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

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## ARTICLE INFO

## 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.

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## 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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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
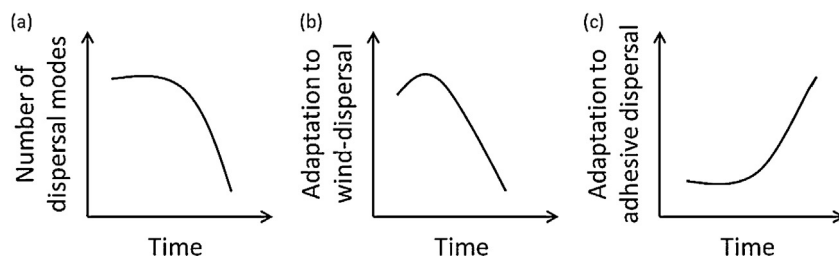
**Fig. 1.** Graphical display of our three hypotheses on the development of dispersal traits during secondary succession from abandoned agricultural sites. We expect that (a) plants using a range of dispersal modes dominate in early successional stages and decrease towards later stages in favour of species specialized on one/few dispersal modes; (b) species well adapted to wind-dispersal peak in abundance in early successional stages; (c) species well adapted to adhesive dispersal (epizoochory) increase with succession.

(May–July) on each plot and site using a Braun-Blanquet scale. Here, we will analyze the time between the year of abandonment and the year 2014. For analyses, we transformed the Braun-Blanquet scale into a rank scale ($r$ to 1; + to 2; 1 to 3, etc.) as a measure of species abundance.

As we were interested in the successional development of plant dispersal modes, knowledge on the occurrence of seed-dispersing animals is desirable. Still, our study sites had initially been established to investigate the successional development of vegetation. Monitoring the occurrence of animals was no focal interest, also because experimental setups to test for the contribution of epizoochory to seed dispersal by animals are extensive (e.g., brushing the fur and hooves of animals, walking dummy animals through vegetation or mechanically shaking animal coats; Tackenberg et al., 2006; de Pablos and Peco, 2007; Hovstad et al., 2009; Picard and Baltzinger, 2012). To our knowledge, there is no published comprehensive list of animals as potential epizoochoric seed dispersers. Nevertheless, a number of studies tested the potential to disperse adhesive seeds for single animal species e.g., roe deer, red deer, wild boar, fox or sheep (Poschlod et al., 1998; Hovstad et al., 2009; Picard and Baltzinger, 2012; Freund et al., 2014). All of these animal species also occur in the area of our study sites and can therefore be assumed to contribute to epizoochory.

### 2.2. Dispersal traits

We used three different dispersal traits as indicators of the ability of species to re-colonize the sites after abandonment: the number of dispersal modes a species can utilize (see Table S1 for an overview of all species found in the study sites and the different dispersal modes a species is able to use) and dispersal ranking indices for anemochory and epizoochory (with both types having being associated with long-distance dispersal; Milton et al., 1997). The number of dispersal modes was derived from the LEDA-traitbase (Kleyer et al., 2008; http://www.leda-traitbase.org), where dispersal modes are assigned to vascular plants of the Northwest

European flora. We did not focus on single dispersal modes and their abundance in the study sites over time because we assumed that species are most successful dispersers in early successional stages when able to utilize many dispersal modes (hypothesis a). For our study species, the number of dispersal modes range from one to six. Dispersal ranking indices for anemochory and epizoochory were taken from D³ – the Dispersal and Diaspore Database (Hintze et al., 2013; http://www.seed-dispersal.info/). These ranking indices show how well a species is adapted to a certain dispersal mode in comparison to other species (either wind-dispersal in the case of anemochory ranking index, or adhesive dispersal in the case of epizoochory ranking index). Anemochory ranking index is based on terminal velocity; epizoochory ranking index is based on attachment potential and retention potential, therefore focusing on adhesive dispersal in woolly hair or fur. As the ranking index of one species is given relative to other species, individual ranking indices change depending on the reference species pool. We used the German flora as reference species pool. The dispersal ranking indices range from 0 (no adaptation to wind-/adhesive dispersal) to 1 (very high adaptation to wind-/adhesive dispersal). If a species has an epizoochory ranking index of e.g., 0.6, this indicates that 40% of all species in the reference pool (in our case: the German flora) are either equally or better adapted to adhesive dispersal than the focal species (Hintze et al., 2013).

### 2.3. Analyses

For each study site, we calculated species richness, mean species abundance, mean number of dispersal modes, mean anemochory ranking index and mean epizoochory ranking index per plot and year. All dispersal variables were analyzed once weighted by species abundance, once not weighted. We assessed the development of each of these variables over time by applying generalized linear mixed-effect models (GLMM; using R-package 'lme4' by Bates et al., 2014), for each study site separately. Plots were taken as random variable; years of succession were taken as fixed variable.

**Table 1**
Characteristics of the four research sites at Bad Lauchstaedt, Bayreuth, Gimritz and Zoeberitz, Germany: Geographic coordinates (Coord.), height above sea level (Elev.), mean annual temperature (Temp.), mean annual precipitation (Prec.), distance to next settlement (Dist.), year of abandonment, and soil type according to IUSS Working Group WRB (2007).

| Site name | Coord. | Elev. [m] | Temp. [°C] | Prec. [mm] | Dist. [m] | Year of abandonment | Soil type | Surrounding habitat type |
|---|---|---|---|---|---|---|---|---|
| Bad Lauchstaedt | N51°23′ E11°52′ | 120 | 8.7 | 480 | 20 | 1995 | Chernozem | Arable fields, meadows |
| Bayreuth | N49°55′ E11°35′ | 355 | 8.2 | 720 | 150 | 1994 | Stagnic Gleysol on sandstone | Meadows |
| Gimritz | N51°33′ E11°50′ | 110 | 9.1 | 490 | 1000 | 1993 | Mosaic of rankers and brown soil | Arable fields, meadows, semi-dry and dry grasslands |
| Zoeberitz | N51°30′ E12°01′ | 110 | 9.1 | 480 | 20 | 1987 | Luvi-glossic Chernozem | Arable fields |

