

PREDICTING SPATIO-TEMPORAL PATTERNS DURING SUCCESSION IN A POST-MINING LANDSCAPE

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Zusammenfassung

Bergbaufolgelandschaften bieten die seltene Gelegenheit den Prozess einer Primärsukzession nach massiver anthropogener Störung zu verfolgen. Die Analyse von Vegetationsmustern in Raum und Zeit ermöglicht Einblicke in die grundlegenden ökologischen Prozesse der pflanzlichen Wiederbesiedlung und trägt damit zum Verständnis von Vegetationsdynamik bei. Obwohl der Sukzessionsprozess auf ehemaligen Bergbauflächen oftmals sehr langsam verläuft, waren bisherige Forschungsprogramme zumeist auf die üblichen Förderzeiträume von drei bis fünf Jahren beschränkt. Die vorgelegte Dissertation präsentiert nun Ergebnisse einer Langzeitstudie zur Sukzession von Sandtrockenrasenbeständen in der Bergbaufolgelandschaft Goitzsche. Es wurden sowohl ökologische Fragen zur raum-zeitlichen Vegetationsdynamik im untersuchten System als auch methodische Aspekte zur Beobachtung und Analyse derartiger Prozesse bearbeitet. Die Entwicklung von Algorithmen zur Überführung von sigmasoziologischen Vegetationsaufnahmen in Markov-Modelle ermöglichte die Bestimmung von Übergangswahrscheinlichkeiten zwischen verschiedenen Vegetationsstadien und somit eine Quantifizierung von Sukzessionsraten und -wegen. Die Analysen zeigten, dass die verschiedenen Pflanzengesellschaften durch ein raum-zeitliches Netzwerk in Verbindung stehen, innerhalb dessen komplexe Übergänge und sowohl progressive als auch regressive Entwicklungen möglich sind. Ein Zeitreihenvergleich von räumlich-expliziten Habitatmodellen zeigte, dass die Bedeutung biotischer Prozesse, wie Konkurrenz und Nachbarschaftseffekte im Sukzessionsverlauf variiert, wodurch Vegetations-Standortbeziehungen modifiziert werden.

Nach mehr als 30 Jahren weitgehend ungestörter Vegetationsentwicklung war das untersuchte System noch immer weitgehend geprägt von frühen Sukzessionsstadien wie Silbergraspionierfluren und Sandtrockenrasen. Dabei handelt es sich jedoch nicht um ein rigides Vegetationssystem, sondern eher um ein mäßig-dynamisches raum-zeitliches Vegetationsmosaik verschiedener Sandtrockenrasenbestände, die miteinander interagieren. Räumliche Vegetationsmuster sowie Sukzessionsraten und -wege waren teilweise durch die am Standort herrschende Bodenazidität determiniert. Die Analysen ergaben aber auch einen erheblichen Anteil an autokorrelativer Musterbildung, was auf starke Nachbarschaftseffekte durch lokale Ausbreitungsprozesse hinweist. Im Laufe der Untersuchungszeit fand jedoch eine zunehmende Standortbindung und -differenzierung der unterschiedlichen Pflanzengemeinschaften statt. Die Wahrscheinlichkeit, dass Vegetationstypen einander ersetzten erhöhte sich mit der Zeit, was auf eine Beschleunigung des Sukzessionsprozesses und/oder stärkere Fluktuationen hinweist. Insgesamt lassen die Ergebnisse darauf schließen, dass die vorgefundenen Vegetationsmuster durch ein Zusammenspiel von Ausbreitungsprozessen, Standortheterogenität und zwischenartlichen Wechselbeziehungen

gen generiert waren, wobei mit fortschreitender Sukzession die Bedeutung von stochastischen Prozessen abnahm, während deterministische Steuerungsfaktoren durch zunehmende biotische Interaktionen an Einfluss gewannen. Schließlich wurde der Effekt von unterschiedlichen Samplingstrategien auf die Vorhersagegüte von Markov-Modellen mittels einer Simulationsstudie untersucht. Stichprobengröße, Länge der Studie und Untersuchungsfrequenz zeigten signifikante und interaktive Effekte auf die Modelgüte. Besonders aber betonten die Ergebnisse die Bedeutung von Langzeitbeobachtungen für die Entwicklung statistischer Modelle sowie deren Evaluierung und Modifikation und letztlich somit für unser Verständnis von Vegetationsdynamik in Raum und Zeit.

Summary

Surface mining is one of the most important human-mediated disturbances that create the conditions for primary succession. Thus, post-mining landscapes provide the unique opportunity for studying spatial and temporal vegetation patterns to gain insights into the underlying ecological processes, with the final aim to understand and to explain vegetation change. However, permanent plot studies in mining sites rarely exceeded the usual funding periods of three to five years or comprised only a limited number of samples. This dissertation presents a long-term study on the succession of a sandy dry grassland system in the post-mining landscape of Goitzsche. Addressing the theoretical ecological questions of long-term processes, special emphasis was put on methodological issues of how to observe and analyse such processes. The development of algorithms for converting multivariate ecological time series into Markov transition matrices offered the possibility to estimate the probability of transition events between stages, resulting in quantification of succession rates and pathways. The system's trajectories are conceived as a network, in which several stages can develop in two or more other stages and both progressive and retrogressive pathways are possible. Subsequently, temporal comparisons of spatially explicit habitat models provided insights into changing biotic community processes in a system that was not at equilibrium with environmental drivers.

More than 30 years after the start of the succession, the study area was still largely covered by acidic dry grassland communities. However, what superficially appeared to be a stable or merely fluctuating system, turned out to rather be a shifting mosaic of different sandy dry grassland stages. Transitions among vegetation types changed significantly in space and over time but both rates and pathways were to a certain degree determined by environmental site factors. In the earlier phase of succession, soil acidity tended to play a minor role in pattern generation than neighbourhood effects. With ongoing succession, a higher confinement of vegetation patterns to a specific environment occurred. The replacement rate of one vegetation type by another tended to increase with time, indicating that the speed of succession accelerated or fluctuations became stronger. The results suggest that the system is formed by an interplay of dispersal, site heterogeneity and species interactions but shifted during succession from being dominated by stochastic processes to a higher degree of deterministic control.

Finally, a simulation study highlighted the effects of different sampling intensity in space and time on the model's power to adequately describe the trajectories. It turned out that all sampling features, i.e. sample size, study length and observation frequency, interactively affected the Markov models' quality. In particular, the results emphasized the importance of long-term studies for model building, but also for model evaluation and adjustment, thus for our ability to understand vegetation dynamics.

