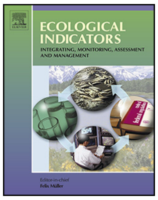
Ecological Indicators xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Dispersal traits as indicators of vegetation dynamics in long-term old-field succession

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ARTICLE INFO

Article history:
Received 30 April 2015
Received in revised form
30 September 2015
Accepted 2 October 2015

Keywords:
Anemochory ranking index
Community assembly
Epizoochory ranking index
Functional traits
Long-term ecological research

ABSTRACT

Succession is a key ecological process that supports our understanding of community assembly and biotic interactions. Dispersal potential and dispersal strategies, such as wind- or animal-dispersal, have been assumed to be highly relevant for the success of plant species during succession. However, research yielded varying results on changes in dispersal modes between successional stages. Here, we test the hypotheses that (a) vascular plant species that use a number of dispersal modes dominate in early stages of succession while species specialized on one/few dispersal modes increase in abundance towards later stages of succession; (b) species well adapted to wind-dispersal (anemochory) will peak in abundance in early successional stages and (c) species well adapted to adhesive dispersal (epizoochory) will increase with proceeding succession. We test these hypotheses in four sites within agriculturally dominated landscapes in Germany. Agricultural use in these sites was abandoned 20–28 years ago, leaving them to secondary succession. Sites have been monitored for plant biodiversity ever since. We analyze changes in plant species richness and abundance, number of dispersal modes and two ranking indices for wind- and adhesive dispersal by applying generalized linear mixed-effect models. We used both abundance-weighted and unweighted dispersal traits in order to gain a comprehensive picture of successional developments. Hypothesis (a) was supported by unweighted but not abundance-weighted data. Anemochory showed no consistent changes across sites. In contrast, epizoochory (especially when not weighted by abundance) turned out to be an indicator of the transition from early to mid-successional stages. It increased for the first 9–16 years of succession but declined afterwards. Species richness showed an opposing pattern, while species abundance increased asymptotically. We suggest that plant-animal interactions play a key role in mediating these processes: By importing seeds of highly competitive plant species, animals are likely to promote the increasing abundance of a few dominant, highly epizoochorous species. These species outcompete weak competitors and species richness decreases. However, animals should as well promote the subsequent increase of species richness by disturbing the sites and creating small open patches. These patches are colonized by weaker competitors that are not necessarily dispersed by animals. The changes in the presence of epizoochorous species indicate the importance of plant traits and related plant–animal interactions in the succession of plant communities.

1. Introduction

Succession is a key ecological process that allows species to establish in “empty”, open habitats. Revealing the mechanisms underlying succession helps understanding community assembly (Cook et al., 2005; Purschke et al., 2013) not only in natural contexts, such as e.g., in primary succession after land-slides, but also in human-dominated contexts, e.g., the secondary succession of spontaneous vegetation after the abandonment of agricultural sites.

Succession has often been seen as a directional process that can be separated into several stages, approaching climax. This long-standing view however, has been challenged and recent review work suggests that there is neither a common mechanism for successional developments, nor a pre-defined climax (Christensen, 2014). Rather, succession seems to be highly context-dependent, depending e.g., on environmental conditions, regional species pools or interactions among species. The direction and speed of succession can be highly variable. Nevertheless, functional ecology identified plant traits that are typically dominant in certain stages of succession: Early successional stages were found to be usually dominated by short-lived herbaceous ruderal species (Grime, 1979) that reproduce by seeds (i.e., therophytes), while later successional stages are usually dominated by highly competitive, long-lived

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http://dx.doi.org/10.1016/j.ecolind.2015.10.003
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species (e.g., Debussche et al., 1996; Prévosto et al., 2011). Generally, the ability of species to colonize open sites should depend on their traits (environmental filtering; cf. Lavorel and Garnier, 2002; Williams et al., 2009). Therefore, traits can reveal mechanisms that govern successional developments as well as underlying reasons of species success or failure in anthropogenic landscapes (e.g., Lososová et al., 2006).

When identifying traits relevant for succession, we have to consider the different steps species have to take: (i) if not already present in the soil seed bank, species have to disperse to an open site; (ii) they have to establish a population in the face of prevailing environmental conditions and competing species, and (iii) they have to be accessible for both their pollinators and dispersal vectors in order to reproduce and successfully colonize other sites. Especially in today's fragmented landscapes, dispersal filters are assumed to be highly relevant for succession (Purschke et al., 2013), and to be key in determining species composition in early successional stages (Latzel et al., 2011). Indeed, early successional stages have been associated with high species' potential of long-distance dispersal and with high frequency of wind-dispersed species (Dolle et al., 2008; Rehounkova and Prach, 2010), while plant species dispersed by animals are supposed to dominate in later successional stages (Martin-Sanz et al., 2015). However, in human-dominated habitats including abandoned agricultural sites in the Czech Republic, wind-dispersal was not associated with species dominating in succession (Prach and Pyšek, 1999) and was found to slightly increase during succession. This was in contrast to expectations (Latzel et al., 2011). Moreover, the increase of animal-dispersal with proceeding succession is mostly related to dispersal after digestion (endozoochory; e.g., Debussche and Isenmann, 1994; Dolle et al., 2008), as sites become more attractive to animals with increasing vegetation cover (Reif et al., 2013). Results on adhesive dispersal (epizoochory) are scarce and not coherent: Prach and Pyšek (1999) showed that epizoochory is weakly associated with species dominating in mid or late succession; Latzel et al. (2011) showed that epizoochory first increases and then decreases during succession but did not explain the pattern; Purschke et al. (2013) identified epizoochory as an indicator of early successional stages. However, Purschke et al. (2013) did not use temporal data and included sites still used for grazing in an arable-to-grassland chronosequence.