GLMMs allow for non-linear error structure and for non-linear (e.g., asymptotic or hump-shaped) dependencies. Depending on data structure, we chose the appropriate model. If several models were possible, we compared them using both Akaike Information Criterion (AIC; Burnham et al., 2011) and $R^2$ (conditional and marginal $R^2$ with the former representing the variance explained by all variables – fixed and random, and the latter representing the variance explained by fixed factors only; Nakagawa and Schielzeth, 2013; Johnson, 2014). We chose the model with the smallest AIC and highest $R^2$ (differences between conditional $R^2c$ and marginal $R^2m$ were similar between models in the sense that it did not make a difference for model selection whether we selected by $R^2c$ or $R^2m$). If AIC and $R^2$ disagreed, models were chosen by AIC (Tables S2–S4

show the different models and the models of choice). *p*-Values for chosen models were obtained by comparing the chosen model to a null-model (no fixed explanatory variable) using analysis of variance.

## 3. Results

### 3.1. Species richness and abundance

Across all plots and throughout the complete study period, species richness ranged between a minimum of 2 and a maximum of 17 species in Bayreuth (mean = 8.5), 2 and 23 species in Bad Lauchstaedt (mean = 7.3), 4 and 32 species in Gimritz (mean = 12.6),
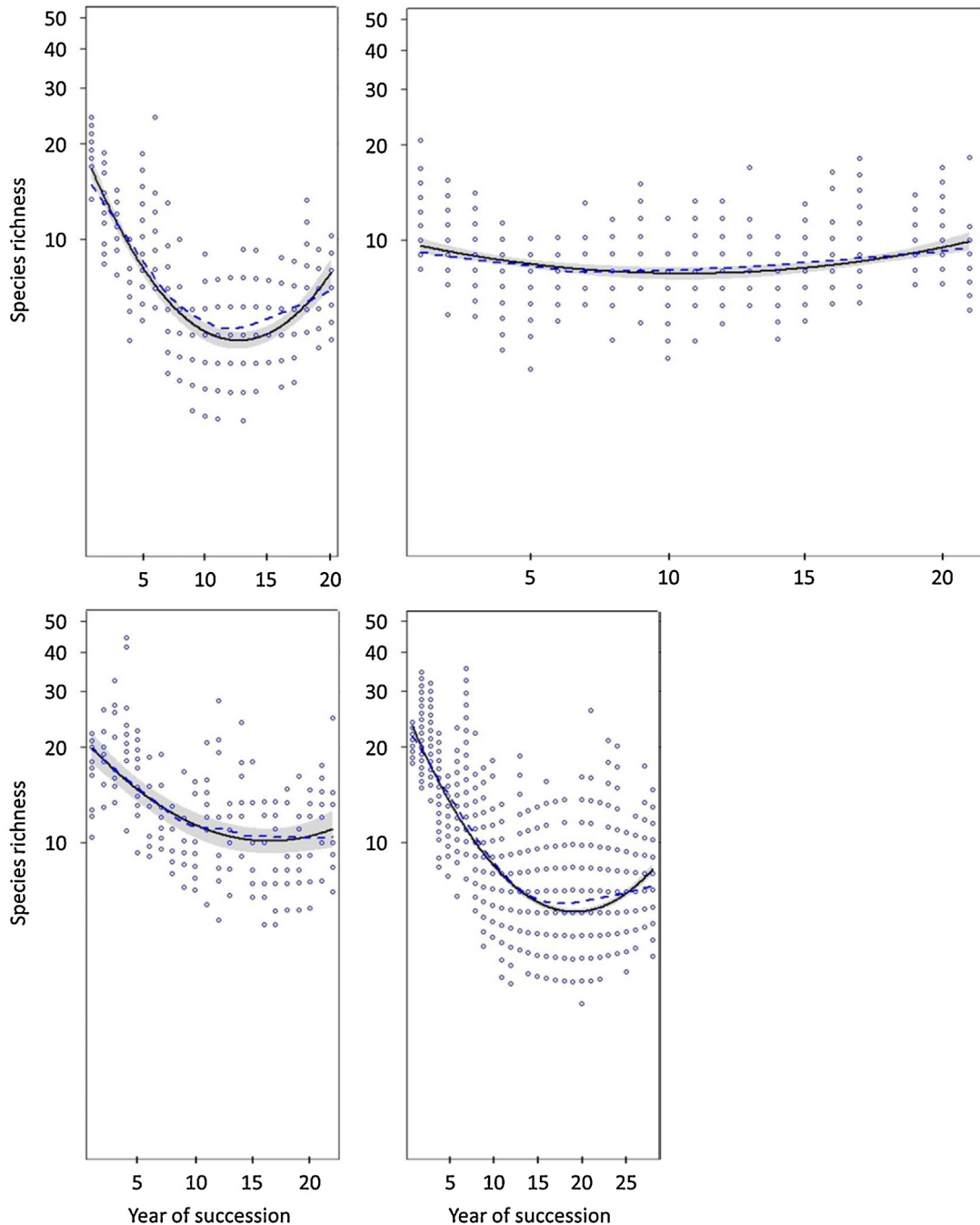


**Fig. 2.** Changes in species richness within 20–28 years of succession on four abandoned agricultural sites in central and southeastern Germany (Bad Lauchstaedt: top left; Bayreuth: top right; Gimritz: down left; Zoeberitz: down right), modelled by generalized mixed models. Points show mean species richness per plot. Grey areas illustrate model residuals with a loess smoother (dashed line).

