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Functional diversity analysis helps to identify filters affecting community assembly after fen restoration by top-soil removal and hay transfer

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ABSTRACT

Top-soil removal followed by species introduction through hay transfer has appeared as a method to restore drained fens. This method addresses abiotic constraints by restoring hydrology and nutrient status, and biotic constraints by removing an unwanted seed bank and counteracting dispersal-limitation. Restoration works by altering environmental filters. Knowledge about the restoration actions effect on functional traits is necessary to understand which types of species may establish. In this study we analyse which factors in top-soil removal followed by hay transfer influence selection and composition of functional traits. Top-soil removal followed by hay transfer from reference sites was conducted at two sites in the Całowanie fen, 33 km SE of Warsaw, Poland. Species and abundance data were recorded for three consecutive years. These data, combined with data on functional traits were used to analyse the effect of the restoration actions on four functional diversity-indices and the community weighted mean of functional traits. Our results reveal a strong habitat filter in the restoration site that follows an elevation gradient. At low elevation this filter selects low values of autochory and specific leaf area and high values of clonal lateral spread, Ellenberg moisture values, and dispersal through hydrochory. The transferred hay differs in trait characteristics compared to the reference site vegetation by having species of higher specific leaf area, lower Ellenberg moisture value and lower dispersal by autochory and hydrochory. The result presented here has three important implications for fen restoration. First, the difference in trait-characteristics between the transferred hay and the reference site it was harvested from limits the restoration potential. Second, since for several fen species important functional traits are filtered along an elevation-gradient, careful planning regarding depth of top-soil removal is needed. Finally the results illustrate how a functional analysis can be used to detect environmental filters acting during ecological restoration.

Introduction

Ecological restoration has a high failure rate (Benayas et al. 2009). The failure to restore a community is many times caused by one or more environmental filters that constrain the restored community from approaching the state of the reference community (Myers and Harms 2009). These filters can be abiotic habitat filters, (e.g. flooding and anoxia), biotic filters (e.g. competition) or dispersal filters (Keddy 1992). In order to improve restoration outcomes, it is important to understand what constrains the restored ecosystem from reaching the state of the reference system. While traditional evaluations of success, based on species identity and abundance did not provide us with an ecological explanation to why certain species successfully establish at the restoration site, while others do not, the advent of functional diversity to community ecology has provided a promising tool for such an analysis (Funk et al. 2008; Hedberg and Kotowski 2010; Hedberg et al. 2013). A classical species identity-focused analysis provides information on how restoration measures or environmental factors affect certain species or communities. However, it does not provide an ecological explanation for these changes, and the results risk being limited by the geographic boundary of the species studied. Switching focus from species to traits that are relevant for the studied ecosystem adds an ecological explanation to observed changes in species composition caused by restoration actions. Ecological restoration is at its very base a method to assist community recovery by changing environmental filters (abiotic, biotic or dispersal) that control the species composition (Myers and Harms 2009). By analysing occurrence of specific traits in a community we can detect environmental filters that operate on them (Diaz et al. 2007),

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whereas functional diversity indices (e.g. Mason et al. 2005) can help to assess the relative importance of habitat versus competition filtering (e.g. Kotowski et al. 2010). Yet, despite the advance of functional ecology, its tools are little used in ecological restoration. In this study we employ them to analyse filtering mechanisms operating during early stages of rich fen restoration by top-soil removal and hay-transfer. Specifically, we want to test whether habitat or competition filtering prevails during restoration.

In riparian fen vegetation, both habitat factors (soil anoxia) and competition for light have been identified as strong environmental filters (Kotowski and van Diggelen 2004; Kotowski et al. 2010), while the dispersal capacity of target species has been found to additionally constrain the restoration process (Klimkowska et al. 2007). An increasingly applied method to restore the hydrology and low trophic status of drained fens, and at the same time counteract dispersal limitation of target species, is to remove the degraded mineralised peat and introduce target species from reference-sites via hay-transfer (Klimkowska et al. 2010a; Rasran et al. 2007). From a filter perspective, top-soil removal should reduce competition compared to degraded sites by removing excess N and P and eliminating potential competitors from the seed bank and standing vegetation. Top-soil removal simultaneously exposes water-saturated peat soils, which increases the abiotic filter of anoxia (habitat filtering sensu Cornwell et al. 2006). Anoxia can further decrease competition filtering by lowering the growth rate of all species during seedling recruitment (Kotowski et al. 2010). Therefore, we hypothesise that competition filtering is lowest in sites, where degraded peat is removed down to the saturated layer, where habitat filtering dominates. This balance is supposed to change in favour of competition filtering if top-soil removal was shallower and an aerated layer remained. In heavily degraded fen sites, such as our area prior to restoration as well as areas at our site that were not restored, we expect that functional diversity is generally low due to habitat filtering by other stress factors, such as draught and K limitation (Van Duren et al. 1997). The second measure, the transfer of hay, is specifically applied to combat the dispersal limitation of the target species. We therefore hypothesise that it will increase functional diversity (as more species can potentially establish). Alternatively, however, it could decrease diversity by increasing competition filtering, when competitive species are introduced with hay.