Chapter I

General Introduction

Processes in natural systems and the resulting vegetation patterns vary in space and time. The fundamental goal of vegetation science is to relate the observations taken at these different scales to an explanatory theoretical framework (e.g. Mueller-Dombois & Ellenberg 1974, Glenn-Lewin & van der Maarel 1992, Pickett & Cadenasso 2005). Studying vegetation patterns, both spatial and temporal, is an important first step to gain insights into the underlying ecological processes, thus, to understand and to explain vegetation change (e.g. Anand & Li 2001, Miller et al. 2002, Mark & Wilson 2005, Seabloom et al. 2005, Kéfi et al. 2007, McIntire & Fajardo 2009). However, scientific understanding of observed reality is not usually an end in itself; there are many practical tasks which challenge our ability to predict vegetation change in certain circumstances. The preservation of species, communities and landscapes depend on our ability to predict the consequences of human activities. Strategies for ecosystem restoration and management need to be deeply rooted in a thorough knowledge of the patterns and processes of vegetation change (e.g. Palmer et al. 1997, Suding et al. 2004, van Andel & Aronson 2006, Lindenmayer et al. 2008, Hobbs & Suding 2009). These patterns and processes have been studied extensively in the field of succession ecology. Succession can be most simply defined as changes of vegetation composition or structure at a certain place over time (e.g. Walker & del Moral 2003). Ecological restoration and management are usually aimed at the purposeful manipulation of these changes, thus are intrinsically linked to succession (e.g. Walker et al. 2007, Prach & Hobbs 2008, Walker & del Moral 2009, Matthews & Endress 2010).

Examples for the intrinsic alliance between restoration and succession research are mining sites (e.g. Cooke & Johnson 2002, Norman et al. 2006, Tischew & Kirmer 2007, Řehouňková & Prach 2010, Tropek et al. 2010). Besides natural disturbances such as floods, earthquakes, hurricanes and volcanic eruptions, surface mining is one of the most important human-mediated disturbances that create the conditions for primary succession (e.g. Walker & del Moral 2003). Sites affected by surface mineral extraction cover around one percent of the Earth's land (ibid.). The direct impacts of surface mining are usually severe with the large-scale removal of soil, vegetation, and animals (e.g. Bradshaw 1997, 2000). In Eastern Germany, surface mining of lignite led to the destruction of entire landscapes and the interlinked ecosystems during the last century (e.g. Hildmann & Wünsche 1996, Hüttl 1998, Stottmeister et al. 2002). An area of around 2000 km² was directly affected by surface mining or by lowering the groundwater table (LMBV 2001). The land destruction has been compared with the mass

turnover during the last ice age (Müller & Eissmann 1991). After the German reunification in 1990, 32 of 39 mining sites across East Germany were shut down (Pflug 1998, Steinhuber 2005). During the last decades, post-mining landscapes offered a unique chance to observe primary succession and have been subject to scientific research on spontaneous or initiated restoration of heavily destroyed sites (e.g. Felinks et al. 1998, Kirmer & Mahn 2001, Wiegleb & Felinks 2001a, Tischew 2004, Esfeld et al. 2008, Kirmer et al. 2008).

However, in spite of a general sentiment among scientists that long-term permanent plot studies are invaluable for the development and testing of ecological theories as well as for the detection of long-term processes and changes (Strayer et al. 1986, Franklin 1989, Bakker et al. 1996, Pickett & Cadenasso 2005, Bekker et al. 2007, Müller et al. 2010), research projects and monitoring schemes often deal with shorter time scales due to constraints in financial resources imposed by funding agencies or because rapid results are required (e.g. in the context of restoration activities). Permanent plot studies in mining sites rarely exceeded the usual funding periods of three to five years (e.g. Wiegleb & Felinks 2001a, Szarek-Łukaszewska & Grodzińska 2007, Felinks & Wiegand 2008) and/or comprised only a limited number of samples (e.g. Kirmer & Mahn 2001). Probably most of projects used chronosequences (space-for-time substituting, Pickett 1989) inferring a successional sequence from a series of plots differing in age, i.e. time since last disturbance (e.g. Wali 1999, Wiegleb & Felinks 2001b, Holl 2002, Tischew & Lorenz 2005, Řehouňková & Prach 2006, Frouz et al. 2008). Although this approach is unquestioned useful for qualitative purposes and for hypothesis generation, it is unfeasible for quantitative analyses of spatial and temporal vegetation dynamics (see also Collins & Adams 1983, Jackson et al. 1988, Pickett 1989, Johnson & Miyanishi 2008). Thus, most projects lack either the long-term perspective or the spatial coverage for a quantitative analysis on vegetation change, both, in the sense of spatial pattern over time and in the sense of temporal pattern in space. Actually, these are not only typical issues of succession research, but a general challenge of any study or monitoring program having to handle the trade-offs between costs and benefits, thus, between study intensity in time and space (e.g. Caughlan & Oakley 2001).

For this dissertation, I have had, and gratefully acknowledge, the opportunity to continue and analyze a permanent plot study in a post-mining grassland system. The “sandy dry grassland” dataset from the post-mining landscape of Goitzsche in East-Germany now covers more than a decade (1995-2007) and has been compiled with the aim to monitor the speed and pathways of primary succession. With this data set at hand I was interested in both addressing theoretical ecological questions of long-term processes and methodological questions in the field of observation and analysis of such processes.