**Table 2**
Changes of species richness and abundance in 20–28 years of succession on four abandoned agricultural sites in central and south-eastern Germany, modelled by generalized mixed models. Type = type of fitted curve for the change of species richness/abundance during succession (negative hump = first decreasing, then increasing; positive hump = first increasing, then decreasing); Vars. = fixed variables (Year$^2$ indicates the use of an exponential function; SSasymp is a function modelling asymptotic data structure implemented within the R-package 'lme4'; Bates et al., 2014); Est. = estimate of fixed variable; SE = standard error of fixed variable; $R^2$c = variance explained by all fixed and random variables; $R^2$m = variance explained by all fixed variables; $p$ = $p$-value showing whether the model is different from a null-model (no fixed explanatory variable) with ***$p < 0.001$.

| | Type | Vars. | Est. | SE | $R^2$c | $R^2$m | $p$ |
|---|---|---|---|---|---|---|---|
| **Species richness** | | | | | | | |
| Bad Lauchstaedt | Negative hump | Year | −0.23 | 0.02 | 0.48 | 0.48 | *** |
| | | Year$^2$ | 0.30 | 0.02 | | | |
| Bayreuth | Negative hump | Year$^2$ | 0.08 | 0.02 | 0.05 | 0.05 | *** |
| Gimritz | Negative hump | Year | −0.19 | 0.02 | 0.35 | 0.28 | *** |
| | | Year$^2$ | 0.12 | 0.02 | | | |
| Zoeberitz | Negative hump | Year | −0.31 | 0.01 | 0.59 | 0.57 | *** |
| | | Year$^2$ | 0.26 | 0.01 | | | |
| **Species abundance** | | | | | | | |
| Bad Lauchstaedt | Asymptotic increase | SSasymp(Year) | −0.04 | 0.003 | 0.29 | 0.29 | *** |
| Bayreuth | Asymptotic increase | SSasymp(Year) | −0.001 | 0.0001 | 0.11 | 0.11 | *** |
| Gimritz | Asymptotic increase | SSasymp(Year) | −0.13 | 0.01 | 0.48 | 0.33 | *** |
| Zoeberitz | Asymptotic increase | SSasymp(Year) | −0.12 | 0.003 | 0.35 | 0.32 | *** |

and 2 and 31 species in Zoeberitz (mean = 9.4). Across all four study sites, species richness increased after a first decline, showing a (negative) hump-shaped curve (Fig. 2). This hump-shaped curve reached the point of turnaround (starting to increase again) after 10 years in Bayreuth, after 13 years in Bad Lauchstaedt, after 16 years in Gimritz, and after 19 years in Zoeberitz. All hump-shaped curves explained a significantly higher amount of variation than null-models (Table 2).

Mean species abundance across all plots and throughout the study period ranged between 2 and 5.5 in Bayreuth (mean = 3.1), 2.1 and 5.5 in Bad Lauchstaedt (mean = 3.5), 1.5 and 4.4 in Gimritz (mean = 2.8), and 1.9 and 5.7 in Zoeberitz (mean = 3.2). Consistently across all sites mean species abundance increased asymptotically without reaching a maximum value (Fig. S1). All asymptotic models were significantly better than null-models (Table 2).

Species richness and mean species abundance were negatively correlated in all four sites (Table S5). Dispersal traits weighted by abundance were thus negatively correlated to species richness but positively to species abundance. When not weighted by abundance, species richness was inconsistently correlated with dispersal traits across sites. This was true for abundance as well, except for the correlation with epizoochory ranking index, which was positive in all sites.

### 3.2. Dispersal traits

The mean number of dispersal modes (not weighted by abundance) across all plots and years ranged between 1 and 5 in Bayreuth and Bad Lauchstaedt (mean = 3.5 and 3.3, respectively) and between 1 and 6 in Gimritz and Zoeberitz (mean = 2.7 and 3.3, respectively). The six dispersal modes present were dispersal by animals (both types: digestive and adhesive dispersal), humans, scatter-hoarding animals, surface currents of water, and by wind. Dispersal by scatter-hoarding animals and by water was less frequent than the other dispersal modes. When not weighted by abundance, the number of dispersal modes slightly increased over time in Bayreuth and slightly decreased in Zoeberitz (Fig. 3). Although statistically different from null-models, these two relationships were very weak (Table 3). In Bad Lauchstaedt and Gimritz, the number of dispersal modes showed a significant hump-shaped development, with a short increase until the sixth year of succession, followed by a clear decrease in Bad Lauchstaedt and a decrease until year 17 turning into a slight increase towards the end of the study period in Gimritz (Fig. 3). When weighted by abundance (Fig. S2), the number of dispersal modes increased asymptotically in both Bayreuth and Zoeberitz, without reaching a maximum value

(i.e., at the end of our study period, it was still increasing). This explained significantly more variance than null-models (Table 3). In Bad Lauchstaedt, the preferable model was hump-shaped, with an increase until year 11 and a decrease afterwards. In Gimritz, although showing a tendency to increase linearly, there was no statistically significant change in the abundance-weighted number of dispersal modes over time.

Anemochory ranking index (not weighted by abundance) ranged between 0.02 and 1 in Bayreuth (mean = 0.66), 0 and 1 in Bad Lauchstaedt (mean = 0.74), 0.02 and 0.99 in Gimritz (mean = 0.61), and 0 and 0.99 in Zoeberitz (mean = 0.60). When not weighted by abundance, mean anemochory ranking index increased asymptotically in Bayreuth and Bad Lauchstaedt but decreased linearly in Gimritz and Zoeberitz (Fig. 4). This decrease was statistically weak for both sites but significantly better than null-models (Tables 3 and S4). When weighted by abundance (Fig. S3), mean anemochory ranking index increased asymptotically in Bayreuth and Bad Lauchstaedt (both models significantly different from null-models; Table 3), with no further increase in Bayreuth in the last two years, but values still slightly increasing in Bad Lauchstaedt at the end of the study period. In Gimritz and Zoeberitz, abundance-weighted anemochory ranking index was hump-shaped, with values increasing until year 16 in Gimritz and year 18 in Zoeberitz, starting to decrease afterwards – with a slight decrease in Gimritz and a stronger decrease in Zoeberitz.

