>37</td>
<td>n.s.</td>
<td>28</td>
<td>31</td>
<td>94</td>
<td>67</td>
</tr>
<tr>
<td>Svartavatn</td>
<td>55</td>
<td>33</td>
<td>44</td>
<td>19</td>
<td>NA</td>
<td>95</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

Note: n.s.: nonsignificant models; NA: not modelled due to sparse data. Note that some predictions were beyond the range spanned by the data, and that some of the models were nonsignificant.

2010; Myster & Pickett, 1994). Furthermore, we obtain a prominent successional gradient along the closely similar first axes of the GNMDs and DCA ordinations which justifies their use for predicting time to recovery (Rydgren, Halvorsen, et al., 2019b) and ensures that the basic assumption of the ordination-based approach for predicting time to recovery (ORBA), that a proxy for the successional gradient is available, is satisfied (Rydgren, Halvorsen, et al., 2019b).

Seven years after the previous census (in 2008) none of the spoil heaps are close to recovery, and full recovery within 1–15 years from 2015, as suggested by earlier linear predictions (Rydgren et al., 2011), is most unlikely. The time-to-recovery predictions obtained by linear models using ORBA extend previous predictions by 8–17 years; full compositional recovery is now predicted to take place between 43 and 60 years after construction. This confirms hypothesis 1. Inclusion of more time points gives more realistic time-to-recovery predictions which explains part of the difference between the linear predictions reported here and the results of Rydgren et al. (2011). However, the fact that taking declining successional rates with
time into account by applying asymptotic models of successional distance, obtaining predictions for time to full compositional recovery from 115 to 212 years, indicates that the major reason for the difference is that successional rates decrease over time (Foster & Tilman, 2000; Myster & Pickett, 1994; Rydgren, Halvorsen, et al., 2019b; Rydgren, Halvorsen, Tøpper, & Njås, 2014). Although it is not possible from our data to conclude which of the models, linear or asymptotic, that gives the most accurate predictions, two strong arguments point in favour of the asymptotic models. First, only the asymptotic models account for decreasing successional rates over time, that is that successions stand out as logarithmic processes. Second, older spoil heaps in the region are still far from full recovery and more than 100 years seem to be needed for full recovery due to the common construction practice of using a coarse top substrate (cf. Rydgren et al., 2013). The definition of recovery also influences predictions of time to recovery. To reach near-zero successional distance from the reference state (TR<sub>88.00</sub> in this study) will of course take longer time than to satisfy a more relaxed criterion (TR<sub>88.10</sub> in this study). In fact, full recovery in the sense defined here may not be possible, feasible or even relevant in all cases (McDonald, Gann, Jonson, & Dixon, 2016). Therefore, adopting a relaxed criterion like +1 standard deviation off the centroid of reference plot scores may sometimes be appropriate.

Our results show that ORBA predictions are influenced by the robustness of ordination methods (DCA and GNMDs), which in turn depends on properties of the data (Eilertsen, Økland, Økland, & Pedersen, 1990; Minchin, 1987; Økland, 1990; Rydgren, 1993) such as the distribution of species’ frequencies. In particular, species that occur in few plots are known to influence the ordination result, and especially so in species-poor or otherwise deviant sample plots (Økland, 1990). We therefore encourage studies on the robustness of ORBA to differences in dataset properties. So far, ORBA has only been tested on a boreal forest dataset (Rydgren, Halvorsen, et al., 2019b). Also in that case, asymptotic models were superior to linear models, and the asymptotic GNMDs-based models fitted the data better than the asymptotic DCA-based models (Rydgren, Halvorsen, et al., 2019b). More studies using ORBA are, however, needed before eventual final conclusions about choice of ordination method can be drawn. A likely outcome of further tests is, however, that no method is consistently better than the other (as for ordination of species data; Økland, 1990; van Son & Halvorsen, 2014) and that two methods should always be used in parallel to secure robustness of the results.

FIGURE 5 Models for species richness of vascular plants (upper panel), bryophytes (middle panel) and lichens (lower panel) as functions of time since disturbance, obtained separately for each of the four spoil heaps. Model predictions are represented by black lines; continuous lines indicate significant (p < .05), whereas dotted lines indicate nonsignificant models. Grey shaded areas indicate 95% confidence intervals. Bryophyte species richness was modelled by a quadratic function. Models were not fitted for spoil heaps in which the species group in question was absent from most plots at the first census. The green dotted horizontal line represents the mean values in the spoil heap’s surroundings in 2015, with ±0.5 standard deviation indicated by light green shading.
4.2 | Time to recovery using univariate metrics

Predictions of time to recovery based upon more generic, univariate metrics are substantially lower than those obtained from ORBA predictions of compositional recovery. Furthermore, the uncertainty of estimates based upon these metrics is larger, confirming hypothesis 2. This result may be due to (a) insufficient understanding of the ecological processes, (mis)leading us to opt for too simplistic models, or (b) that the relevant processes do not follow a simple monotonic pattern. While both species richness and total cover of bryophytes and lichens increase relatively fast after disturbance, reaching reference levels within 13–58 years after disturbance, recovery of soil organic matter and pH is predicted to take up to 111 years. The relatively fast recovery of species richness, particularly for bryophytes, is due to the appearance of pioneer species as well as species typical of established vegetation relatively soon after disturbance. Later, as seen at the last census in 2015, bryophyte species richness drops when pioneer species go locally extinct. This shows that recovery of species richness is decoupled from species compositional recovery and, accordingly, that richness recovery does not imply recovery of an ecosystem with functions and a species composition in dynamic equilibrium with its environment.

The two cover variables follow a similar pattern; in two of the four spoil heaps the reference level is predicted to be reached relatively fast, within 55 years. The reason is that the cover of pioneer and established species follow the same pattern as species richness with shifts in the species groups that contribute to cover over time. In addition, the highly persistent seeded grass species contribute considerably to the total cover over the entire time period (Rydgren et al., 2016).

