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

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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, Llambí, 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 Philippi, 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, & Njøs, 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_e and re-analysed with respect to the species composition s times after disturbance (plots $j = 1, ..., n$; time points $t = 1, ..., s$, corresponding to recordings of species made v_t years after disturbance). The matrix $\mathbf{M}$ thus contains $n \cdot s$ columns, one for each restoration plot × time (RP × T) combination jt. 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 $u \cdot s$ 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 $n \cdot s + u$ 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 (Økland, 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 × time (RP × T) combination jt, the successional distance $d_{jt,0}$, that is the distance along the successional gradient, from the position x_0 that represents the reference to x_{jt}, is calculated (Figure 1a; see Appendix S1 for computer code):

$$d_{jt,0} = x_0 - x_{jt} \tag{1}$$

The position x_0 may be the centroid of observations in $\mathbf{Q}$. Thereafter, model $d_{jt,0}$ as a function of v_t, 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_L—obtained as a linear model with untransformed response variable (Figure 1b). According to M_L, the composition of restoration plots changes at a constant rate so that these plots first approach the reference, then reach recovery ($d_{jt,0} = 0$) and thereafter depart from the reference again ($d_{jt,0} < 0$). (ii) The asymptotic model M_A—obtained as a linear model with logarithmically transformed response variable (Figure 1b). Predictions from M_A approach $d_{jt,0} = 0$ 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 TR_L and TR_A—time to recovery predicted by use of the linear response model M_L and the asymptotic model M_A, respectively—are obtained by a two-step procedure: (a) Define a threshold value for the successional distance $d_{jt,0}$ at which restoration is regarded as successful. (b) The predictor TR is the value of v_t, the predicted number of years since disturbance which, according to the model in question, corresponds to $d_{jt,0}$. Threshold values may be defined in at least three different ways: (a) The reference itself that is successional distance $d_{jt,0} = 0$ (Figure 1a). (b) A fixed successional distance c from the threshold, that is, $d_{jt,0} = c$. (c) A "statistical threshold" s 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 value difference from the mean, or quantiles. 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 $d_{jt,0} = 0$. 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 TR_{L0}, TR_{Ls}, and TR_{Ac} and TR_{As}, 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 TR_{As+1}. One plausible choice of fixed successional distance c is 0.01 from the threshold, which we will denote $TR_{Ac+0.01}$.

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, Økland, & Hestmark, 2004). The dataset comprises records of the species composition of 80 permanently marked plots, each 0.25 m^2. A nested sampling design was used, with 10
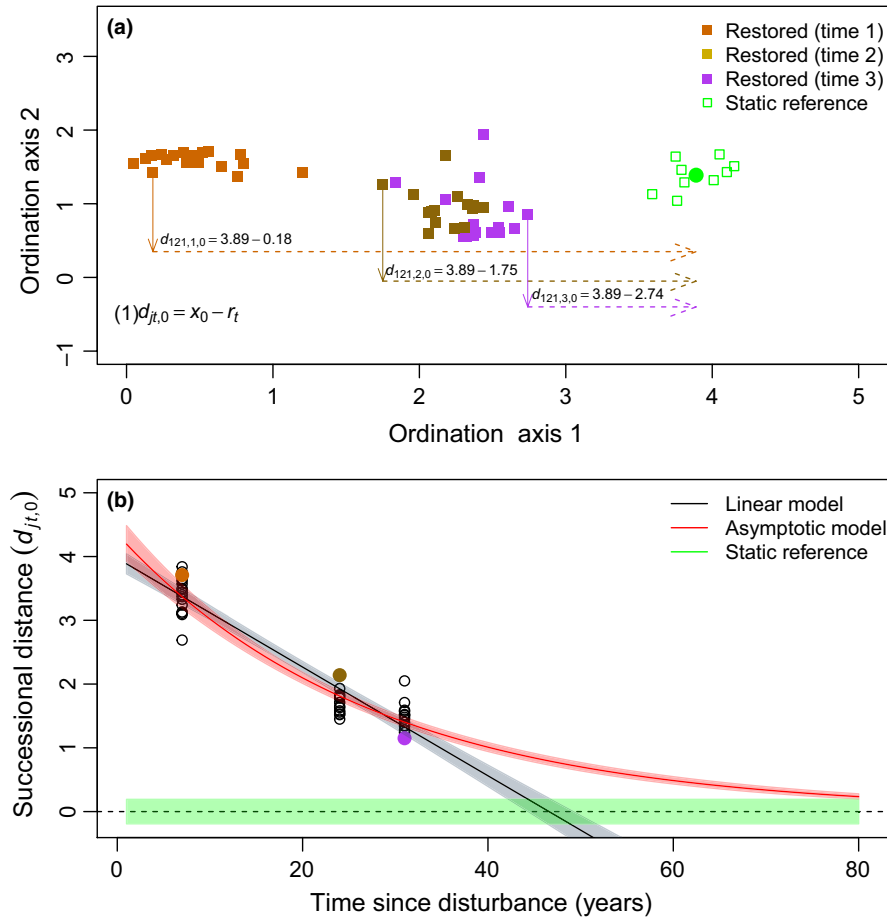
FIGURE 1 Graphic illustration of the rationale behind the new approach for predicting time to recovery, exemplified by a dataset with restoration plots analysed at three different time points using a static reference with the centroid as large green circle (a) Calculation of successional distance, obtained by Equation (1), along the first ordination axis, which represents the successional gradient, between restored plots and the centroid of the reference plots. (b) Two models for successional distance as a function of time since disturbance; a linear model shown by the black line with grey 95% confidence interval and an asymptotic (nonlinear) model shown by the red line with red confidence interval. The three points of which we demonstrated the calculation of successional distance in (a) is shown as closed circles in their respective colours. Predicted time to recovery occurs when the modelled response reaches the confidence limit around the restoration target, indicated by the green band (of breadth +1 SD off the centroid of reference plot scores) or, alternatively, intersects or approaches the restoration target itself ($y = 0$)