Epizoochory ranking index (not weighted by abundance) ranged between 0 and 1 in Bayreuth, Bad Lauchstaedt and Zoeberitz (mean = 0.66, 0.69 and 0.61, respectively), and between 0 and 0.99 in Gimritz (mean = 0.65). When not weighted by abundance, it increased asymptotically in Bayreuth but first increased and then decreased in the three other sites (Fig. 5). Epizoochory ranking index increased until year 9 in Bad Lauchstaedt, year 11 in Gimritz and year 16 in Zoeberitz. When weighted by abundance (Fig. S4), epizoochory ranking index increased asymptotically (significantly better than null models; Table 3) in Bayreuth and Gimritz, without reaching a maximum value. In Bad Lauchstaedt and Zoeberitz, epizoochory ranking index showed a significant hump-shaped development over time, increasing until year 8 in Bad Lauchstaedt and until year 18 in Zoeberitz and decreasing afterwards.

The mean values of dispersal traits per plot and year weighted by species abundance were all positively correlated to each other (for all four study sites; Table S5). Dispersal traits not weighted by abundance were inconsistently correlated to each other except anemochory and epizoochory ranking index, which were positively correlated across sites.

**Table 3**

Changes of dispersal traits, i.e., number of dispersal modes (derived from LEDA; Kleyer et al., 2008), anemochory and epizoochory ranking index (Hintze et al., 2013) in 20–28 years of succession on four abandoned agricultural sites in central and south-eastern Germany, modelled by generalized mixed models. Type = type of fitted curve for the change of species richness/abundance during succession (negative hump = first decreasing, then increasing; positive hump = first increasing, then decreasing); Vars. = fixed variables (Year$^2$ indicates the use of an exponential function; SSasymp is a function modelling asymptotic data structure implemented within the R-package 'lme4'; Bates et al., 2014); Est. = estimate of fixed variable; SE = standard error of fixed variable; $R^2$c = variance explained by all fixed and random variables; $R^2$m = variance explained by all fixed variables; $p$ = $p$-value showing whether the model is different from a null-model (no fixed explanatory variable) with $p > 0.5$ n.s.; ***$p < 0.001$.

### Number of dispersal modes – not weighted by abundance

| Site | Type | Vars. | Est. | SE | $R^2$c | $R^2$m | $p$ |
|---|---|---|---|---|---|---|---|
| Bad Lauchstaedt | Positive hump | Year | −0.17 | 0.02 | 0.23 | 0.23 | *** |
| | | Year$^2$ | −0.12 | 0.02 | | | |
| Bayreuth | Linear increase | Year | 0.06 | 0.02 | 0.08 | 0.02 | ** |
| Gimritz | Negative hump | Year | −0.14 | 0.02 | 0.26 | 0.14 | *** |
| | | Year$^2$ | 0.08 | 0.03 | | | |
| Zoeberitz | Linear decrease | Year | −0.03 | 0.009 | 0.08 | 0.003 | ** |

### Number of dispersal modes – weighted by abundance

| Site | Type | Vars. | Est. | SE | $R^2$c | $R^2$m | $p$ |
|---|---|---|---|---|---|---|---|
| Bad Lauchstaedt | Positive hump | Year | 0.43 | 0.19 | 0.26 | 0.26 | *** |
| | | Year$^2$ | −2.40 | 0.22 | | | |
| Bayreuth | Asymptotic increase | SSasymp(Year) | −0.17 | 0.01 | 0.41 | 0.38 | *** |
| Gimritz | Linear increase | Year | 0.04 | 0.01 | 0.12 | 0.04 | n.s. |
| Zoeberitz | Asymptotic increase | SSasymp(Year) | −0.02 | 0.001 | 0.17 | 0.05 | *** |

### Anemochory ranking index – not weighted by abundance

| Site | Type | Vars. | Est. | SE | $R^2$c | $R^2$m | $p$ |
|---|---|---|---|---|---|---|---|
| Bad Lauchstaedt | Asymptotic increase | SSasymp(Year) | 1.5e$^{-4}$ | 1.4e$^{-5}$ | 0.26 | 0.26 | *** |
| Bayreuth | Asymptotic increase | SSasymp(Year) | 0.003 | 0.0002 | 0.29 | 0.25 | *** |
| Gimritz | Linear decrease | Year | −0.03 | 0.004 | 0.57 | 0.08 | *** |
| Zoeberitz | Linear decrease | Year | −0.03 | 0.002 | 0.17 | 0.08 | *** |

### Anemochory ranking index – weighted by abundance

| Site | Type | Vars. | Est. | SE | $R^2$c | $R^2$m | $p$ |
|---|---|---|---|---|---|---|---|
| Bad Lauchstaedt | Asymptotic increase | SSasymp(Year) | −0.07 | 0.005 | 0.36 | 0.36 | *** |
| Bayreuth | Asymptotic increase | SSasymp(Year) | −0.03 | 0.002 | 0.29 | 0.27 | *** |
| Gimritz | Positive hump | Year | 0.10 | 0.02 | 0.43 | 0.08 | *** |
| | | Year$^2$ | −0.07 | 0.02 | | | |
| Zoeberitz | Positive hump | Year | 0.13 | 0.007 | 0.27 | 0.20 | *** |
| | | Year$^2$ | −0.17 | 0.008 | | | |

### Epizoochory ranking index – not weighted by abundance

| Site | Type | Vars. | Est. | SE | $R^2$c | $R^2$m | $p$ |
|---|---|---|---|---|---|---|---|
| Bad Lauchstaedt | Positive hump | Year | −0.10 | 0.01 | 0.52 | 0.49 | *** |
| | | Year$^2$ | −0.18 | 0.01 | | | |
| Bayreuth | Asymptotic increase | SSasymp(Year) | −0.03 | 0.001 | 0.55 | 0.54 | *** |
| Gimritz | Positive hump | Year$^2$ | −0.02 | 0.006 | 0.33 | 0.05 | *** |
| Zoeberitz | Positive hump | Year | 0.01 | 0.002 | 0.19 | 0.12 | *** |
| | | Year$^2$ | −0.04 | 0.002 | | | |