Dry acidic grasslands and the study site

Dry acidic grassland communities dominated by grey hair-grass, *Corynephorus canescens* used to be widespread on European inland sand dunes. Due to habitat destruction, afforestation and atmospheric nitrogen deposition these grasslands became increasingly rare and are currently more endangered than bogs or calcareous grasslands (Szymank et al. 1998, Jentsch & Breyschlag 2003). Besides military training areas (e.g. Jentsch et al. 2009), post-mining sites often constitute the last larger remnants of these grassland communities (e.g. Wiegand & Felinks 2001a, Tischew 2004). In the northern mining regions of the Central-German lignite area dry acidic grasslands are relatively widespread. The study site is part of the post-mining landscape of Goitzsche located in Saxony-Anhalt between the towns Bitterfeld and Delitzsch (Plate 1). Until 1974 the investigated area was used first for brown coal surface mining and then to dump overburden layers that consisted of mixed Quaternary and Tertiary material. Since 1993, the process of succession of sandy dry grasslands has been observed at the site (e.g. Mahn & Tischew 1995, Jakob et al. 1996, Schmiedeknecht 1996, Tischew & Mahn 1998, Fromm et al. 2002, Tischew et al. 2004a). Based on small-scale vegetation sampling, a spatial mosaic of plant communities has been observed (see Plates 2-5), which are considered a temporal sequence in grassland succession on inland sand dunes (Passarge 1960, Fukarek 1961, Berger-Landefeldt & Sukopp 1965, Ellenberg 1996). Like on dunes, pioneer stages are dominated by *Corynephorus canescens* forming either the *Spergulo morisonii-Corynephorum canescens* typicum Tx. (1928) or the *Spergulo morisonii-Corynephorum canescens* *cladonietosum* Tx. (1928) 1955 when additionally covered by the moss *Polytrichum piliferum* and *Cladonia* lichen species. For sites of more favourable nutrient supply a rapid development into *Festuco-Sedetalia*-communities characterized by different herbaceous species (e.g. *Helichrysum arenarium*, *Trifolium campestre* and *T. arvense*, *Artemisia campestris*) has been proposed (Fromm et al. 2002, Tischew et al. 2004a). However, merely a description of spatio-temporal grassland stages and their characteristic species is given, while the turnover of stages has rarely been observed. Since 1995, additionally to relevés of small homogeneous plots which are usually taken to study succession, sigma relevés visually estimating the areal extension of pre-defined vegetation types have been collected from the study site. Sigma relevés have been collected in a 10 m-grid on the total area of 4.8 hectare (160 m x 300 m) every three years starting 1995 up to 2007. This method offers the advantage of the census of vegetation complexes to monitor shifts in the dispersion and dominance patterns at a larger scale than feasible with usual relevés of small homogeneous plots. However, statistically sound analyses of spatial and temporal patterns on the basis of sigma relevés have not been made yet. Thus, one challenge was to transfer methodological approaches that are often based on small-scale investigations of species at the level of plant communities. The reduced mapping effort is more time efficient and therefore more feasible in long-term monitoring studies, however, it remains to be seen whether such analyses still provide sufficient detailedness for model building and hypothesis testing.

Plate 1. Central German lignite mining district
(LMBV 2008, modified)

Red circle: post-mining landscape of Goitzsche
Red star: location of the study site
Light green areas: mining sites in recultivation
Brown areas: active mining sites
Olive-green / beige areas: post-mining sites

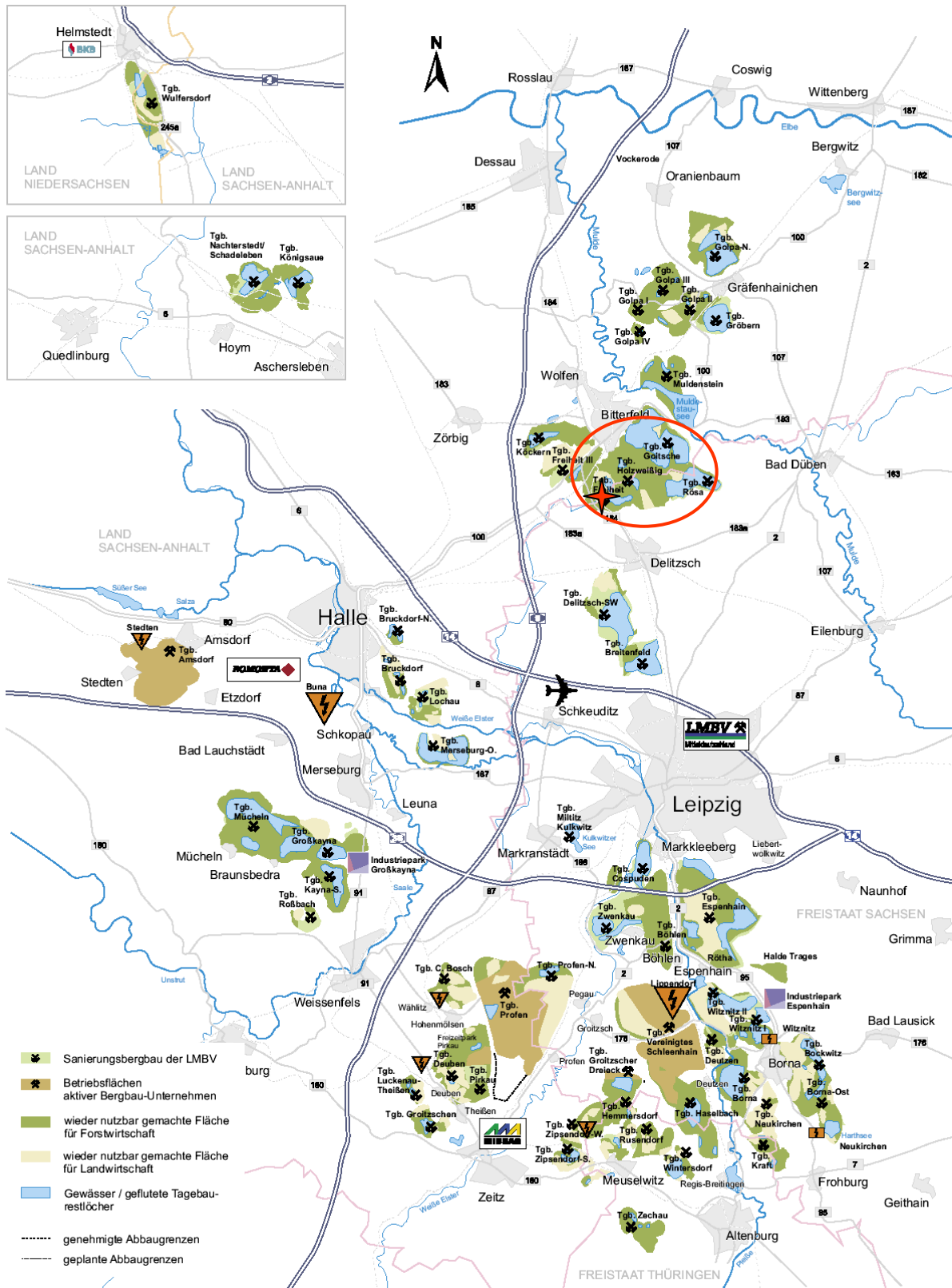




Plate 2. Dry grassland succession stages in the post-mining area of Goitzsche (Saxony Anhalt, Germany), 34 years after start of the succession (August 18, 2008). In the front: Spatial mosaic of bare soil and pioneer communities with *Corynephorus canescens* and cryptogams. To the right: Small patch with *Calamagrostis epigeios*. In the background: Areas dominated by shrubs and trees, mainly *Pinus sylvestris* and *Betula pendula*.