Our results indicate that univariate metrics for the physical environment (here: soil organic matter and pH) are more relevant for modelling the recovery process than properties of the biotic environment. There are two reasons for this: (a) that environmental conditions known to be important for the species composition are important in their own right when the recovery status is assessed; and (b) that the physical properties seem to follow a monotonic trajectory (e.g. continuously increasing soil organic matter content and decreasing soil pH). Based upon metrics for the physical environment, recovery is predicted to take place many years later than predicted from the univariate, biotic variables, and closer to the predicted recovery of the species composition, confirming hypothesis 3. This accords with ecological theory, e.g. the gradient analytic perspective (Halvorsen, 2012; Whittaker, 1967), according to which the species composition of an ecosystem in dynamic equilibrium reflects the environmental conditions closely.

The long recovery time for soil properties found in this study reflects a major challenge in ecological restoration (Aradottir & Hagen,
2013; Becker & Pollard, 2016; Dobson, Bradshaw, & Baker, 1997; Fagan, Pywell, Bullock, & Marrs, 2008; Jorgenson & Joyce, 1994). At the studied soil heaps, persistently unfavourable soil conditions are probably the main obstacle to re-establishment of many of the local vascular plant species (Rydgren et al., 2013, 2011). This also accords with results of Gretarsdottir, Aradottir, Vandvik, Heegaard, and Birks (2004) and Alday, Marrs, and Martinez-Ruiz (2011). Generally, soil development on newly formed land proceeds more slowly than indicated by the changes in soil organic matter and pH. Like soil development in alpine glacier forelands (Matthews, 1992), re-establishment of fully developed soils on soil heaps may take centuries. Typically, dominant species in the surroundings such as the Vaccinium spp. prefer soils with high content of organic matter and high moisture retention capacity for successful recruitment (Eriksson & Fröborg, 1996). For these species, conditions for establishment and growth at soil heaps are still rather unsuitable 40 years after soil heap construction. Soil development therefore appears as a major bottleneck for recovery (Rydgren et al., 2013, 2011) of the species composition on alpine soil heaps, emphasizing why knowledge about soil development is crucial for understanding recovery processes (Forbes, Ebersole, & Strandberg, 2001).

4.3 | Time to recovery—which metric to use?

The four categories of metrics used to predict time to recovery in this study give widely different results. The relatively fast recovery of species richness and total cover contrasts the slow recovery of properties of the physical environment and the species composition. Although species richness is the most commonly used metric to assess restoration success (Waldén & Lindborg, 2016), it is not regarded as a core metric for evaluating restoration outcomes (SER, 2004). Our study clearly demonstrates that species richness and total cover may reach pre-disturbance levels and suggest successfully accomplished restoration, whereas the succession of plant species and re-establishment of environmental conditions are still in relatively early stages. In contrast, the plant species composition is an indicator of the basic properties of the ecosystem and should therefore be regarded as ‘the principal obligation of restorationists’ (Clewell & Aronson, 2013). We advocate using species compositional data and soil conditions to predict time-to-recovery, and advise against using species richness and total cover as unique metrics of successful restoration (cf. Piqueray et al., 2011). However, we acknowledge that species richness and other generic variables may be valuable metrics shedding light on the restoration process when restoring the species composition is not feasible (Halpem, Antos, Kothari, & Olson, 2019). For example when ecosystems are considerably degraded, appropriate reference systems do not exist and full recovery will neither be attainable or desirable (McDonald et al., 2016). Another promising development for estimating time-to-recovery may be to use functional-trait based metrics, which may serve as indicators of ecosystem function (cf. Funk et al., 2017) and, therefore, also provide relevant indicators of recovery status.

The ordination-regression based approach (ORBA) used for predicting time to species compositional recovery in this study provides promising results, but further exploration, most notably of later phases of restoration successions, is needed to generalize about the precision of the predictions. Anyway, our results clearly support the view that, to advance restoration ecology, we should move beyond simple biodiversity measures (Brudvig, 2017) and develop methods for predicting time to recovery that take the full plant species composition into account (cf. Urban, 2006).

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AUTHORS’ CONTRIBUTIONS

K.R., I.A., L.N.H. and J.S. collected the data. K.R. and J.P.T. analysed the data; K.R. led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT


ORCID

Knut Rydgren https://orcid.org/0000-0001-8910-2465

REFERENCES


The ecology of recently-deglaciated terrain.


**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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PAPER III

Sulavik, J., Auestad, I., Halvorsen, R., Rydgren, K.

2021.

Assessing recovery of alpine spoil heaps by vascular plant, bryophyte, and lichen functional traits.

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Assessing recovery of alpine spoil heaps by vascular plant, bryophyte, and lichen functional traits

Jan Sulavik1,2,3, Inger Auestad1, Rune Halvorsen2, Knut Rydgren1

Functional traits are linked to ecosystem processes and services and therefore relevant in recovery assessment. However, traits of bryophytes and lichens, important components of many ecosystems, have received less attention than those of vascular plants. We explored the use of functional traits of multiple important organism groups in recovery assessment. We combined data on traits and species composition for vascular plants, bryophytes, and lichens from four alpine spoil heaps and their undisturbed surroundings in western Norway, collected at three time-points spanning more than two decades. We studied changes in community-weighted mean (CWM) trait values and distribution of trait-category optima over time. We analyzed temporal variation in joint functional trait composition using the ordination regression-based approach (ORBA) to predict time to recovery. We observed functional shifts along the successional gradient for all organism groups, e.g. from wind-dispersed propagules shortly after disturbance to vegetative reproduction at later successional stages. Over time, the similarity between dispersal-related traits of vascular plants and bryophytes on the spoil heaps and in their surroundings increased, indicating that propagule influx is important in alpine restoration. The joint functional trait composition of all spoil heaps converged towards that of their surroundings: one spoil heap had recovered 34 years after construction, while the predicted time to recovery for the other three was 59–74 years. Our results indicate that inclusion of multiple organism groups improves trait-based recovery assessments and time-to-recovery predictions. Further development of trait databases is essential for future use of joint functional trait composition in recovery assessment.

