

Changing importance of environmental factors driving secondary succession on molehills

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Abstract

Question: Species composition during secondary succession is influenced by a number of factors, such as soil moisture, disturbance timing and surrounding vegetation. How does the importance of these factors change over the course of succession?

Methods: We set up a full-factorial block design using molehills differing in (a) disturbance timing, (b) soil moisture and (c) composition of surrounding vegetation, and recorded the cover of all species present on the molehills over 3 years. Multiple regression analyses on the dissimilarity matrices of community composition and of environmental factors were applied for each of five age classes of molehills to estimate the effect of the single factors at different stages of succession.

Results: The timing of disturbance did not significantly affect community composition at any stage of succession. In contrast, the effects of soil moisture and surrounding vegetation changed significantly over time, with moisture being more important at earlier stages of succession and surrounding vegetation at later stages.

Conclusion: The importance of environmental factors for species composition change significantly over the course of secondary succession. Instead of aggregating the effects of environmental factors over time, future studies should consider underlying dynamics of recolonization more comprehensively.

Keywords: Community composition; DCA; Disturbance timing; Mantel test; Molehills; Soil moisture

Nomenclature: Jäger & Werner (2002).

Introduction

Disturbance size and timing, surrounding vegetation, soil characteristics, nutrient availability and other environmental factors are known to affect vegetation dynamics during secondary succession (e.g. Hillier 1990; Lavorel et al. 1994; Hobbs & Mooney 1995; Crawley 2004; Prach & Rehoukova 2006). However, most previous studies investigated the influence of these factors only during a short time span after disturbance and thus missed the temporal development of their importance on community composition (but see Cook et al. 2005; Zobel & Antos 2009). This focus on aggregated effects of environmental factors has led to a more static view of secondary succession than the dynamic nature of succession would suggest.

In this study, we hypothesise that effects of determinants such as the timing of disturbance or abiotic conditions in controlling species abundances are likely to change with the stage of succession, since both the availability of diaspores and the conditions on the disturbed patch vary over time. To test this hypothesis, we quantified the relative effects of the factors soil moisture, surrounding vegetation and disturbance timing over the course of recolonization of disturbed, small-scale patches. As a research system, we used the widespread but rarely studied disturbances caused by the European mole (*Talpa europaea*) in wet meadows in central Germany.

Molehills occur in large numbers throughout most of the year in the studied areas. During the first months after disturbance, differences in soil moisture are pronounced on molehills, due to the missing buffering effect of plant cover (K. Schiffers, unpubl. data). With increasing plant cover, the drier conditions on disturbed patches are ameliorated (for positive effects of vegetation cover on disturbed patches see e.g. Villarreal-Barajas & Martorell 2009) so that soil moisture may be reduced in importance over the course of succession. In contrast, the effect of the surrounding species composition on vegetation dynamics on molehills is likely to increase over time. According to the concept of the competition/colonization trade-off (Gleason & Tilman 1990;

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Turnbull et al. 1999, 2004, 2005), species are either good gap exploiters, with high dispersal abilities, or are well adapted to high vegetation cover and competitive pressure. At early successional stages, pioneer species with usually good dispersal ability are favoured (e.g. Leishman 1999), so that the surrounding area that acts as potential seed source is large and the contribution of seeds for recolonization from directly adjacent individuals is relatively low. With increasing vegetation cover, the suitability of trait combinations for recolonization shifts to more competitive species (Turnbull et al. 2004). The generally lower dispersal ability of competitive species limits the area acting as a seed source to the immediate surroundings of the disturbed patch. Thus, the impact of surrounding vegetation on species composition should increase with increasing dominance of late-successional species.