Plate 3. Pioneer stages dominated by grey hair-grass *Corynephorus canescens* – left-hand: *C. canescens* on bare soil, right-hand: *C. canescens* and *Polytrichum piliferum*.

(F. Kommraus, 2005).



Plate 4. Sandy dry grassland communities characterized by different herbaceous species – left-hand: with *Helichrysum arenarium*, right-hand: with *Trifolium arvense*.

(A. Baasch, 2008)

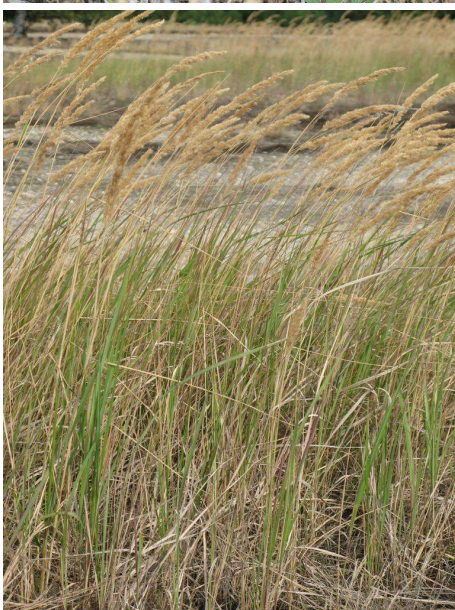


Plate 5. Degenerate phases of sandy dry grasslands – left-hand: *Calamagrostis epigeios* dominance stand, right-hand: sapling of *Pinus sylvestris*.

(A. Baasch, 2008)

Conceptual framework of succession theory

Developed at the beginning of the twentieth century, succession is one of the oldest concepts in ecology (Johnson 1979). Since then, succession ecology has experienced a series of concept developments and is characterized by “a succession of ideas about succession” (Walker & del Moral 2003). Numerous studies on primary succession are provided in the literature from many different sites, e.g. volcanic deposits (e.g. Whittaker et al. 1989, del Moral 2009), dunes (e.g. van der Maarel et al. 1985, Lichter 2000), glacial forefields (e.g. Chapin et al. 1994, Mori et al. 2008), and mining sites (e.g. Prach 1987, Felinks & Wiegand 2008), and several textbooks summarize the current knowledge (e.g. Glenn-Lewin et al. 1992, Walker & del Moral 2003, van der Maarel 2005). It is out of reach to give a complete outline here; therefore I will highlight only some aspects that have influenced my own work.

The first conceptual framework and comprehensive theory of plant succession was offered by Clements during the first three decades of the twentieth century (Clements 1904, 1916, 1928). Succession was viewed as a highly directional, deterministic and predictable process towards a stable climax, which is controlled solely by the regional climate (see also Clements 1936). This concept was challenged by Gleason’s reductionistic approach, which focused on the unique, individualistic behaviour of species and the importance of chance events leading to indeterminate and unpredictable processes (Gleason 1917, 1926, 1927, 1939). With the corresponding shift towards more reductionist perspectives, proximate causes and mechanisms of vegetation change were emphasized and several non-mutually exclusive theories were put forward. An alternative to Clements’ successional concept of waves of species colonizing after the previous species have altered the habitat conditions (relay floristic) was presented by Egler (1954). Egler suggested that succession might be simply the consequence of differential longevity and processes of population dynamics, leading to the sequential conspicuousness of species that all arrive at the beginning but grow at different rates (initial floristic composition). The competitive-sorting model introduced by Margalef (1963, 1968) stressed the importance of species competition causing a temporal gradient in level of community organization and predictability. Pickett (1976) proposed succession as being a gradient-in-time where biological characteristics of species explain their distribution along temporal gradients. Finally, several approaches concentrated on the role of disturbance to explain spatial patterns during succession (e.g. Pickett & White 1985).

Even so, the shift of focus from holistic explanations to more reductionistic and mechanistic approaches was connected with a strong emphasis on prediction as a central issue in studying vegetation dynamics (Glenn-Lewin et al. 1992). Ecologists paid more attention to components rather than generalities and predictions were based on empirical site-specific information. Anyway, the ratio between deterministic and stochastic processes during succession is still being discussed (e.g. Hobbs et al. 2007a, Woods 2007, MacDougall et al. 2008). Deterministic factors include soil properties and biotic processes such as competition or facilitation that can alter species responses. These factors can be

assessed and used to predict vegetation patterns (e.g. del Moral 2009). However, studies on early primary succession have often failed to detect strong correlations between vegetation and environmental site factors (e.g. del Moral et al. 1995, Wiegleb & Felinks 2001b, Tischew et al. 2004b, del Moral & Lacher 2005), suggesting that stochastic processes dominate. However, there is uncertainty about the subsequent importance of deterministic processes in pattern generation (e.g. Lepš & Rejmánek 1991, Tischew et al. 2004b). A related question is concerned with the ratio of exogenous processes (e.g. soil properties) to endogenous processes (e.g. dispersal, biotic community processes) during succession, since spatial patterns usually result from a mixture of both (e.g. Fortin & Dale 2005). Indeed, these questions are quite difficult to answer, since the most of frequently used statistical tools remain phenomenological rather than mechanistic and do provide a static view on a dynamic world, i.e. dynamic aspects of ecological reality such as dispersal or species interaction are not directly represented (e.g. Guisan & Zimmermann 2000, Austin 2002, Guisan & Thuiller 2005, Dormann et al. 2007). Therefore, in my work I sought for methodological approaches that allowed for including dynamic components (see “The choice of methodological approaches” and **chapter II**).