We aim to test the above predictions with the analysis of community weighted means (CWM) (Garnier et al. 2004, 2007) of the functional traits, which are supposed to determine species response to the analysed environmental filters, and their functional diversity indices proposed by Mason et al. (2005) and Laliberté and Legendre (2010).

The four functional diversity indices we use measure different aspects of functional diversity. Functional richness (FRic) measures the size of the filled niche space. For a single trait it is the difference between the maximum and minimum value of the trait, whereas for two or more traits it is the minimum area (two traits) or volume (more than two traits) that covers all trait values (Mason et al. 2005; Villéger et al. 2008). Functional evenness (FEve) is a measure of how evenly the biomass of a community is distributed within a niche-space. Assuming evenly distributed resources, a low FEve indicates, that some parts of the niche space are under-utilised, which increases risk of invasion of new species (Mason et al. 2005). Functional divergence (FDiv) measures the distribution of abundance within a niche-space. For a single trait, high FDiv occurs when the most abundant species have trait-values on the extreme ends of the trait-axis (Mason et al. 2005; Villéger et al. 2008). In a multivariate context, FDiv is measured as the average distance of each species to the centre of gravity of the trait-space (Villéger et al. 2008). Functional dispersion (FDis) is similar to FDiv in that it measures dispersion in a multivariate trait-space as the average distance of each species to a centre-point. The two indices differ in that FDiv measures the average distance of each species to the centre of gravity of the trait space, whereas FDis measures the average distance of each species to the centroid of all species. FDis is independent of the convex hull concept, which makes it less sensitive to outliers compared to the other three functional diversity indices (Laliberté and Legendre 2010). Community weighted mean (CWM) is a measure of the dominant trait-value in a community (e.g. Garnier et al. 2004, 2007; Diaz et al. 2007).

Based on the structure and functioning of the functional diversity indices, we assume that low habitat filtering can be detected by high values of FRic and FDis when tested against a restoration action or an abiotic variable associated with the restoration action. Increased competition should be expressed in increased FEve and FDiv. The functional analysis is used as a complement to the classical analysis that presents the results in averages of species richness, as well as ordination techniques for the restored, reference and control communities.

Methods

Study site

Całowanie fen (52° 0′41.80″N, 21°21′11.26″E), 33 km SE of Warsaw, Poland is a soligenous former rich fen in the Wisła ice-marginal valley (Oświt and Dembek 2001; Żurek 1990). The average temperature for Jun–Aug is 17.5 °C, and the average temperature for Dec–Feb is −2.5 °C, while the average annual rainfall is 555 mm (Olszewski 2003). Due to degradation caused by drainage, the site has a large seasonal groundwater level variation (Klimkowska et al. 2010a). Prior to the restoration, the degraded parts where top-soil removal was carried out, had vegetation dominated by *Urtica dioica* L., *Festuca rubra* L., *Anthoxanthum odoratum* L. and *Salix cinerea* L.

Experimental design

Two areas of 0.5 ha each were restored through top-soil removal followed by hay-transfer. These sites are hereafter referred to as the restoration-sites. The top-soil was removed in December 2008 with an average depth of 60 cm. The surface of the restoration sites was not levelled, and both restoration sites had a significant within site variation in elevation. This elevation gradient, connected with a gradient in moisture (or flooding depth), was used as a predicting abiotic factor in our analyses.

In spring and early summer of 2009 two nearby donor meadows (hereafter referred to as reference sites) were monitored for species presence and abundance. One reference site was mown in August 2009 and the other was mown in September 2009. Samples of the mown hay from both reference sites were collected for a species content analysis. The species content analysis was done by incubating eight trays with hay spread over commercial peat-soil (with a control for species content in the soil) in a greenhouse and a climate-chamber and identifying emerging seedlings, whose abundance was estimated using the Londo scales (Londo 1976). After mowing, the restoration sites were divided into 15 m wide belts, and hay was spread evenly on every second belt. Within each belt two 2 m × 2 m permanent plots were placed out.

Control plots (five with – and five without hay transfer) were placed on degraded sites (hereafter referred to as the control sites) adjacent to each of the two restoration site. Five plots were placed at each of the two reference sites as well. Monitoring of the full control plots (control-plots without hay-transfer) and the reference sites started one year later than other plots. Due to boars (*Sus scrofa* L.) destroying 10 plots in one control site (five plots with hay transfer