Apart from spatial seed limitation, also temporal seed limitation might change over the course of succession: the timing of molehill occurrence clearly defines which species are available for initial recolonization (Busing & Clebsch 1983; Squiers 1989). However, several authors argue that these results cannot be directly translated to compositional changes over longer time periods. For example, even if seedling emergence at a particular time is increased on disturbed areas, density-dependent processes such as mortality and reproduction at later life stages may neutralize this effect (Alexander & Schrag 2003; Maron & Kauffman 2006). However, since early-successional individuals affect conditions for later-successional species (e.g. Bezemer et al. 2006), an attenuating effect of timing will probably persist throughout the whole course of succession.

Based on the above expectations, we formulated the following hypotheses:

- (i) Moisture has a stronger effect during the early phase of succession when vegetation cover is low and the susceptibility of recolonizing individuals to drought is higher.
- (ii) Species composition adjacent to molehills is most important at later stages of succession, when conditions on the disturbed area become more similar to the surrounding vegetation matrix.
- (iii) The effect of timing of mole disturbance is most pronounced soon after disturbance but persists throughout the whole succession.

We tested these hypotheses by assessing the effect size of the three environmental factors on community composition. The results of this work

will help to gain a more predictive understanding of succession dynamics on small-scale disturbances. Moreover, the study may serve as an impulse for future investigations on succession dynamics to explicitly consider the changing importance of factors influencing succession over time.

Methods

Study area

The study area is located in a nature reserve (1315 km²) in western Brandenburg, Germany (52°71'66"N, 12°21'66"E). It represents an island between two arms of the River Havel and is characterized by slightly undulating terrain with extensively used grassland, dominated by *Arrhenatheretalia*- and *Diantho-Armerietum* communities. Dominant species in the dry grasslands at higher elevations are the grasses *Agrostis capillaris* and *Poa angustifolia*, and the forbs *Rumex acetosella*, *Achillea millefolium*, *Plantago intermedia* and *Cerastium arvense*. Wetter grasslands at lower elevations are dominated by the forbs *Rumex thyrsiflorus*, *Leontodon autumnalis* and *Potentilla reptans*, and the grasses *Agrostis stolonifera*, *Holcus lanatus* and *Alopecurus pratensis*. Soils are predominantly sandy and nutrient-poor (Burkart et al. 2003). The meadows are traditionally mown once a year in June. Lower elevations are subject to flooding of the River Havel during the winter months and have higher soil moisture throughout the year. In addition to flooding, moles constitute a common and widespread disturbance agent within the study site.

Sampling design and data collection

To test the effect of different timing of molehill occurrence, soil moisture and surrounding species composition on subsequent succession and community structure on molehills, we conducted a 3-year data collection. The basic design incorporated two sites separated by around 1.5 km and having differing species composition, probably due to their different history of land use. These two sites represent the factor "surrounding vegetation" for our analyses. At both sites, two blocks of 50 m x 50 m were marked, with one block being at a lower elevation (moister soil) and the other block at higher elevation (drier soil). In August 2004, November/December 2004, April/May 2005 and July/August 2005, in each of the blocks, five plots were marked

permanently. Plots were centred on fresh molehills and were 15 cm x 15 cm in size. Due to relatively low mole activity, it was not always possible to find five fresh molehills at each time point in all five blocks. The total molehill number resulted in 29 plots, with 11 of the plots being situated in the two blocks at lower elevation and higher soil moisture, and 18 at higher elevation with drier soil. The average water content of the soil in the wet plots was 11.5% (± 6.1 SD) and in the dry plots was 5.5% (± 2.3 SD).

Floristic measurements were made bi-monthly from August 2004 until June 2007, with breaks during periods of snow and flooding of surrounding areas, resulting in a total of 668 recordings. None of the experimental blocks were flooded during that time. All vascular plants growing in the plots were recorded and their cover was estimated using a continuous percentage scale.

Statistical analysis

The data were analysed to estimate the effects of disturbance timing, surrounding vegetation and soil moisture on community composition for different stages of succession. Community data were pooled to five age classes of molehills (5 ± 1 , 8 ± 1 , 14 ± 1 , 17 ± 1 and 25 ± 1 months), each containing at least three replicates of all treatment combinations. Community composition data were not transformed prior to the analyses.