Another topic I paid attention to in my work was the predictability of temporal patterns, thus the successional sequence of a system. Knowledge of succession rates and pathways is crucial for devising restoration strategies of highly disturbed ecosystems, such as surface-mined land. Restoration ecologists wish to know both, rates and pathways, because these determine to what extent and when a site will fulfil desired functions (e.g. Zedler & Callaway 1999). Vegetation scientists are interested in deriving general rules and conclusions by comparing results across different site-specific successional seres (e.g. Walker & del Moral 2003, Prach et al. 2007). Studies suggest that rates and trajectories are affected by several site-specific factors such as site heterogeneity (e.g. Elgersma 1998, Lepš et al. 2000), proximity to colonists (e.g. del Moral et al. 1995, Prach & Řehouňková 2006, Vojtěch & Lepš 2009), priority effects and local dominance patterns (e.g. Wiegleb & Felinks 2001a, Trowbridge 2007, del Moral et al. 2009). Trajectories can be characterized by the following properties (see Walker & del Moral 2003). Vegetation that initially varies in species composition may become increasingly dominated by the same set of species, i.e. individually trajectories converge to resemble one vegetation type (convergence, e.g. Christensen & Peet 1984, Hatton & West 1987, Poli Marchese & Grillo 2000). Likewise, composition can become increasingly heterogeneous with time (divergence, e.g. Lepš et al. 2000, Sarmiento et al. 2003, del Moral 2007) or may develop from distinct starting points to distinct endpoints (parallel trajectories, e.g. Elgersma 1998). Trajectories also can form networks when one stage develops in two or more stages (e.g. Bliss & Gold 1994, Fastie 1995). There may be not only progressive but also retrogressive trajectories, cyclic patterns and fluctuations (e.g. Lough et al. 1987, Mark & Wilson 2005, Walker & Reddell 2007).

Unfortunately, most studies about succession refer to rates in a general way without references to absolute time (Walker & del Moral 2003). Likewise, succession schemes are often expressed without

quantification (e.g. Wiegleb & Felinks 2001a), i.e. without stating the expected time to reach a certain stage or without weighting of multiple trajectories (see also “Methodological approaches”). Wiegleb & Felinks (2001a) presented a conceptual model of spontaneous vegetation development in the Lusatian post-mining landscape inferred from on a comprehensive 4-year survey and analysis of chronosequences (see Fig. I.1). Likewise, Tischew & Lorenz 2005 review the results of several studies on succession in more than 100 mining sites in eastern Germany (e.g. Tischew & Kirmer 2003, Tischew 2004, see also Tischew & Kirmer 2007) and presented a succession model mainly based on classification and ordination analyses of chronosequences (see Fig. I.2).

Both studies showed that *Corynephorus* pioneer stages are often the starting point for many different pathways. In particular, under extreme site conditions (dry, extremely acid) which act as a filter and only allow the colonization and persistence of a few specialist communities of dry psammophytic grasslands, the *Corynephorus* pioneer stages can remain stable for a long time. On sites of intermediate site quality first-comer effects of plants with clonal growth (e.g. *Calamagrostis epigejos*) or high seed production (e.g. *Betula pendula*) play a decisive role for the first seral stages. Wiegleb & Felinks (2001a) also stressed the unique position of *Calamagrostis* being dominant likewise in pioneer stages and also in temporary final stages, inhibiting the invasion of woody species. With ongoing succession the transition to initial woody stages with birch or pine can be expected. However, the exact duration of each stage and the probability of developing into the next stages were not yet quantifiable, because only a few transitions have actually been observed within the study periods. Therefore, one goal of my study was to seek for methodological approaches to quantify successional rates and pathways on the basis of sigma-relevés (see “The choice of methodological approaches” and **chapter III**).

Moreover, I was also interested in the question to which extent results of field studies provide a sufficient basis to derive general rules for both, reconstructing past events and forecasting future developments of a system. It is well known that the quality of all inferences strongly depend on study intensity in time and space (e.g. Abella & Covington 2004, MacKenzie & Royle 2005). The choice of field methods, study length, observation frequency and sample size is a fundamental challenge in planning and implementation of any study or monitoring program (e.g. Block et al. 2001, Archaux & Bergès 2008). While some studies have tested the effects of different techniques or field methods on study results (e.g. Kercher et al. 2003, Korb et al. 2003, Carlsson et al. 2005, Vittoz & Guisan 2007, Milberg et al. 2008, Godínez-Alvarez et al. 2009), surprisingly few case studies have addressed the interactive effects of study frequency, study length and sample size (but see Gerrodette 1987, Mac Nally 1997, Mac Nally et al. 2004). Making use of the “sandy dry grassland” data set with its high number of replicates both in space and time I addressed these issues by creating different sets of study scenarios with varying sampling effort (see **chapter V**).