Key words: alpine, functional trait composition, multiple organism groups, ordination regression-based approach (ORBA), prediction, recovery assessment, spoil heap, time to recovery

Implications for Practice

• Analysis of joint functional trait composition is recommended for recovery assessments in all types of ecosystems in which multiple organism groups (e.g. vascular plants, bryophytes, and lichens) are important for ecosystem functioning.
• The ordination regression-based approach (ORBA) for assessing progress in ecological restoration is recommended for analysis of data on functional trait composition because it allows for inclusion of multiple organism groups and provides predictions of time to recovery.
• Recovery assessment based on species composition and on functional trait composition are complementary approaches and should be used in parallel to improve decision-making in ecological restoration.

Introduction

Ecosystem degradation caused by human population growth and infrastructure development poses a major threat to future generations, and its mitigation is therefore a global priority (Díaz et al. 2019). Active use of ecological restoration should play a central role in reducing negative anthropogenic impacts on the environment (Palmer et al. 2004). Alpine ecosystems are particularly vulnerable to degradation because the short growing season and slow biological processes prolong the recovery period (Hagen & Evju 2013; Rydgren et al. 2013). Development of hydropower, an energy source with substantial potential in mountainous areas (Kumar et al. 2011), causes major disturbance in alpine ecosystems. Surplus rock material from hydropower development is often deposited on site in spoil heaps, which have a considerable ecological and visual impact.
Assessing recovery by functional trait composition

(Skjerdal & Odland 1995; Rydgren et al. 2011). Spoil heaps have attracted research interest as model ecosystems for alpine restoration (Auestad et al. 2018), and long-term data suitable for assessing progress towards recovery are therefore available (Rydgren et al. 2020). The slow recovery of alpine ecosystems means that the consequences of restoration failure are long lasting, and recovery should therefore be monitored regularly by comparing measurable properties of degraded sites with restoration targets (Nilsson et al. 2016).

Multiple ecosystem properties have been proposed as suitable for use in recovery assessments (Rydgren et al. 2020). They include both univariate properties, e.g. species richness (Ruiz-Jaen & Aide 2005), and multivariate properties, e.g. species composition (Shackelford et al. 2013). Functional traits, i.e. morphological, physiological, or phenological features of individuals that influence their fitness through their effects on reproduction, growth, and survival (Violette et al. 2007), have recently been recognized as useful indicators of ecosystem functioning (de Bello et al. 2010; Funk et al. 2017). Functional traits are directly associated with key ecosystem processes, e.g. primary production (Lavorel & Garnier 2002; Funk et al. 2017), and ecosystem services, e.g. carbon sequestration (de Bello et al. 2010). There is therefore growing interest in functional trait targets in the context of ecological restoration (Laughlin 2014). Functional trait composition is a measurable multivariate ecosystem property that is particularly suitable for recovery assessment because of its direct links with changes in species composition and ecosystem functioning during the restoration (Zirbel et al. 2017).

Over the past two decades, the development of trait databases has facilitated analysis of multiple traits, which is an essential basis for assessment of functional trait composition. Evaluation of restoration success by means of functional trait composition has been explored in several studies (e.g. Pywell et al. 2003; Hedberg et al. 2013; Engst et al. 2016), though generally only vascular plants have been considered. Non-vascular cryptogams (i.e. bryophytes and lichens, cf. Cornelissen et al. 2007) have received considerably less attention in trait research (but see Lang et al. 2009; Hedberg et al. 2013; Roos et al. 2019), despite their important functional roles as essential components of many ecosystems. Bryophytes and lichens constitute a substantial fraction of the biomass at high latitudes and elevations, have complex interactions with vascular plants and other biota, and influence soil temperature, hydrology, and biogeochemistry, e.g. through nitrogen input from symbiotic bacteria (Cornelissen et al. 2007; Asplund & Wardle 2017).

To the best of our knowledge, no previous study has assessed ecosystem recovery through changes in joint functional trait composition of vascular plants, bryophytes, and lichens. All of these organism groups are relevant in a comprehensive assessment of the recovery of alpine ecosystems (Rydgren et al. 2011). However, joint analysis of the functional traits of multiple organism groups is methodologically challenging due to group-specific sets of traits and ecological and morphological differences between organisms (Hedberg et al. 2013). This challenge can be addressed through ordination methods, which are tools for the extraction of gradient structure (Økland 1990; van Son & Halvorsen 2014) applicable to any kind of compositional data, including data on functional trait composition (e.g. Fukami et al. 2005; van Son et al. 2013). If a clear successional gradient can be identified in the compositional data, the distances between restored and reference sites in the ordination space can be analyzed using the novel ordination-regression-based approach (ORBA; Rydgren et al. 2019). Predictions of time to recovery provided by ORBA can be used to assess the restoration process (Rydgren et al. 2019).

In this study, we combined data on species composition for vascular plants, bryophytes, and lichens collected during the restoration of four alpine spoil heaps with database and literature data on functional traits to explore changes in joint functional trait composition. The main aim of our study was to explore the potential of using the joint functional trait composition of multiple organism groups in assessing ecosystem recovery. We sought to answer the following questions:

(1) How does the functional composition of vascular plants, bryophytes, and lichens differ between spoil heaps and their surroundings, and how does it change over time?
(2) Are there any parallels in temporal development in related traits across the three organism groups?
(3) Is ORBA useful for analyzing data on the joint functional trait composition of multiple organism groups for use in assessments of ecosystem recovery?