For each of the age classes, we performed a detrended correspondence analysis (as PCA analysis gave a strong horseshoe effect) to determine the association between recolonizing species and molehills differing in the three environmental factors.

In a second step, for each age class, distance matrices for both the community data and the environmental variables were calculated using Euclidean distance for numerical variables and Gower distance for categorical variables (since Gower distances do not represent ecological distances as well as Euclidean distances, see e.g. Faith 1997). On the resulting matrices, multiple regressions were applied (based on Mantel tests), using community composition as response variables and the three observed factors as explanatory variables (Legendre et al. 1994). The fitted regression coefficients for disturbance timing, moisture and surrounding vegetation were plotted against the age of the molehills, i.e. the stage of succession. Permutation tests (1000 iterations) were used to test the significance of these factors in affecting the species composition.

For both analyses, we used the statistical package R, version 2.6.2 (R Development Core Team 2008) with the additional packages “ecodist” (Goslee & Urban 2007), “cluster” (Maechler et al. 2005) and “vegan” (Oksanen et al. 2009).

Results

For molehills with an age of 5 months, community composition did not differ between any of the three investigated factors (Fig. 1). Starting with an age of 8 months, a differentiation between molehills on wet and dry blocks became discernible. Species such as *Plantago lanceolata* and *A. millefolium* were more strongly associated to molehills with lower soil moisture and did not appear on wet plots. At an age of 14 months, molehills clustered mostly according to attributes of the two investigated sites (indicating different surrounding vegetation): while at one site *P. reptans* and *H. lanatus* were the most characteristic species, molehills from the other site are mainly marked by species such as *Veronica serpyllifolia* or *Myosotis discolor*. In the two classes of oldest molehills, four groups of hills emerged: along the first ordination axis, hills separated according to the two investigated sites, while along the second ordination axis they separated according to soil moisture. Representative species of the two moister blocks were *H. lanatus* for site 1 and *Lychnis flos-cuculi* for site 2; dominant species in the drier blocks were *A. millefolium* for site 1 and *Elytrigia repens* for site 2.

Soil moisture had a significant effect on community composition on molehills from month 8 to month 25, with a peak at month 8 (Fig. 2). The regression coefficients for the timing of disturbance were slightly negative for all considered age classes and none of them was significantly different from zero. Surrounding vegetation had no significant impact on community composition during early stages of succession. However, from month 14 onwards, it replaced moisture as the factor with the highest regression coefficients.

Overall, only a small part of the total variation in community composition could be explained by the investigated factors; r^2 -values for the Mantel tests ranged between of 0.015 (5 months) and 0.07 (8 months).

Discussion

Our results demonstrate that the importance of environmental factors can change significantly over the course of succession. However, the outcome of