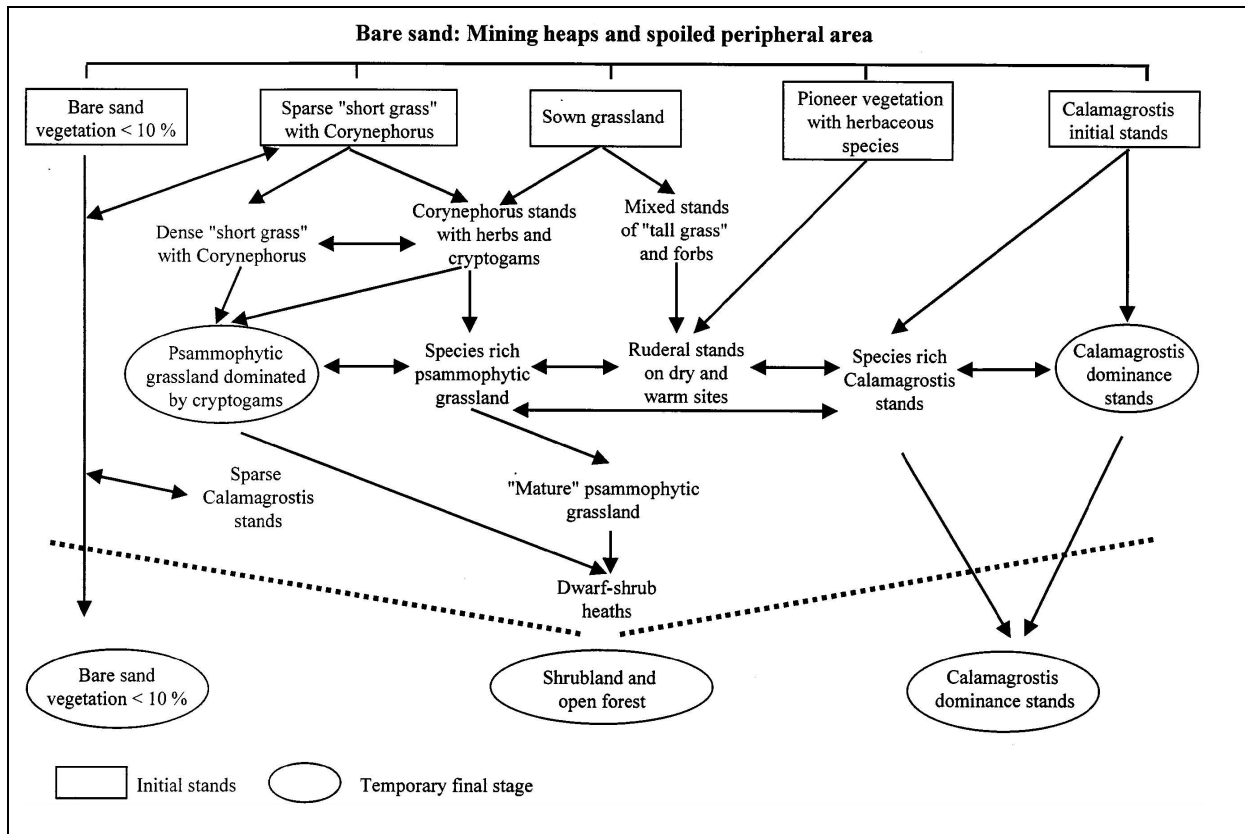


Fig. I.1. Successional pathways in the terrestrial open areas of the Lower Lusatian post-mining landscape. From Wiegleb & Felinks 2001a.

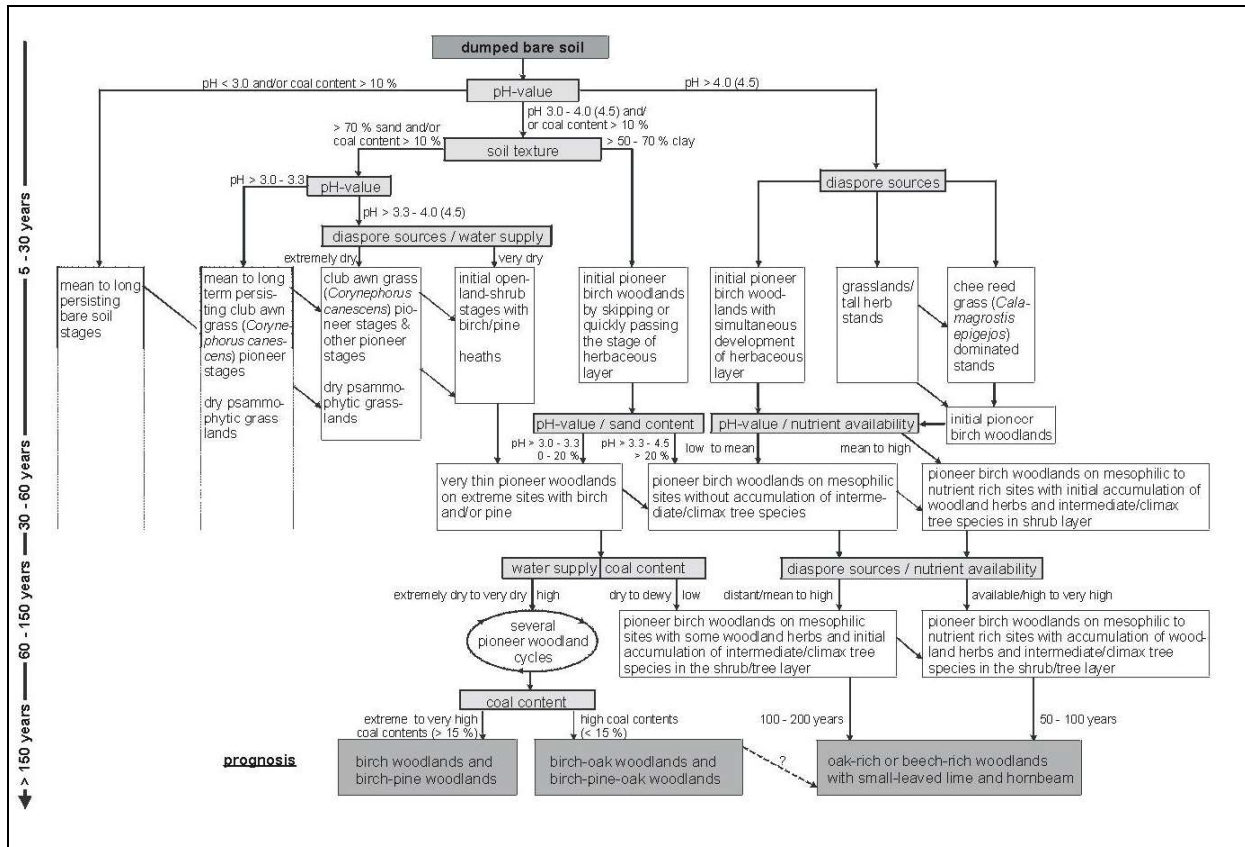


Fig. I.2. Successional scheme for primary succession in post-mining landscapes of eastern Germany. From Tischew & Lorenz 2005, see also Tischew & Kirmer 2007.

The choice of methodological approaches

Most modelling approaches developed for predicting spatial vegetation patterns have their roots either in statistically quantifying species–environment relationships (e.g. habitat models: Guisan & Zimmermann 2000, Austin 2002, Guisan & Thuiller 2005) or in quantifying neighbourhood relationships which belong to the domain of spatial statistics (e.g. Cressie 1993, Fortin & Dale 2005). The strength of habitat models is their ability to predict the realized niches of species that are actually observed in nature, relying on Hutchinson’s view of species being excluded from a part of their fundamental niche by biotic interactions (Ellenberg 1953, Hutchinson 1957, Malanson et al. 1992, Malanson 1997, Silvertown 2004). Hence, the observed pattern is affected not only by environmental factors but also by dispersal, competition, facilitation and other ecological interactions. The domain of spatial statistics is to quantify the pattern itself regardless whether caused by exogenous processes (e.g. soil properties), endogenous processes (e.g. dispersal, biotic community processes) or a combination of both (e.g. Fortin & Dale 2005). Combining both approaches can be expected to allow inferences of the relative importance of environmental factors and endogenous community processes in pattern generation (e.g. Legendre 1993, Lichstein 2002, Dormann et al. 2007). However, a spatial pattern is usually “a single realization” of a process or a combination of processes at one given time (e.g. Fortin et al. 2003). Data are usually sampled during a limited period of time, thus models only reflect a snapshot view of the expected relationships (e.g. Fortin & Dale 2005, Guisan & Thuiller 2005). Therefore, situations with successional dynamics can only be modelled with difficulty (e.g. Guisan & Zimmermann 2000, Perry & Millington 2008). Nevertheless, to do justice to a successional system – or to vegetation change in general – concepts and models should include a temporal component. This could be achieved by a series of “snapshots” along a temporal gradient. However, so far, I am not aware of any study on succession that carried out a temporal comparison of spatially explicit habitat models (**chapter II**).