By answering these questions, we aim to advance the understanding of functional changes occurring during restoration of ecosystems with multiple important organism groups, and thus contribute to the improvement of functional trait-based recovery assessments.

Methods

Study Area

The study was carried out at four alpine spoil-heap sites in western Norway (Figs. S1 & S2, Table S1). The spoil heaps, each covering 2.2–4.1 ha, were established between 1974 and 1984. The bedrock in the study area comprises a mixture of granite, gneiss, phylite, and other metamorphic rocks (NGU 2018), and all spoil heaps were made up of local rock material. Three spoil heaps consisted of blasted rocks and one (Kleådalalen) was made up of fine-grained material from full-profile drilling (Skjerdal & Odland 1995). Spoil heaps differed from their surroundings in soil organic matter content and pH; soil organic matter content was most similar to the surroundings in the Kleådalalen spoil heap, and pH was most similar in the Fossane spoil heap (Rydgren et al. 2020). Annual precipitation in the study area in the period 1971–2000 ranged between approximately 1,500 and 1,900 mm (NVE 2018).

All spoil heaps were seeded with a commercial grass mixture and fertilized with artificial fertilizer, without prior addition of topsoil (Skjerdal & Odland 1995). The Kleådalalen, Svartavatn, and Fossane spoil heaps received additional fertilizer in 2002 and 2007, while Kleådalalen received an extra 6 kg of seeds in 2002 (Rydgren et al. 2011). Thirty Salix shrubs were planted
at Fossane in 2005 (Rydgren et al. 2011). All the study sites are in alpine areas used as summer pasture for free-ranging domestic sheep. No active measures (e.g. fencing) have been taken to exclude sheep from the spoil heaps, and there has been low-intensity grazing at all study sites.

Species Composition Dataset
Species composition was sampled at all four study sites at three time-points: 1990s (1991 for Fossane, Kleådalen, and Svartavatn, 1994 for Øydalen), 2008 and 2015. In the 1990s, only spoil heaps were sampled, while in 2008 and 2015, we sampled both spoil heaps and their undisturbed surroundings; these are classified as two statistical “treatments” in this study. In the 1990s, stratified random sampling along baselines was used instead of sampling in blocks (Skjerdal & Odland 1995). In 2008, we subjectively placed eight blocks (each 5 × 10 m) at each site (Rydgren et al. 2011): five blocks on each spoil heap to cover variation in vegetation and ecological conditions, and three in the surroundings to provide a reference for recovery. Blocks in the surroundings were placed in well-drained locations where hydrological conditions were similar to those on the generally dry spoil heaps (Rydgren et al. 2011). In the 1990s, 10–20 non-permanent plots were placed on each spoil heap (total n = 64). In 2008, we placed three plots randomly within each block on the spoil heaps and in the surroundings (total n = 96), and permanently marked them with metal tubes. Permanent plots were resampled in 2015, except for three plots in one block on the Kleådalen spoil heap, which were buried under newly deposited rock material between 2008 and 2015. All plots measured 0.5 × 0.5 m and were divided into 16 equal-sized subplots. At each time-point, all species (or species aggregates for genera in which species could not be distinguished, see Supplement S1) of vascular plants (n = 107), bryophytes (n = 89), and lichens (n = 48) in each subplot were recorded. Presence in subplots (0–16) represented species abundance. The species composition dataset consisted of 253 plot-by-time combinations, which formed 20 “plot groups,” i.e. combinations of 4 sites × 3 time-points × 2 “treatments” (for the time-point 1990s, only 1 “treatment,” i.e. spoil heap, was sampled).

Trait Dataset
We selected traits for the trait dataset using the following criteria: (1) relevance for growth, reproduction, and survival; (2) relevance for successional and ecosystem processes (Violle et al. 2007); and (3) data availability. We used trait data from databases and other literature sources deriving primarily from Norway, Northern Europe and European alpine regions, i.e. the Alps and the Carpathians. As most traits were categorical and we analyzed community-level averages of trait values, the potential bias due to intraspecific trait variation was considered negligible (cf. Auger & Shipley 2013). Missing species-by-trait combinations (n = 35) were replaced by the median value for the given trait for species from the same genus and alpine vegetation zone present in the trait dataset (n = 15) or present in a database/other literature source (n = 19). For one missing species-by-trait combination without a suitable replacement (n = 1), we used the median value for the trait for all species present in the trait dataset (cf. van Son et al. 2013). We aggregated several originally distinct traits/trait categories into compound traits (for details about trait data, see Table 1).

Vascular plant traits included maximum height, seed mass, specific leaf area, main dispersal mode, lateral spread, and growth form. At our study sites, tall bushes and trees do not reach the potential maximum heights reported in the databases. We therefore used 1 m as an approximation for the local maximum height of all tall shrub species (Juniperus communis, Salix phylicifolia, and S. pentandra), and 2 m for tree species (Betula pubescens).

Bryophyte traits included maximum size, mean spore size (i.e. the mean of maximum and minimum spore size values), frequency of sporophytes, frequency of vegetative propagules, sexuality, and growth form.

Lichen traits included maximum thallus size, mean reproduction type, photobiont association and growth form. No trait database was available for lichens (Branquinho et al. 2015), and we used trait data from multiple sources (Table 1). Maximum thallus size was included because of associations with specific thallus mass, water-holding capacity, and production of secondary compounds (Asplund & Wardle 2017) and because similar (but not fully analogous) traits were used for vascular plants and bryophytes. The other three traits were included because of their relevance for growth, survival, and reproduction (Ellis & Coppins 2006; Koch et al. 2013; Nelson et al. 2015b). The trait dataset consisted of 1,368 species-by-trait combinations.