A range of plant species is able to disperse by a multitude of dispersal modes (an example being *Rumex acetosella* L. s.l. – a species whose seeds have been shown to be dispersed by wind, water, humans or animals (after digestion, adhesive or scatter-hoarding); cf. LEDA-traitbase; Kleyer et al., 2008; http://www.leda-traitbase.org). With respect to dispersal, such plant species are generalists and should have better dispersal potential than specialized species that use one dispersal mode only. Theory predicts that generalists will dominate over specialists if costs for establishment are low (Bersini, 2008). During succession, costs should increase because competition among species increases with time (Dinnage, 2009). Also, according to classical ecological theory (reviewed in Cavender-Bares et al., 2009), environmental filtering should dominate in early successional stages and select for functionally similar species; in later stages with increasing competition, species should become less similar because the specialization into different niches will decrease the pressure of competition. Indeed, specialists have been found to replace generalists in a chronosequence of restored semi-natural grasslands in Belgium (Helsen et al., 2013) and to increase over time in secondary succession in old-fields in Hungary (Csecserits and Redei, 2001).

In summary, although it is generally assumed that dispersal traits are highly relevant for succession, there is no consensus about the development of dispersal traits within successional plant communities.

Here, we test whether common patterns exist in the successional development of dispersal traits. From literature, we derive the expectations (Fig. 1) that

(a) vascular plant species that use a number of dispersal modes dominate in early stages of succession while species specialized on one/few dispersal modes increase in abundance towards later stages of succession (based on the findings by Csecserits and Redei, 2001; Bersini, 2008; Dinnage, 2009; Helsen et al., 2013);
(b) species well adapted to wind-dispersal will peak in abundance in early successional stages (as found by e.g., Dolle et al., 2008);
(c) species well adapted to adhesive dispersal (epizoochory) will increase with proceeding succession (as suggested by the studies of Prach and Pyšek (1999) and Martin-Sanz et al. (2015)).

We test these hypotheses in four research sites within agriculturally dominated landscapes, where agriculture was abandoned 20–28 years ago (secondary succession). We test both abundance-weighted and unweighted dispersal traits (i) in order to gain a comprehensive picture of successional developments and (ii) because other studies showed that environmental parameters predict some trait values or Ellenberg indicator values better when weighted by abundance but others when not weighted by abundance (Häring et al., 2013; Carpenter and Goodenough, 2014; Pakeman et al., 2009).

We discuss whether dispersal traits mark transitions from one successional stage to the next and we discuss the mechanisms governing changes in dispersal traits over time. At our study sites, progressive succession resulted in species rich plant assemblages within a relatively short time span and therefore provides ideal means for studying patterns and processes of community assembly (Dinnage, 2009).

2. Materials and methods

2.1. Study sites and species data

All four study sites are located in Germany on former arable land and were intensively used for agricultural crops (maize, cereals and clover) until the date of abandonment. Three sites (Bad Lauchstaedt, Gimritz and Zoeberitz) are located in the central German lowlands ("Mitteldeutsche Tiefebene"), close to the city of Halle (Saale) and are included in the long-term ecological research network LTER. One site (Bayreuth) is located in the south-east German uplands, close to the city of Bayreuth and is not included in the LTER-network so far. All four sites are located in an intensively used agricultural landscape, in a distance of 20 m to 1 km from the next settlement or building. The surrounding agricultural landscape is either dominated by crop farming (Zoeberitz), meadow farming (Bayreuth) or a mixture of both (Bad Lauchstaedt and Gimritz). In addition, at Gimritz, small porphyritic hillsides dominated by semi-dry and dry grasslands occur in the nearby surroundings.

Agricultural use at the sites was abandoned between 1987 and 1995 (Table 1). In the year of abandonment, the sites were ploughed and harrowed once at a total area of 40 m × 100 m to initiate succession. Since then, the abandoned sites were not management at all to enable a succession process that is undisturbed by human activities. Nevertheless, animal disturbances (e.g., by wild boars, hares, mice or roe deer) occurred irregularly over the past years on all sites. Within the abandoned area, nested experimental plots of 2 m × 2 m each were established (18 plots in Bad Lauchstaedt, 25 plots in Bayreuth, 10 plots in Gimritz, 100 plots in Zoeberitz). Starting in the year of abandonment, vascular plant species identity and abundance were recorded annually during the main vegetation period

Please cite this article in press as: Knapp, S., et al., Dispersal traits as indicators of vegetation dynamics in long-term old-field succession. Ecol. Indicat. (2015), http://dx.doi.org/10.1016/j.ecolind.2015.10.003