There is a broad set of tools for studying vegetation dynamics including multivariate approaches as well as analytical and statistical models (e.g. Glenn-Lewin & van der Maarel 1992, Walker & del Moral 2003, Taylor et al. 2009). Ordination methods were frequently used to infer rates and trajectories of succession (e.g. Řehouňková & Prach 2006, del Moral 2007, Matthews & Endress 2010). Most methods for estimating succession rates are based on measures of species turnover (e.g. Anderson 2007), calculate (dis)similarity between successive samples (e.g. Sarmiento et al. 2003) or simply compare the changes in cover or abundance between sample points (e.g. Prach et al. 1993). A shortcoming of these methods is the lack of any estimation of probabilities of events, which are required for quantifying pathways. Thus, rates and pathways are merely expressed in general ways. There are two principal modelling approaches that provide probabilities. Firstly, population dynamic models treat every species separately and then integrate the single models in a community model (e.g. van Hulst 1992). Secondly, statistical models that find stochastic expressions for the transitions from one state to

another state, so-called Markov models (e.g. Usher 1992). Because succession processes can be conceived as a chain of discrete displacement events, the latter approach seems to be the method of choice for quantifying successional trajectories. Markov models are the best-known models which incorporate stochasticity and can be built on the basis of observed changes in the field. However, Markov models are usually based on point observations on single individuals. Thus, data from sigma relevés are not directly convertible into Markov transition matrices (see Usher 1992). Therefore, a great challenge was to find a satisfying solution for converting multivariate ecological time series into transition matrices (**chapter III**).

Thesis objectives

The objectives of this thesis were derived from the open questions as outlined in the preceding chapters. One general aim was to use the long-term dataset to analyse spatial and temporal vegetation patterns and to gain insights into the processes of vegetation change and its underlying driving factors. Another overarching aim was to provide novel and innovative approaches in the field of monitoring vegetation change, with a strong emphasis on methodological issues. The specific objectives of this study can be grouped in three different research topics:

Spatial patterns in time

- How well are vegetation patterns linked to environmental site factors, e.g. soil acidity?
- Do vegetation types shift their realized niche with time?
- Does the relative importance of stochastic and deterministic processes change within time, i.e. is the match between vegetation and environment becoming better in the course of succession?
- Which processes determine the generation of spatial patterns during primary succession?
- How can the relative importance between different processes in pattern generation be assessed?

Temporal pattern (in space)

- What are the main trajectories in sandy dry grassland succession?
- Are trajectories and rates determined by environmental site factors, i.e. soil acidity?
- Do the trajectories and rates vary within time?
- How can the successional rates and different pathways be quantified?
- To which degree can the future development of the system be predicted?

Monitoring intensity in time and space

- How well does a survey reflect successional processes if the sampling effort varies a) in space b) in length of the total observation period, c) in observation frequency, and d) in a combination of these factors?
- What are the practical implications of the above mentioned issues for devising monitoring programs?

The dissertation presented is a cumulative work. In principle, Chapters II to V each are independent papers referring to spatial patterns in time (Chapter II), temporal patterns (Chapter III und IV) and the effects of survey intensity on study results (Chapter V).

In chapter II, we will use a temporal comparison of spatially explicit habitat models for assessing the effect of biotic processes on habitat specificity of species or communities. The issue of the ratio between stochastic and deterministic factors during succession will be addressed.

Chapters III and IV refer to rates and pathways of the sandy dry grassland succession. A solution for converting multivariate ecological time series into transition matrices is presented. The chapters focus on the Markov approach's applicability for measuring rates, quantifying pathways and weighting multiple trajectories as well as for reconstructing past events and forecasting the future development of the system. In addition, rates and trajectories with respect to soil conditions are assessed.

Chapter V presents the results of a simulation approach to highlight the effects of different survey intensities in time and space. A stepwise reduction of sample size, survey lengths and observation frequency is simulated and the effects on Markov models' quality are assessed. The results are discussed with respect for drawing practical implications for devising monitoring programs.

Finally, a synthesis is presented in chapter VI making clear the relationships between the partial results and creating the necessary frame for the joint discussion.

Chapter II

Insights into succession processes using temporally repeated habitat models: results from a long-term study in a post-mining landscape

Baasch, A., Tischew, S. & Bruelheide, H. 2009.
Journal of Vegetation Science 20: 629-638.

Abstract

Questions: The early phases of primary succession are governed by chance events and dispersal-related processes in an environment that is largely free of competition. Thus, the predictability of vegetation patterns using environmental site factors can be expected to be low and spatial autocorrelation to be high. We asked whether the match between vegetation and environment becomes better in the course of succession, and whether vegetation types shift their realized niche with time.

Location: Lignite mining region in Central Germany, the post-mining landscape of Goitzsche (Saxony-Anhalt).

Methods: Vegetation types were mapped in a 10-m grid (total area 4.8 ha), starting in 1995, at 3-year intervals until 2007. We used a temporal comparison of habitat models. We applied: GLS regression to partition the variation in coverage of vegetation types into environmental (soil pH) and spatial components; logistic regression to model the presence/absence of vegetation types along a soil acidity gradient; and autologistic regression allowing for soil acidity and neighbourhood effects.

Results: For most vegetation types, the proportion of variation explained by space was high but declined during succession. The outcome of autologistic models suggests that soil acidity often plays a minor role compared to neighbourhood effects in the earlier phase of succession than 12 years later. For four vegetation types, the pH range in which the type was expected to be dominant clearly became smaller with time. These trends support the view that the role of processes related to chance and dispersal decrease with time, while those related to environmental filtering mediated by biotic interactions increase.

Conclusions: We conclude that temporal comparisons of spatially explicit habitat models provide insights into changing biotic community processes and their effects on habitat specificity of species or their communities. Thus, this approach may be particularly important for analysis of ecological systems that are not in equilibrium with their environmental drivers.

Keywords: Acidic dry grassland; Competitive sorting; Dispersal; Environmental filtering; Environmental range; GLS; pH; Realized niche; Spatio-temporal analysis; Vegetation dynamics.

Nomenclature: Wisskirchen & Haeupler (1998)

Abbreviations: GLS=generalized least-squares.

Chapter III

Twelve years of succession on sandy substrates in a post-mining landscape: a Markov chain analysis

Baasch, A., Tischew, S. & Bruelheide, H. 2010.
Ecological Applications 20: 1136-1147.