Statistical Analyses of Changes in Joint Functional Trait Composition
The joint functional trait composition dataset was prepared in two steps. In the first step, we transformed continuous trait data into categorical data to ensure comparability with a priori categorical traits. Values for each continuous trait for all species were sorted in ascending order, and divided into five categories based on sample quintiles (cf. van Son et al. 2013): small, medium-small, medium, medium-large, and large. Each species was subsequently assigned to one category per trait. A priori categorical traits were left untransformed. In the second step, we obtained the joint functional trait composition of each plot-by-time combination by calculating trait-category abundances as the weighted averages of trait categories with species abundances as weights (for details, see Supplement S2). The joint functional trait composition dataset consisted of 70 trait categories × 253 plot-by-time combinations.

Recovery assessment using the ordination regression-based approach (ORBA; Rydgren et al. 2019) required a successional gradient quantified by ordination methods. To quantify the successional gradient, we subjected the joint functional trait composition dataset to multiple parallel ordination (MPO; van Son & Halvorsen 2014), using detrended correspondence analysis (DCA; Hill & Gauch 1980) and global (GNMDS; Minchin 1987) and local (LNMDs; Sibson 1972) non-metric

<table>
<thead>
<tr>
<th>Trait</th>
<th>Relevance</th>
<th>Description (scale)</th>
<th>Units or Categories</th>
<th>Data Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vascular plants</td>
<td></td>
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<tr>
<td>maximum height</td>
<td>G, R, S</td>
<td>cont. (ratio)</td>
<td>m</td>
<td>V8, V10</td>
</tr>
<tr>
<td>seed mass</td>
<td>R</td>
<td>cont. (ratio)</td>
<td>mg</td>
<td>V1, V5, V8, V11, V14</td>
</tr>
<tr>
<td>specific leaf area</td>
<td>G, S</td>
<td>cont. (ratio)</td>
<td>mm²/mg</td>
<td></td>
</tr>
<tr>
<td>main dispersal mode</td>
<td>R</td>
<td>cat. (nominal)</td>
<td></td>
<td></td>
</tr>
<tr>
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<td>G, R</td>
<td>cat. (nominal)</td>
<td>1) small (&lt;0.01 m/year) 2) medium (0.01–0.25 m/year) 3) large (&gt;0.25 m/year) 4) unspecified</td>
<td>V4, V9</td>
</tr>
<tr>
<td>growth form (F, C)</td>
<td>G, S</td>
<td>cat. (nominal)</td>
<td>1) chamaephyte, 2) phanerophyte 3) hemiepiphyte, 4) geophyte 5) therophyte, 6) semi-parasite</td>
<td>V3, V6, V8, V11</td>
</tr>
<tr>
<td>Bryophytes</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>maximum size</td>
<td>G, S</td>
<td>cont. (ratio)</td>
<td>mm</td>
<td></td>
</tr>
<tr>
<td>mean spore size (C)</td>
<td>R</td>
<td>cont. (ratio)</td>
<td>µm</td>
<td></td>
</tr>
<tr>
<td>frequency of sporephore</td>
<td>R</td>
<td>cat. (nominal)</td>
<td>1) very rare, 2) rare, 3) occasional, 4) frequent, 5) abundant</td>
<td></td>
</tr>
<tr>
<td>frequency of vegetative propagules (C)</td>
<td>R</td>
<td>cat. (nominal)</td>
<td>1) N/A, 2) very rare, 3) rare, 4) occasional, 5) frequent</td>
<td></td>
</tr>
<tr>
<td>sexuality</td>
<td>R</td>
<td>cat. (nominal)</td>
<td>1) monoious, 2) dioicios 3) aquatic, 4) turf, 5) solitary, 6) mat</td>
<td></td>
</tr>
<tr>
<td>growth form (F, C)</td>
<td>G, S</td>
<td>cat. (nominal)</td>
<td></td>
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<tr>
<td>Lichens</td>
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<tr>
<td>maximum thallus size</td>
<td>G, S</td>
<td>cont. (ratio)</td>
<td>mm</td>
<td>L2, L3</td>
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<td>R</td>
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<td>L1, L3</td>
</tr>
<tr>
<td>photobiont association</td>
<td>G, S</td>
<td>cat. (nominal)</td>
<td>1) cyanobacteria, 2) green algae, 3) cyanobacteria and green algae (tripartite)</td>
<td>L1, L3</td>
</tr>
<tr>
<td>growth form (C)</td>
<td>G, S</td>
<td>cat. (nominal)</td>
<td>1) crustose, 2) folioise, 3) fruticose</td>
<td>L1, L3</td>
</tr>
</tbody>
</table>

multidimensional scaling (NMDS). The MPO procedure, in which more than one ordination method is applied to the same dataset, facilitated artifact detection and established a consolidated gradient structure (van Son & Halvorsen 2014). We conducted all ordinations using package “vegan” (Oksanen et al. 2017). For details of ordination methods, see Supplement S3. Based on the selection process described in Supplement S3, we chose the two-dimensional LNMDS for interpretation and further analyses.

To confirm that the LNMDS ordination adequately quantified the successional gradient, we used linear mixed-effects models (LMM) as implemented in package “lme4” (Bates et al. 2015). Separate models were obtained for LNMDS axes 1 and 2, using plot scores as response variables. As the fixed effect, we used time-point x “treatment” combinations, i.e. a factor variable with five levels: 1990s spoil heap (1990s surroundings not sampled), 2008 spoil heap, 2008 surroundings, 2015 spoil heap, and 2015 surroundings. To address repeated sampling, i.e. using non-permanent plots in the 1990s and permanent plots in 2008 and 2015, we randomly assigned permanent plot IDs to the non-permanent plots from the same site in the models. Repeated surveys of plots and the hierarchical sampling design (plots nested in blocks nested in study sites) were accounted for by including appropriate random effects in the models. We assessed differences between fixed-effect factor levels by multiple comparisons between all pairs of means using Tukey contrasts, as implemented in the function “glht” of package “multcomp” (Hothorn et al. 2008).