### Epizoochory ranking index – weighted by abundance

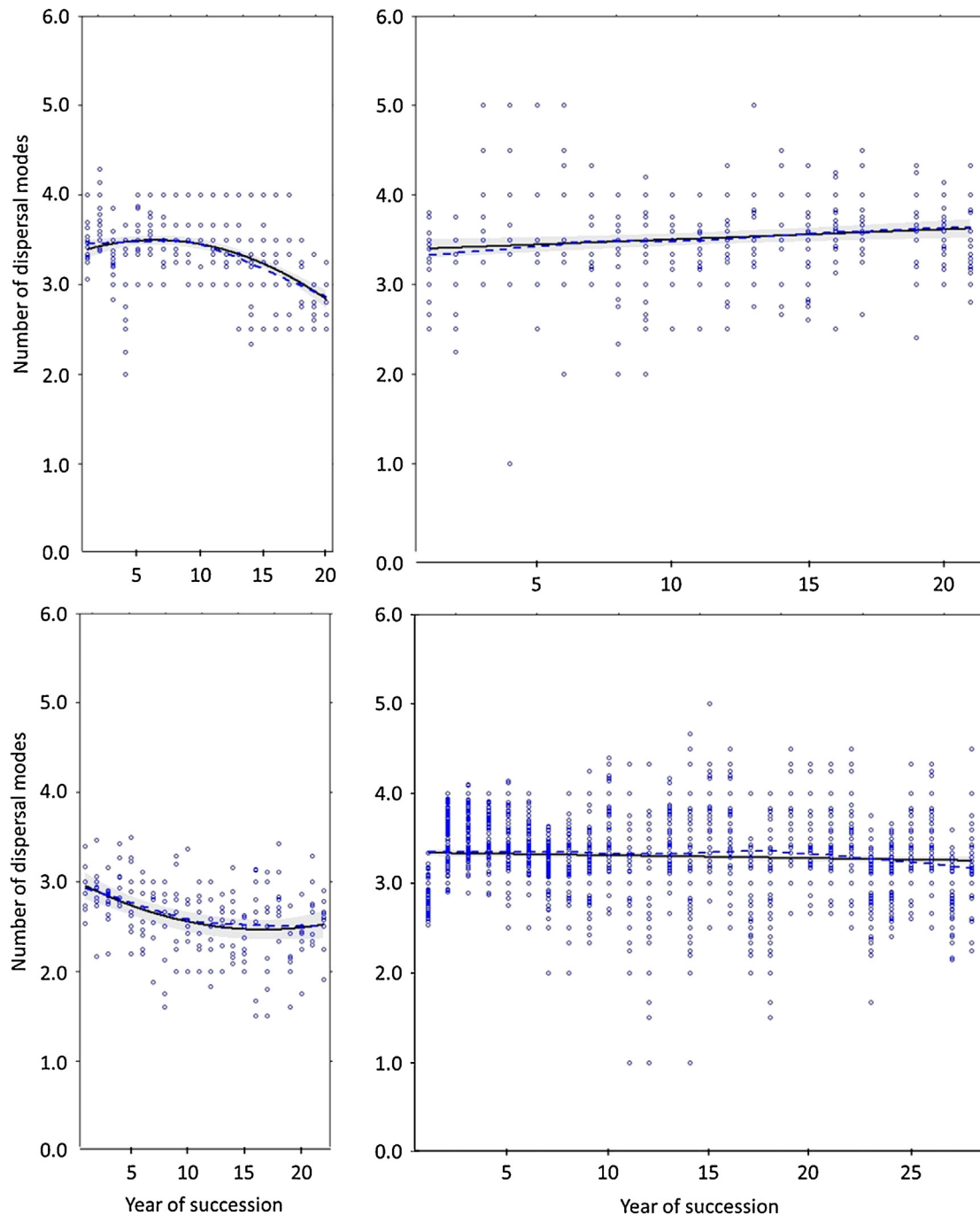| Site | Type | Vars. | Est. | SE | $R^2$c | $R^2$m | $p$ |
|---|---|---|---|---|---|---|---|
| Bad Lauchstaedt | Positive hump | Year | −0.36 | 0.05 | 0.50 | 0.47 | *** |
| | | Year$^2$ | −1.01 | 0.06 | | | |
| Bayreuth | Asymptotic increase | SSasymp(Year) | −0.18 | 0.007 | 0.54 | 0.53 | *** |
| Gimritz | Asymptotic increase | SSasymp(Year) | −0.33 | 0.04 | 0.40 | 0.21 | *** |
| Zoeberitz | Positive hump | Year | 0.26 | 0.01 | 0.36 | 0.31 | *** |
| | | Year$^2$ | −0.28 | 0.01 | | | |

**Fig. 3.** Changes in the number of dispersal modes (not weighted by species abundance) within 20–28 years of succession on four abandoned agricultural sites in central and south-eastern Germany (Bad Lauchstaedt: top left; Bayreuth: top right; Gimritz: down left; Zoeberitz: down right), modelled by generalized mixed models. Points show the mean number of dispersal modes per plot. Grey areas illustrate model residuals with a loess smoother (dashed line).

## 4. Discussion

### 4.1. Changes in dispersal traits during secondary succession

While the development of plant species richness and abundance was consistent across study sites, the development of dispersal traits varied. Our expectation that species using a range of dispersal modes will dominate early stages of succession but decrease afterwards (hypothesis a) was supported by the sites in Bad Lauchstaedt, Gimritz and very weakly in Zoeberitz, but only when data were not weighted by species abundance. Our sites thus provide evidence that in the course of succession, the richness