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 $\mathbf{MQ_b}$ 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 $\mathbf{MQ_b}$ 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 τ 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 $|\tau| > 0.7$ and both were confidently interpreted as

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 $d_{jt,0}$ 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, $t = 1, ..., 9$. For one plot, the value $d_{jt,0} = 0.000$ (obtained for T1 disturbance in year $t = 9$) was replaced by $d_{jt,0} = 0.001$ 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_L 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 $\ln(d_{jt,0})$ 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 $d_{jt,0}$ increased (for 2 years with GNMDS and 3–6 years with DCA), before starting to decrease gradually. The maximum single-plot $d_{jt,0}$ 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 they, 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 $d_{jt,0}$ values within +1 SD off the centroid of reference plot along the successional gradient (Figure 3).

The linear and asymptotic models M_L and M_A of successional distance $d_{jt,0}$, 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
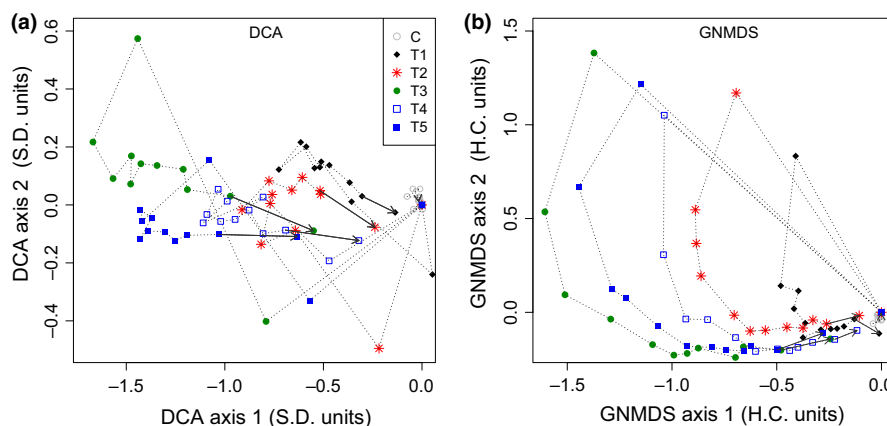