In the multiple comparisons, the LNMDS-axis 1 scores differed significantly between all fixed-effect factor levels, except...
for the comparison between the surroundings in 2008 and 2015 (Fig. S3A). Plot-score means increased along LNMDS-axis 1 from spoil heap plots sampled in the 1990s, via 2008 and 2015 to plots in the surroundings (Fig. S3A). We found no significant differences in plot scores along LNMDS-axis 2 between the spoil heaps and the surroundings (Fig. S3B). We therefore concluded that plot scores along LNMDS-axis 1 adequately represent the successional gradient, which is required for recovery assessment using ORBA.

We used the distance along LNMDS-axis 1 between each spoil-heap plot-by-time combination and the centroid of plots from the corresponding surroundings, referred to as successional distance (Rydgren et al. 2019), to assess the recovery status of a given spoil-heap plot at a given time-point. As the surroundings were not sampled in the 1990s, scores for the surroundings in 2008 were used to estimate successional distances in the 1990s (for justification, see Supplement S4). We defined recovery as reached when the successional distance between the centroid of spoil-heap plots and the centroid of plots from the corresponding surroundings (at a given site and time-point) was lower than or equal to a threshold. As the threshold, we used the mean absolute deviation (MAD), that is, the mean distance of the plots from the surroundings to their centroid in 2015.

We used ORBA with a dynamic reference (Rydgren et al. 2019) to model the recovery process (see Fig. S4). Time to recovery was modeled separately for each spoil-heap site using an asymptotic LMM. We used log-transformed successional distances as the response and spoil-heap age as the fixed effect. Repeated and spatially nested sampling was accounted for by specifying plot nested within block within site as random effects (Rydgren et al. 2020). We calculated 95% confidence intervals (95% CI) around model predictions as ±1.96 × SE of fitted values.

**Variation in Single Traits**

To explore variation in continuous traits (Table 1) over time and between spoil heaps and their surroundings, we first calculated the community-weighted mean (CWM; Garnier et al. 2004) for each trait in each plot-by-time combination. Continuous trait values from the trait dataset were centered and standardized by subtracting the mean and dividing by the SD before calculating the CWM, using species abundances as weights. We applied LMM to each trait and each site with plot-wise CWM values as the response, “plot group” affiliation (i.e., combination of site × time-point × “treatment”) as fixed-effect factor, and plots nested in blocks as random effects. We subsequently assessed differences between “plot groups” within each site by multiple comparisons of means using Tukey contrasts (Hothorn et al. 2008).

Changes in a priori categorical traits (Table 1) along the successional gradient were studied by comparing positions of trait-category optima. These optima were estimated as weighted averages (WA) of LNMDS-axis 1 scores using trait-category abundances as weights, as implemented in function “wascorers” in package “vegan” (Oksanen et al. 2017). We divided the WA values, sorted in ascending order, by sample quintiles into five successional stages (early, early-intermediate, intermediate, intermediate-late, and late). This reflected the successional gradient from “young” spoil heaps to the vegetation of the surroundings. However, as the successional gradient is continuous, any division into discrete stages is arbitrary, serving illustrational purposes only.

All analyses were conducted in R version 3.2.0 (R Core Team 2015). For flowchart of datasets and analyses, see Figure S5.

**Results**

**Variation in Single Traits of Vascular Plants, Bryophytes, and Lichens**

In general, trait community-weighted means (CWMs) of spoil-heap plots became more similar to the surroundings over time (Fig. 1). However, CWMs of several continuous traits differed between spoil heaps, with respect to both change over time and difference from their surroundings.

The specific leaf area (SLA) of vascular plants decreased over time on the spoil heaps towards the level in the surroundings (Fig. 1A). Seed mass on the spoil heaps gradually converged towards that of the surroundings at all sites except Svartavatn, where, however, there was no significant difference between the spoil heap and the surroundings at any time-point. Seed mass increased at Klæadal and Øydalen, and decreased at Fossane and Svartvatin spoil heaps (Fig. 1B). Bryophyte maximum size increased with time on all spoil heaps, becoming more similar to that in the surroundings. However, at Fossane and Øydalen, there were still significant differences between lichen and bryophyte maximum size on the spoil heaps and in their surroundings in 2015 (Fig. 1C, E). Mean bryophyte spore size on the spoil heaps became gradually more similar to that in the surroundings, but the convergence pattern was weaker than for vascular plant seed mass, and differed between sites. In 2015, there was still a significant difference in bryophyte spore size between the spoil heaps and their surroundings at Fossane and Klædal (Fig. 1D).

The distribution of optima of a priori categorical traits along the successional gradient revealed functional shifts (Fig. 2; for details, see Table S2). The early-successional stage was associated with epizoochorous dispersal of vascular plants and abundant production of sporophytes of bryophytes, while anemochorous dispersal and frequent production of sporophytes prevailed in the early-intermediate stage. The importance of vegetative reproduction increased towards the intermediate-successional stage for both vascular plants (lateral spread) and bryophytes (frequency of vegetative propagules). The optimum for lichen reproduction by vegetative propagules (soredia and isidia) was observed in the early-intermediate stage, and for sexual reproduction (by apothecia and perithecia) in the intermediate stage. The intermediate-late stage was characterized by vegetative reproduction by fragmentation of lichens and by infrequent sporophyte production by bryophytes. The late-successional stage was associated with
endozoochorous dispersal of vascular plants and occasional sporophyte production by bryophytes. Hemicryptophytes (forbs, e.g. *Alchemilla alpina*) and turf-forming bryophytes (e.g. *Polytrichum alpinum*) were common at the early-successional stage, while foliose lichens (e.g. *Peltigera* spp.) characterized the early-intermediate stage. Cushion-forming bryophytes (e.g. *Dicranoweisia crispula*) and crustose lichens (e.g. *Psoroma hypnorum*) were common in the intermediate stage. Phanerophytes (trees and tall shrubs, e.g. *Salix lapponum*), mat-forming bryophytes (e.g. *Barbilophozia lycopodioides*), and fruticose lichens (e.g. *Cladonia* spp.) characterized the intermediate-late stage. Chamaephytes (dwarf shrubs, e.g. *Vaccinium myrtillus*) and weft-forming bryophytes (e.g. *Hylocomium splendens*) were common in the late-successional stage.