of dispersal generalists decreases in favour of more specialized species. However, this pattern differed markedly among sites. There was no common time frame when decrease changed into increase or vice versa. Therefore, the number of dispersal modes does not seem to be useful as consistent indicator of successional stages, which is also valid for the anemochory ranking index. When weighted by species abundance, it basically showed the same pattern as abundance alone, not providing any additional information. An exception was Zoeberitz, where mean abundance-weighted anemochory ranking index decreased after an initial increase as hypothesized. Zoeberitz is the study site with the longest successional period (28 years of abandonment). We therefore expect
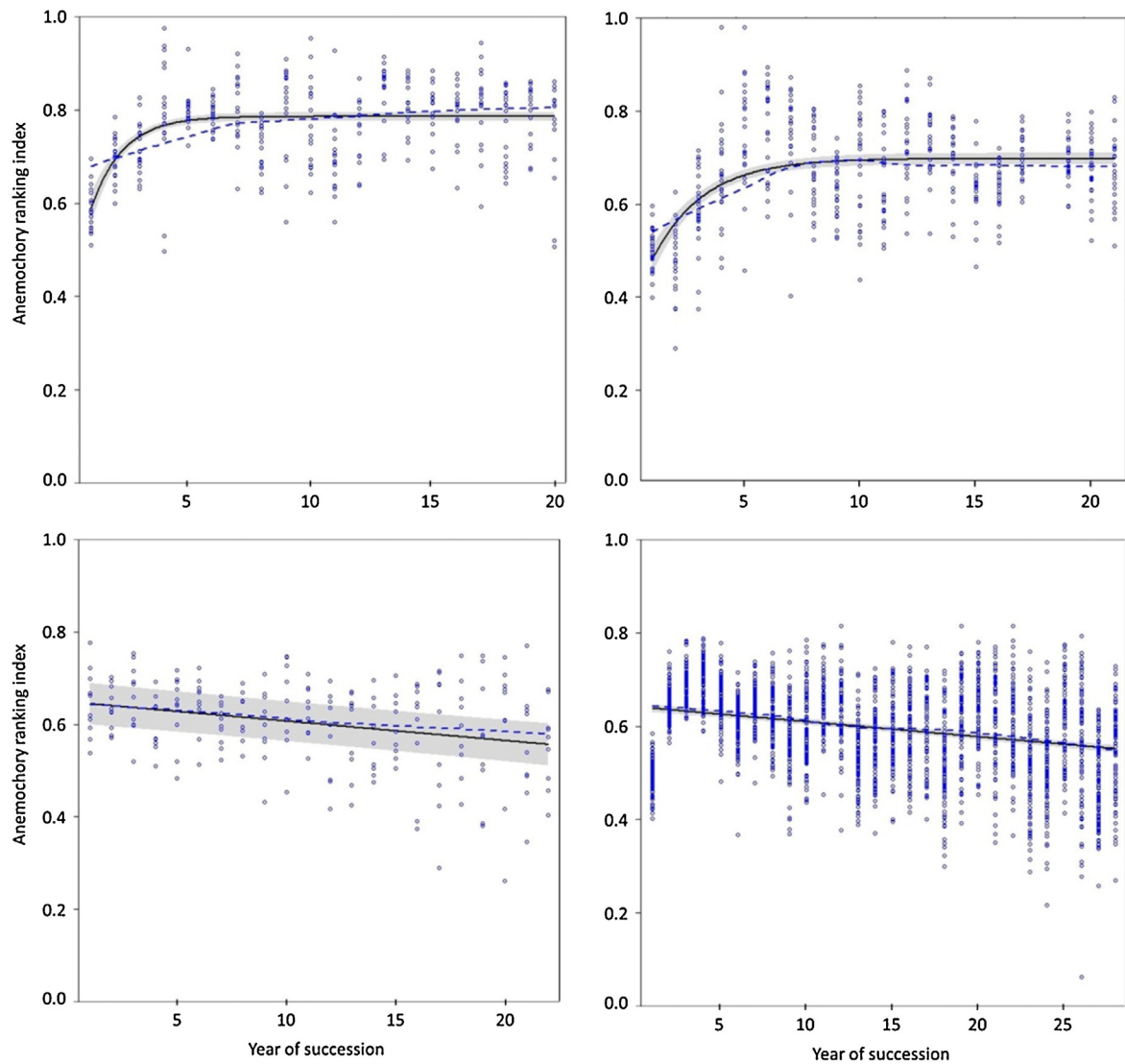
**Fig. 4.** Changes in anemochory ranking index (Hintze et al., 2013) within 20–28 years of succession on four abandoned agricultural sites in central and south-eastern Germany (Bad Lauchstaedt: top left; Bayreuth: top right; Gimritz: down left; Zoeberitz: down right), modelled by generalized mixed models. Points show the mean anemochory ranking index per plot (not weighted by species abundance). Grey areas illustrate model residuals with a loess smoother (dashed line).

that in the other sites, abundance-weighted anemochory ranking index has not reached its peak, yet but will follow our hypothesis after the next five to ten years have passed. When not weighted by abundance, anemochory ranking index was either lower in the first four to five years after abandonment than in later years, or slightly decreased from the beginning. We conclude that on the one hand, the richness of wind-dispersed species in secondary succession is site-specific; i.e., different reactions might depend on the regional species pool available for colonization and differences in this pool among sites (which would be in line with the view that succession is context-dependent; cf. Christensen, 2014). On the other hand, our successional time series might be too short to show common reactions of wind-dispersed species (as expected in hypothesis b).

In contrast, epizoochory ranking index (especially when not weighted by abundance) pointed towards similar transitions between successional stages as species richness. The changes in epizoochory ranking index contradict our expectation (hypothesis c) that epizoochorous species become more frequent as succession proceeds. Rather, it supports the finding of Latzel et al. (2011) that epizoochory first increases and then decreases during succession. This pattern, together with the opposing trend