FIGURE 2 Ordination of the full example dataset (69 taxa × 1,031 plots): trajectories of restoration plots and control plots in (a) detrended correspondence analysis (DCA) and (b) global nonmetric multidimensional scaling (GNMDS) ordination spaces, illustrated by mean resultant displacement of each combination of treatment (T1–T5) and control (C), and year since disturbance. Ordination axes 1 and 2 are shown. Successive years for the same treatment are connected by broken lines except for the two last years of observation ($t = 12$ and $t = 18$), which are connected by solid lines ending with an arrow
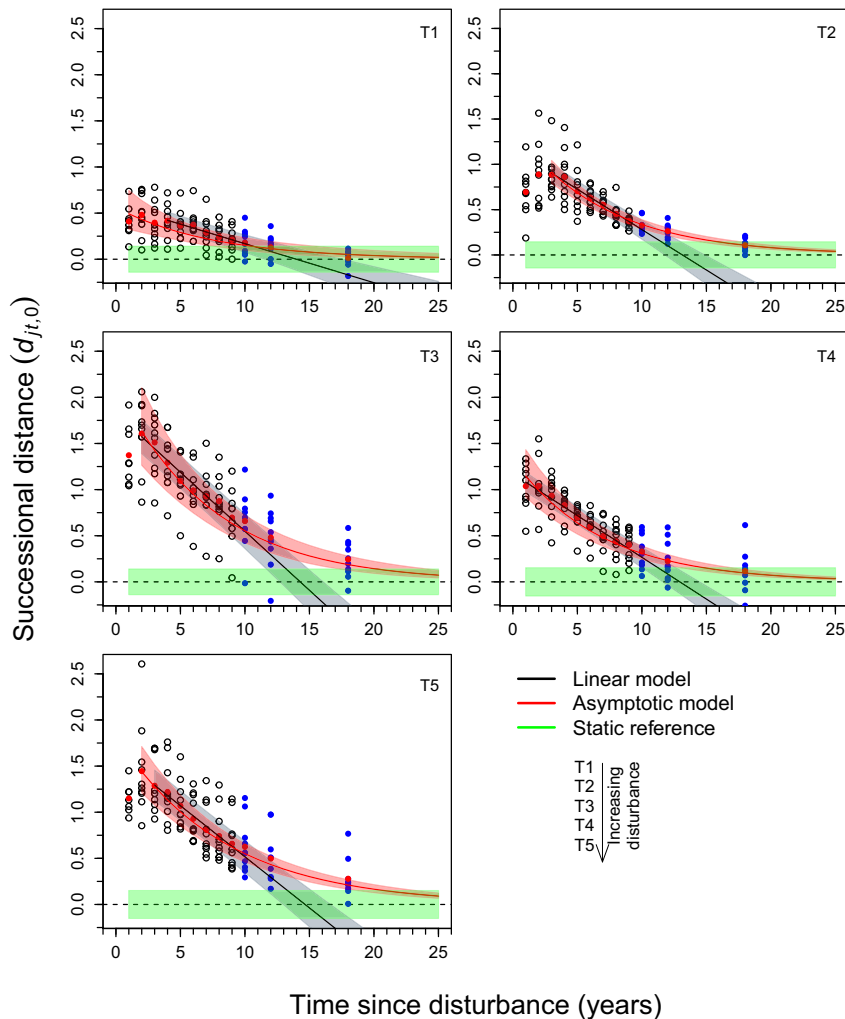
FIGURE 3 The example dataset: Best linear (black lines) and asymptotic models (red lines) for successional distance (distance along the successional gradient represented by the first global nonmetric multidimensional scaling (GNMDS) ordination axis) as a function of time since disturbance, with 95% confidence 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

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_{L0} predictions for time to full recovery (5 treatments × 2 ordination methods) ranged between 13 and 29 years, whereas the 10 TR_{Ls+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 $TR_{Ac+0.01}$ and TR_{As+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).

5 | DISCUSSION

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

TABLE 1 Model evaluation results based upon the detrended correspondence analysis (DCA) and the global nonmetric multidimensional scaling (GNMDS) ordinations: difference in successional distance $d_{jt,0}$ between the mean plot position 18 years after disturbance for the five treatments (T1–T5) and the corresponding predictions from the linear and asymptotic models M_L and M_A

Treatment	DCA		GNMDS	
	M_L	M_A	M_L	M_A
T1	0.44	0.03	0.18	−0.04
T2	0.59	0.12	0.54	0.00
T3	−0.10	−0.24	0.72	0.06
T4	0.09	−0.07	0.58	0.02
T5	−0.05	−0.10	0.65	0.04

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.

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_A predictors that are based on an asymptotic model (M_A), as best choices. The minimum data requirement for M_A 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, & Austad, 2016; Kirmer, Rydgren, & Tischew, 2018). In succession, 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, & Martínez-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, & Klinger, 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, & Řehounková, 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.

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AUTHORS' CONTRIBUTIONS

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DATA ACCESSIBILITY

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

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