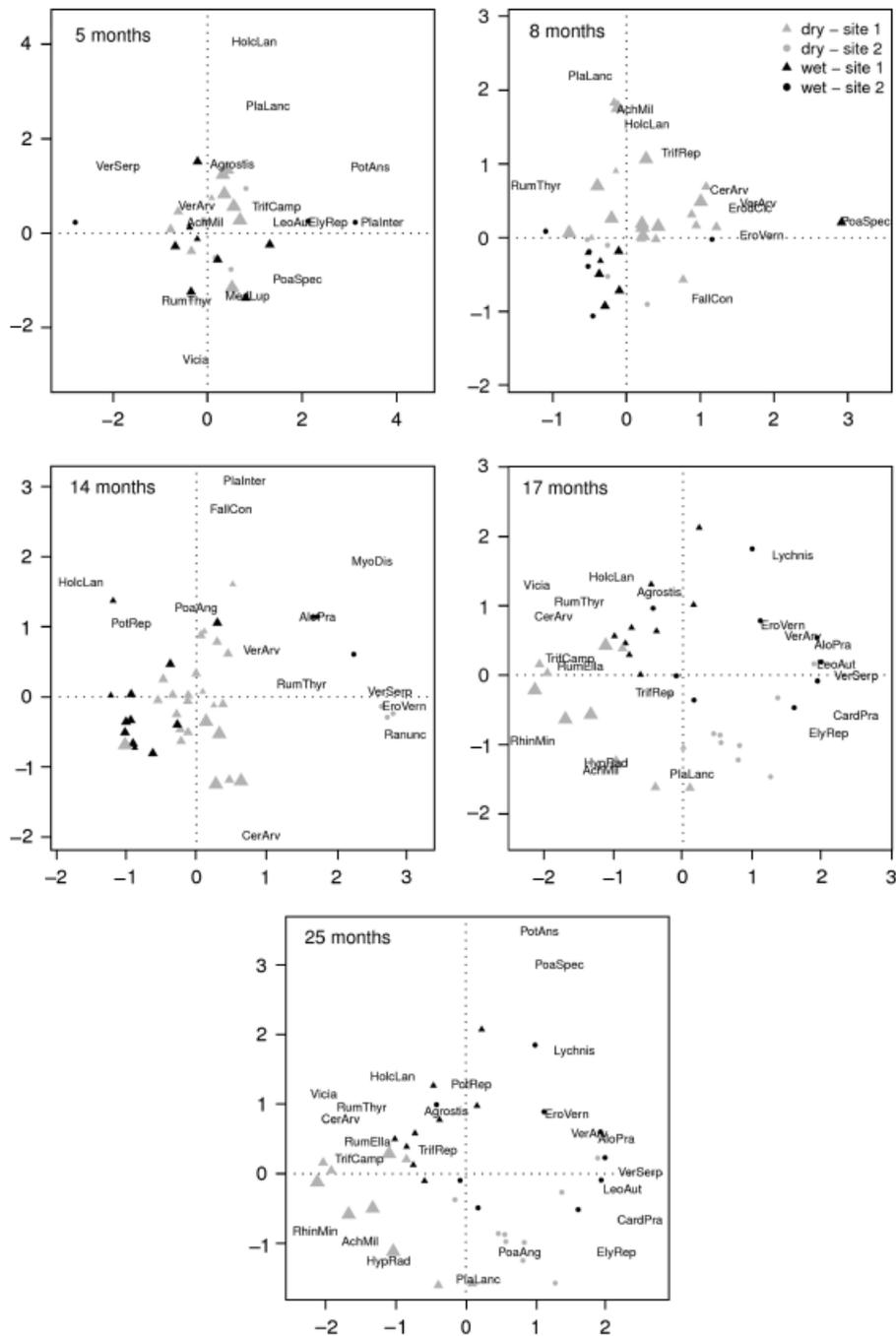


Fig. 1. Ordination diagrams from detrended correspondence analyses on community data of each of five age classes of the molehills. Increasing size of symbol indicates later occurrence of molehills during the year.

the multiple regression analyses contradicts our expectation in two respects: first, in the generally small effect of all factors soon after disturbance, and second, in the lack of effect of disturbance timing on community composition.

The limited effect of the investigated factors on species composition during the first months after disturbance might be due to a large overlap in the

first colonizing species across the plots and the generally small number of individuals present on the patches during early stages of succession. Independent of soil moisture, surrounding vegetation and disturbance timing of the molehills, annual species such as *Erophila verna* or *Veronica arvensis* were often the first species recorded on the hills. Apart from these, other species occurred only sporadically,