of species richness (first decreasing, then increasing) suggests that the role and richness of seed dispersers differs among successional stages. Snails, for example, are potential dispersers of seeds in agro-environmental habitats (Türke et al., 2013) and were shown to be richer in species in mid-successional (defined as 5–15 year old) than early successional (defined as 1–3 year old) brownfields across European urban areas (Lososová et al., 2011). For ants, site attractiveness should increase when management is ceased, with species richness increasing as sites are not disturbed anymore (Zwiener et al., 2012; Wiezik et al., 2013). This raises the question about the main dispersers of plant species in our study sites, especially for those few plant species that dominate succession in the time of highest epizoochory ranking index. These dominant plant species were *Arrhenaterum elatius* (L.) P. Beauv. ex J. Presl & C. Presl (epizoochory ranking index = 0.82) in Bad Lauchstaedt, Gimritz and Zoeberitz, *Calamagrostis epigejos* (L.) Roth (0.88) in Zoeberitz, *Hieracium pilosella* L. (0.98) in Gimritz, *Poa pratensis* L. (0.77) in Bayreuth and Zoeberitz and *Solidago canadensis* L. (0.98) in Bad Lauchstaedt and Bayreuth. The dispersules of these species are dispersed by ants (for *S. canadensis* and *H. pilosella*; cf. www.floraweb.de) or they work like burrs that
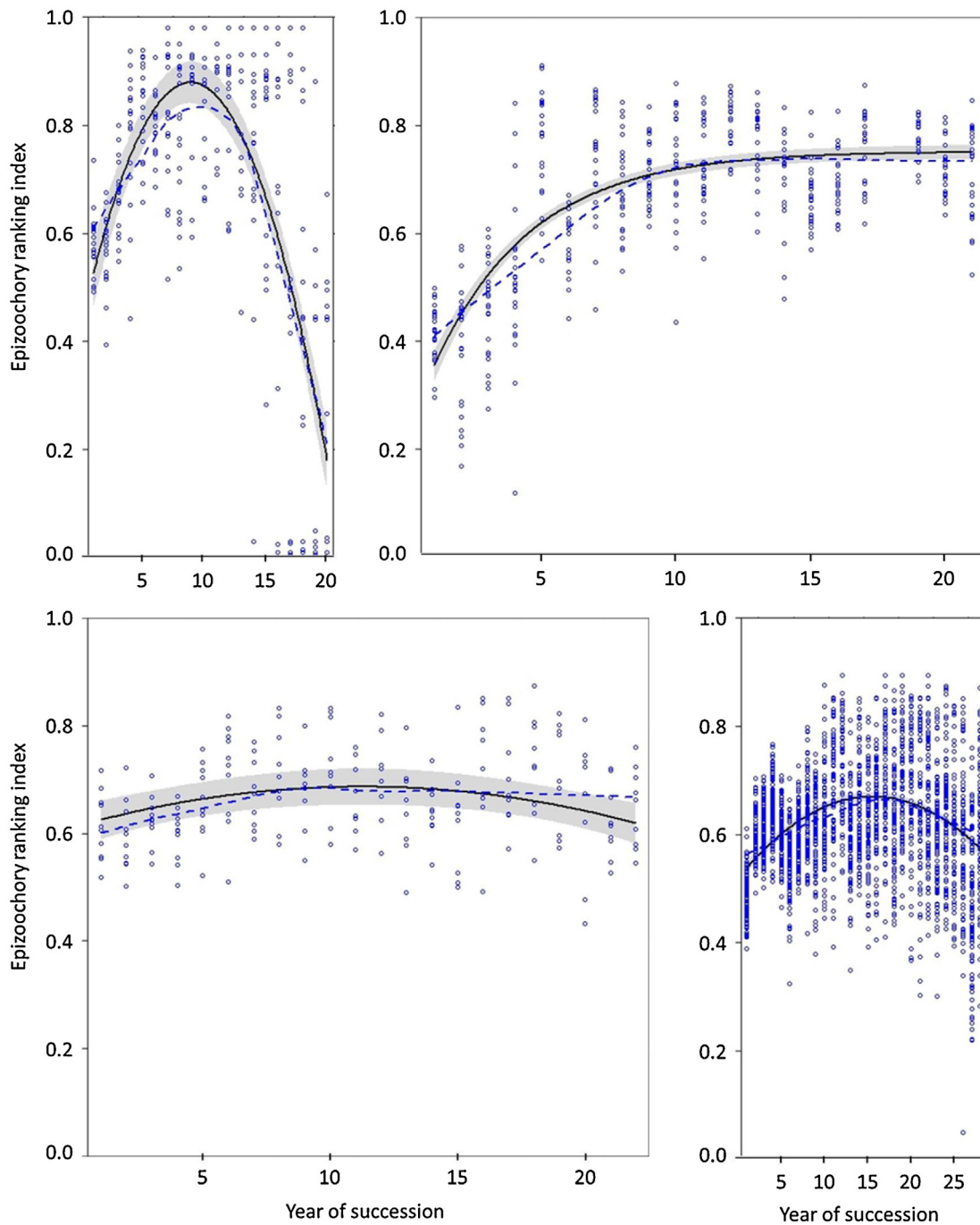
**Fig. 5.** Changes in epizoochory ranking index (Hintze et al., 2013) within 20–28 years of succession on four abandoned agricultural sites in central and south-eastern Germany (Bad Lauchstaedt: top left; Bayreuth: top right; Gimritz: down left; Zoeberitz: down right), modelled by generalized mixed models. Points show the mean epizoochory ranking index per plot (not weighted by species abundance). Grey areas illustrate model residuals with a loess smoother (dashed line).

can stick to fur or to clothes and should mainly be dispersed by mammals.

Wild mammals known to occur in the vicinity of our study sites are e.g., moles (*Talpa europaea* L.), rodents (e.g., the common vole *Microtus arvalis* Pallas), wild rabbits (*Oryctolagus cuniculus* L.), hare (*Lepus europaeus* Pallas), foxes (*Vulpes vulpes* L.), badgers (*Meles meles* L.), roe deer (*Capreolus capreolus* L.) and wild boars (*Sus scrofa* L.; Dean et al., 1997; Milton et al., 1997). Also, several snail species such as *Helix pomatia* L. and *Cepaea spec.* and ant species have been observed, e.g., *Lasius* and *Formica* spp. (Dean et al., 1997; Petter, 2012). These species might all be potential dispersers of

epizoochorous seeds (e.g., purposeful in order to stock seeds or accidentally, e.g., burrs), amongst them seeds of strong competitors such as *S. canadensis* or *A. elatius*. However, wild animals were reported to have a very limited capacity of dispersing plant seeds (reviewed by Poschlod et al., 1998), with e.g., ants dispersing many seeds but over small distances only (Buisson et al., 2006). In contrast, sheep were shown to be very effective dispersers of both endo- and epizoochorous seeds over short and long distances (Poschlod et al., 1998; Freund et al., 2014). As just two of our four study sites (Bayreuth and Gimritz) have been visited by sheep several times within the study period (sites at Bad Lauchstaedt

and Zoeberitz are fenced and therefore not accessible to sheep), we suggest that both wild animals (as shown by Hovstad et al., 2009; Picard and Baltzinger, 2012) and livestock contribute to the observed successional development of epizoochory ranking index as well as to the development of species richness and abundance.