Recovery Assessment Based on Joint Functional Trait Composition Although the spoil-heap plot scores along LNMDS-axis 1 gradually became more similar to the scores of plots in the surroundings (Fig. 3), they were still significantly different in 2015 (Fig. S3A). Only the Kleådalen spoil heap had reached the recovery threshold in 2015 (Fig. 4B). According to ORBA estimates, the threshold was reached in 2010, 29 years after establishment (95% CI: 24–34 years). For the other three spoil heaps (Fig. 4A,C,D), the predicted time from establishment to recovery varied from 74 years (95% CI: 69–80 years) at Fossane and 65 years (95% CI: 60–72) at Øydalen to 59 years (95% CI: 52–69) at Svartavatn. The uncertainty of predictions expressed as the 95% CI varied from 10 years for Kleådalen to 17 years for Svartavatn (Fig. 4, Table S3).
Figure 2. Association of selected categorical trait optima with successional stages (delimited by quintiles of optima sorted in ascending order). Green: Vegetative reproduction and dispersal; red: Sexual reproduction and dispersal; blue: Growth forms. Abbreviations: (vascular plants) disp., dispersal; lat., lateral; S, small; M, medium; L, large; (bryophytes) veg., vegetative; R, rare; O, occasional; F, frequent; a, abundant; (lichens) frag., fragmentation.

Figure 3. (A)–(D). The two-dimensional LNMDS ordination of the joint functional trait composition dataset, illustrated by separate diagrams for each site (A–D). Study plots are indicated by points, and envelopes show minimum convex hulls of site-wise “plot groups” (i.e. the smallest convex polygons enclosing all plots within a “plot group”). Point symbols (circle vs. square), line types (continuous vs. dashed) n and colors (gray vs. green) distinguish spoil-heap plots from plots in the surroundings. Patterns of polygon hatching show time-point (vertical – 1990s, diagonal – 2008, and horizontal – 2015). “Plot-group” centroids are indicated by “+” for spoil-heap “plot groups” and “*” for those of the surroundings.
Discussion

Variation in Single Traits of Vascular Plants, Bryophytes, and Lichens

Patterns of functional traits of vascular plants observed in this study generally agreed with those reported in other studies of succession (Garnier et al. 2016). There was a gradual decrease in community-weighted mean (CWM) values of specific leaf area (SLA) on the spoil heaps, reflecting a shift from rapid acquisition to increased conservation of resources (Navas et al. 2010). At all sites, the CWM values for seed mass on the spoil heaps either became more similar to those of their surroundings, or were not significantly different from the surroundings to start with (Svartavatn). In the former case, the increasing similarity resulted from a combination of increasing (Kleådalen, Øydalen) and decreasing (Fossane) spoil-heap CWM values over time. A plausible explanation for this paradoxical result is that recovery of the vascular plant community on the spoil heaps is primarily mediated by local seed influx from the surroundings, possibly with dispersal mechanisms varying between sites. The importance of anemochory and epizoochory in early-successional stages highlights the role of wind and animals (e.g. domestic sheep) in local seed dispersal. Plant establishment on the spoil heaps may thus be limited by the availability of suitable microsites rather than by seed availability (Rydgren et al. 2011), as might be expected in an open, wind-exposed alpine landscape (Erschbamer et al. 2008). The sequence of optima for vascular plant growth forms along the successional gradient, and the increasing abundance of tree and (dwarf) shrub species that are dominant in the surroundings, correspond to the general successional pattern (Garnier et al. 2016).

The significant differences between bryophyte and lichen maximum size on the spoil heaps and in the surroundings at Fossane and Øydalen suggest that the bryophyte and lichen communities on these spoil heaps are not yet functionally restored. The abundant sporophyte production and smaller spores observed early in early-successional stages are consistent with the inverse relationship between spore mass and dispersal potential reported by During (1992). However, the pattern of convergence is weaker for spore mass than for seed mass, indicating that sexual reproduction plays a smaller role in bryophytes than in vascular plants (During 1992). The difference between mean spore size on the Kleådalen spoil heap, which is close to functional recovery, and in its surroundings, may reflect the increasing importance of vegetative reproduction as succession proceeds. This may result from a trade-off between the production of sporophytes and of vegetative propagules (Austrheim et al. 2005b). The sequence of bryophyte growth form optima along the successional gradient, ending in wefts, fits with patterns typical of the establishment of closed vegetation during primary succession (Gimingham & Birse 1957).

Like Nelson et al. (2015a), we found that lichen species reproducing by soredia prevailed in the early-successional stage...
from the sequence typical of succession, i.e. crustose functional trait composition. Nevertheless, the decrease over time in successional rates observed at all sites shows that this general property of succession reveals that the two metrics provide somewhat different signals about ecosystem recovery at the study sites. This is interesting, as the two metrics are closely related. For example, based on the mass ratio hypothesis (Grime 1998; Garnier et al. 2004), species abundances are used in calculating functional trait CWMs, which represent functional trait composition. There are examples indicating that recovery assessment based on functional trait composition alone may be misleading, e.g. if invasive alien species are present in the restored area (Laughlin et al. 2017). However, recovery assessment based on species composition alone may fail to reveal situations where a restored ecosystem has achieved functional similarity with the reference, but with a different species composition (Caldotte et al. 2011; Engst et al. 2016). We therefore recommend the use of functional trait composition and species composition in parallel, and suggest that the two approaches should be considered as complementary (cf. Engst et al. 2016). In alpine and other ecosystems where bryophytes and lichens are fundamental elements (Cornelissen et al. 2007), we recommend using joint functional trait composition rather than vascular plant functional trait composition alone for recovery assessments.