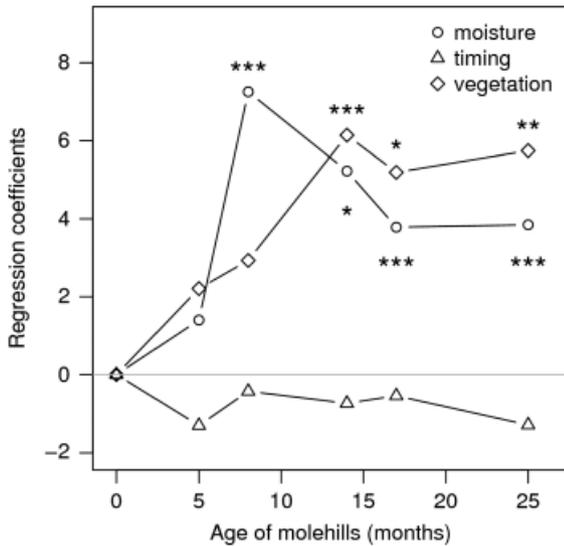


Fig. 2. Coefficients for the three environmental variables, moisture (circle), timing (triangle), and surrounding vegetation (diamond), calculated by multiple regressions on distance matrices and plotted over the age of the molehills.

lacking any pattern with respect to the explanatory variables.

The effect of timing might have been reduced by the existence of seed bank species (Nathan & Muller-Landau 2000). For example, Kalamees & Zobel (2002) showed that 36% of the regeneration in small gaps was due to the seed bank. In an experiment conducted by Pakeman & Small (2005), the seed bank contributed 43% of the developing cover after 1 year. Data from a germination experiment accompanying our study (unpublished results) indicate that germinable seeds from a number of species (e.g. *A. stolonifera*, *R. acetosella*, *Trifolium repens*, *A. millefolium*, *C. arvensis*) are contained in the soil of the disturbed patches. The fact that all molehills that occurred at different points in time but on the same site have the same seed bank, might partly uncouple the recolonization from the species-specific dispersal seasons so that the impact of disturbance timing on species composition is reduced.

Integrating the results, a picture of vegetation development constituting three main stages arises. (1) Soon after disturbance, none of the investigated environmental factors were good predictors of the species composition of the first colonizers. An inspection of community data shows that, generally, annuals such as *E. verna* or *V. arvensis* were the most abundant species on freshly disturbed soil, independent of timing, moisture conditions or surrounding vegetation (see also Milton et al. 1997; Canals & Sebastia 2000). (2) After around 8 months, vegetation composition was significantly different

between wet and dry plots, with species such as *P. reptans* dominating under moist conditions and species such as *A. millefolium* and *P. lanceolata* dominating under dry conditions. (3) From approximately 1 year after disturbance onwards, surrounding vegetation was the best predictor of species composition on the molehills. In this last stage, species such as *A. capillaris*, *A. pratensis*, *P. angustifolia*, *P. lanceolata* and *A. millefolium* became dominant, dependent on composition of the surrounding vegetation matrix.

Several aspects have to be considered when interpreting our findings: The results presented here are based on observations of molehills classified by natural variability rather than experimental treatment. This entails that in order to substantiate the causal relationship between dependent and independent variables, further experimental work is needed. Subsequent studies are also necessary to test for the impact of other environmental variables on community composition over the course of recolonization. Clearly, more than the three factors singled out for this study may affect the vegetation structure at different stages of succession and might even have higher predictive power. Finally, we used whole blocks with their respective community composition as explanatory variables for species composition on molehills. However, in order to estimate the impact of the surrounding vegetation as a seed source for recolonization in more detail, information on the spatial distribution of species around the disturbed patches would be desirable. For future studies, we suggest direct evaluation of the effect of community composition in the area surrounding the disturbed patches as explanatory variable and comparison of the explanatory power of the compositions of surrounding areas of different sizes. Also, the inclusion of species regenerative traits into the analysis (see e.g. Latzel et al. 2008) is a promising approach in order to understand the interplay between abiotic conditions, species pool and succession dynamics.

Conclusion

The results of this study show that the succession on molehills is a function of inter-specific differences in water requirement and local dispersal limitations, as described by Gravel et al. (2006). In order to transfer this knowledge to other study systems, more experimental work is required. However, a general and important result of our study is that the effect of the influencing factors can significantly

change over time. Therefore, we argue that future studies on succession should account for the changing importance of such factors, since a deeper knowledge of temporal shifts in importance of factors influencing species composition will enhance our predictive understanding of succession.

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