Moreover, animal activity does not only influence seed dispersal but also leads to vegetation disturbance e.g., due to trampling, grubbing or grazing activities (Whelan, 1989): Disturbance resets small patches within the vegetation community to initial successional stages and leads to the accumulation of nutrients (e.g., by faeces or anthills, which were shown to be richer in nutrients than surrounding soils by Dean et al. (1997); or by transporting nutrients from lower soil layers to the top). Molehills, anthills, burrows, boar grubbing, animal trampling or grazing open new windows of opportunity for the colonization and establishment of less competitive species (Milton et al., 1997; Jentsch et al., 2002; Ferguson et al., 2010). This is supported by several experimental studies using animal exclosures, which showed that trampling and grazing by livestock decrease the abundance of highly competitive species and increase soil heterogeneity, thus increasing species richness as opposed to sites without trampling or grazing (Faust et al., 2011; Golodets et al., 2011). Our findings indicate that especially plant species less adapted to epizoochory can enter as a result of disturbance, e.g., by wind or by resprouting from the soil seed bank. Other studies support these findings; e.g., boar grubbing was shown to support self-dispersed plant species (Milton et al., 1997). Anthills were shown to support poor competitors in the presence of highly competitive grasses (Dean et al., 1997; Dostal, 2007), therefore increasing species richness (Sebastia and Puig, 2008). Consequently, in our sites, species richness increases again after the initial decline, while mean epizoochory ranking index decreases.

Humans are potential dispersers of seeds, too and a range of primarily animal-dispersed species can be dispersed by humans, such as burr-like dispersules (Hodkinson and Thompson, 1997). However, our study sites are fenced, located on former or active research stations or far from any path. Partly, vegetation is very dense (e.g., stands of *S. canadensis*). Therefore, although we accessed the sites for vegetation survey once a year, and although our study sites are located relatively close to settlements (max. 1 km), human-mediated dispersal should be negligible.

### 4.2. Changes in species richness and abundance during secondary succession

Different succession studies showed that species richness can either decrease or increase with successional age. Decreases of species richness have been reported by numerous studies as e.g., Foster and Tilman (2000) who analyzed 14 years of succession at Cedar Creek long-term ecological research site in Minnesota, USA; by Debussche et al. (1996) investigating 12–14 year-old successional old fields in Mediterranean France; Bartha et al. (2003) reporting on plant colonization windows in an old-field succession started in 1958 in the US (Buell-Small Successional Study) or by Pornaro et al. (2013) who analyzed abandoned pastures subjected to natural forest succession in the Italian Alps. In contrast, species richness increased in a 5–270 years arable-to-grassland chronosequence in Sweden (Purschke et al., 2013). However, results of chronosequences, i.e. space-for-time approaches, cannot generally be transferred to real long-term successional data and especially patterns of species richness can differ among chronosequences and long-term data (Foster and Tilman, 2000; Bartha et al., 2003). Our study sites have a successional age of 20–28 years and are still far from dense bush or tree encroachment. However, in our study sites vegetation was recorded annually since abandonment, providing long-term ecological data that enables studying real temporal developments instead of surrogates such as chronosequences.

Our results show that the successional development of species richness is neither a pure decrease nor a pure increase but indicates transitions between successional stages. We suggest that the direction of this transition is determined by abiotic and biotic factors which interact differently during succession (cf. Christensen, 2014). In our study, the point of turnaround, where species richness increases again, falls between 10 and 19 years after abandonment and therefore supports the results by Foster and Tilman (2000) and Debussche et al. (1996), where species richness decreased for the complete 14-years study period. The congruency of the results point to site conditions similar to our study sites, which are relatively dry due to low annual precipitation and/or shallow, nutrient poor soils, inhibiting earlier shrub and tree development (especially in Bayreuth and Gimritz, shrub and tree development is delayed, while it is faster in Bad Lauchstaedt and Zoeberitz where soils are nutrient rich; Fig. S5).

The asymptotic increase in species abundance shows that abundance increases especially fast in the first years after abandonment, when species richness decreases. This asymptotic increase seems to be typical for succession (Foster and Tilman, 2000) and is an effect of pre-abandonment conditions (e.g., type of crop or season of abandonment) or treatment (e.g., plowed or left intact after abandonment; Meiners et al., 2015). Similarly, Schadek et al. (2009) found for urban successional sites in Germany that species richness decreased with increasing vegetation density. The few plant species that became highly abundant within our sites have the potential to outcompete early successional species and hamper colonization by less competitive species. Disturbances of the vegetation through animal activities, as discussed above, can create small open sites that can subsequently be colonized by other plant species.

## 5. Conclusions

Species richness and epizoochory ranking index (Hintze et al., 2013) turned out to be indicators of the transition from early to mid-stages of secondary succession in abandoned agricultural sites suggesting that common patterns exist in the successional development of dispersal traits on old fields. On the contrary, wind-dispersal and high dispersal potential did not show common patterns across study sites, pointing towards context-dependency of succession. The dual role of animals as dispersers and disrupters facilitates the spread of highly competitive species but then partly represses the very same species, supporting the establishment of weak competitors and the increase of species richness. The changes in the presence of epizoochorous plant species indicate the importance of plant traits and related plant-animal interactions in the succession of plant communities.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.10.003.

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