Recovery Assessment Based on Joint Functional Trait Composition

The joint functional trait composition of vascular plants, bryophytes, and lichens on all spoil heaps converged towards that of their surroundings, although at different speeds at different sites. Similar patterns were found for the temporal dynamics of total cover, species richness, and physical environment on the spoil heaps (Rydgren et al. 2020). The fact that the ordination regression-based approach (ORBA) provides ecologically plausible results for joint functional trait compositional data suggests that it is an appropriate analytical method for such data.

Only one of the spoil heaps studied, Kleådalen, had reached the recovery threshold for functional trait composition by 2015, the last time-point. A likely explanation for the rapid recovery at Kleådalen is that local soil characteristics, especially the more fine-grained topsoil, facilitated plant establishment and accumulation of organic matter (Rydgren et al. 2013; Rydgren et al. 2020). In addition, Kleådalen is the study site at the lowest altitude, and the longer growing season may encourage the establishment of vegetation. Joint functional trait composition at Kleådalen shows an interesting late-successional pattern, with successional distances apparently stabilizing around the recovery threshold. However, more data will be needed to follow post-recovery developments, and to identify the causes of any deviations from the current ORBA models, e.g. persistent differences in environmental conditions between the spoil heaps and their surroundings. Nevertheless, the decrease over time in successional rates observed at all sites shows that this general property of succession (Rydgren et al. 2019) also applies to successional gradients in functional trait composition.

Joint Functional Trait Composition: Relationship With Species Composition and Use in Recovery Assessment

We observed faster recovery in functional trait composition than in species composition at the same study sites (Rydgren et al. 2020), in accordance with Engst et al. (2016). Furthermore, ordering the sites by time to recovery gives different results for the two metrics. For example, the Svartavatn spoil heap was found to show the second fastest recovery of functional trait composition, but the slowest recovery of species composition (Rydgren et al. 2020).

Thus, a comparison between our results for functional traits composition and those of Rydgren et al. (2020) for species composition reveals that the two metrics provide somewhat different signals about ecosystem recovery at the study sites. This is interesting, as the two metrics are closely related. For example, based on the mass ratio hypothesis (Grime 1998; Garnier et al. 2004), species abundances are used in calculating functional trait CWMs, which represent functional trait composition. There are examples indicating that recovery assessment based on functional trait composition alone may be misleading, e.g. if invasive alien species are present in the restored area (Laughlin et al. 2017). However, recovery assessment based on species composition alone may fail to reveal situations where a restored ecosystem has achieved functional similarity with the reference, but with a different species composition (Caldotte et al. 2011; Engst et al. 2016). We therefore recommend the use of functional trait composition and species composition in parallel, and suggest that the two approaches should be considered as complementary (cf. Engst et al. 2016). In alpine and other ecosystems where bryophytes and lichens are fundamental elements (Cornelissen et al. 2007), we recommend using joint functional trait composition rather than vascular plant functional trait composition alone for recovery assessments.

Time-to-recovery predictions by ORBA for our study sites showed similar degrees of uncertainty, expressed as 95% CI of model estimates, for functional trait composition (this study) and species composition (Rydgren et al. 2020). Laughlin et al. (2017) found functional trait-based metrics to be less variable and more predictable than species composition-based metrics for a variety of restoration treatments, while Abella et al. (2018) questioned the existence of a general hierarchy of predictability. Thus, the two types of metrics should be considered as complementary for predictions of time to recovery as well as for recovery assessments. Predictions based on both functional trait composition and species composition provide a more reliable basis for making decisions on restoration than predictions based on either metric alone. If there is substantial disagreement between recovery assessments based on the two metrics, the results should be discussed in the context of specific restoration goals, such as ecosystem functioning or conservation of particular species or species groups.

Outlook for the Functional Trait-Based Approach to Recovery Assessment

It is only possible to use joint functional trait composition in recovery assessments if reliable, relevant trait data can be obtained from trait databases. While the number of vascular plant species and traits covered by available databases has increased strongly in recent years, information about intraspecific (including regional) variation in traits remains sparse (Moran et al. 2016). This variation may be substantial (de Bello et al. 2011; Asplund & Wardle 2017). However, interspecific trait variation generally dominates in the presence of a strong gradient (Auger & Shipley 2013), such as a successional...


Assessing recovery by functional trait composition


Nelson PR, McCune B, Swanson DK (2015b) Lichen traits and species as indicators of vegetation and environment. The Bryologist 118:252–263


Assessing recovery by functional trait composition


Supporting Information

The following information may be found in the online version of this article:

Table S1. Overview of studied spoil heaps.
Table S2. Optima for categorical traits as WA-scores at LNMDS-axis 1.
Table S3. Predicted time to recovery (model estimate and 95% CI) in years since establishment (i.e. spoil heap age).
Figure S1. Map of the study area and locations of the four study sites in western Norway
Figure S2. The four studied spoil heap sites.
Figure S3. Multiple comparisons of means of LNMDS-axis scores
Figure S4. Illustration of the data input for regression step in ordination regression-based approach (ORBA)
Figure S5. Flowchart of datasets and analyses
Supplement S1. Species aggregates
Supplement S2. Preparation of the joint functional trait composition dataset
Supplement S3. Ordinations – justification and settings
Supplement S4. Successional distances in the 1990s – justification

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van Son TC, Halvorsen R (2014) Multiple parallel ordinations: the importance of choice of ordination method and weighting of species abundance data. Sommerfeltia 37:37