Abstract

Knowledge of succession rates and pathways is crucial for devising restoration strategies of highly disturbed ecosystems, such as surface-mined land. As these processes have often only been described in qualitative terms, we used Markov models to quantify transitions between successional stages. However, Markov models are often considered not attractive for some reasons, such as model assumptions (e.g. stationarity in space and time, or the high expenditure of time required to estimate successional transitions in the field). Here we present a solution for converting multivariate ecological time series into transition matrices and demonstrate the approach's applicability for a dataset that resulted from monitoring the succession of sandy dry grassland in a post-mining landscape.

We analyzed five transition matrices, four one-step matrices referring to specific periods of transition (1995-1998, 1998-2001, 2001-2004, 2004-2007), and one matrix for the whole study period (stationary model, 1995-2007). Finally, the stationary model was enhanced to a partly time-variable model. Applying the stationary and the time-variable models, we started a prediction well outside our calibration period, beginning with 100% bare soil in 1974 as the known start of the succession, and generated the coverage of twelve pre-defined vegetation types in three-year-intervals.

Transitions among vegetation types changed significantly in space and over time. While the probability of colonization was almost constant over time, the replacement rate tended to increase, indicating that the speed of succession accelerated with time or fluctuations became stronger. The predictions of both models agreed surprisingly well with the vegetation data observed more than two decades later. This shows that our dry grassland succession in a post-mining landscape can be adequately described by comparably simple types of Markov models, although some model assumptions have not been fulfilled and within-plot transitions have not been observed with point exactness.

The major achievement of our proposed way to convert vegetation time series into transition matrices is the estimation of probability of events – a strength not provided by other frequently used statistical methods in vegetation science.

Keywords: Acidic dry grassland; Markov models; Prediction; Succession; Transition matrix; Vegetation dynamics.

Chapter IV

Long-term monitoring of sandy dry grassland in a post-mining landscape

Baasch, A., Tischew, S. & Bruelheide, H. 2008. In Declerck K. (ed.): Short papers of SER. Proceedings of the 6th European Conference on Ecological Restoration. Ghent, No. 157, pp. 1-4.

Abstract

We applied the Markov approach to a dataset that resulted from monitoring the succession in a post-mining landscape in East Germany. The data have been compiled over more than a decade. We calculated probabilities of processes that determine succession (e.g. colonization, replacement). More than 30 years after start of succession, the study area is still largely covered by acidic dry grassland communities. Particularly at sites characterized by a high substrate acidity, the speed of succession is low and communities with high conservation priority persist over decades. The preservation of suitable sites for such rare communities should be an important goal in restoration schemes for mining areas.

Chapter V

How much effort is required for proper monitoring? Assessing the effects of different survey scenarios in a dry acidic grassland

Baasch, A., Tischew, S. & Bruelheide, H.
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Abstract

Questions: The quality of any inferences derived from field studies or monitoring programs depends on the expenditure of time and effort to make the underlying observations. Here, we used a long-term dataset that resulted from a succession monitoring scheme to assess the effect of different survey scenarios. We address the following questions: (1) How well does a survey reflect successional processes if the sampling effort varies a) in space b) in length of the total observation period, c) in observation frequency, and d) in a combination of these factors? (2) What are the practical implications for devising monitoring programs?

Location: Lignite mining region of Central Germany, post-mining landscape of Goitzsche (Saxony-Anhalt)

Methods: Based on our full data set we constructed subsamples. For the full dataset and all subsets, we constructed Markov models and compared them based on the predictions they made. We assessed the effects of survey intensity on model performance by using generalized linear models and multiple logistic regressions.

Results: Exploring the effects of different survey scenarios revealed significant effects of all three main features of survey intensity (sample size, length, frequency). The most important sampling feature was study length. However, we found interactive effects of sample size with study length and observation interval on model predictions. This indicates that for long-term observations with multiple recording intervals a lower sample size in space is required to reveal the same amount of information as required in a shorter study or one with fewer intervals. Conversely, a high sample size may to some degree compensate for relatively short studies.

Conclusions: Monitoring activities should not be restricted to an intensive sampling over only a few years. With clearly limited resources a decrease of sampling intensity in space and stretching these resources over a longer period would probably pay off much more than totally abandoning monitoring activities after an intensive but short campaign.

Keywords: Markov models; Monitoring; Observation frequency; Sampling intensity; Study length; Succession; Vegetation dynamics.

Chapter VI

Synthesis

This chapter starts with a short summary of study results presented in chapters II to V. Thereafter, I consolidate and discuss the results of my thesis. This discussion does not only repeat the interpretations already discussed in the previous four chapters, but rather takes a broader view and focuses on integrative aspects. Throughout the chapter, I also point out the questions that still remain and give an outlook on future studies.

Summary of results

In **chapter II** I combined the strength of habitat models and of spatial statistics for predicting spatial vegetation patterns. Using a series of model “snapshots” along a temporal gradient and taking into account dynamic ecological processes overcame the restrictions of static statistical models. I showed that temporal comparisons of spatially explicit habitat models allow insights into changing biotic community processes and their effects on the match between vegetation and environment. In the earlier phase of succession soil acidity often played a minor role in pattern generation than neighbourhood effects. However, deterministic control of vegetation patterns increased during succession. Most vegetation types shifted their realized niche with time exhibiting an increasing restriction to particular site conditions, resulting in an increasing match between vegetation and environment during succession. These results suggest that the role of processes related to chance and dispersal decrease with time, while those related to environmental filtering mediated by biotic interactions became increasingly important.

An approach for converting multivariate ecological time series into Markov transition matrices is presented in **chapter III**. The successional system could be adequately described by comparably simple types of Markov models, although some model assumptions had not been fulfilled and within-plot transitions had not been observed with point exactness. I found that trajectories and rates of succession were varying in space and over time. While the rate of colonization was almost constant over time, it changed in space, because environmentally favourable sites developed more quickly than stressful sites. The replacement rate tended to increase with time and was also varying in space, i.e. the probability of replacement events was lower at sites with high soil acidity.

In **chapter IV** I showed that not only rates but also pathways are determined by environmental site factors. Trajectories in harsh environments are more restricted than those observed under favourable conditions. Finally, I demonstrated that simple stationary Markov models, despite their power to measure rates, quantify pathways and reconstruct past events, have limited use in forecasting the future development of the system, making time-variable models indispensable (**chapter III**).

In **chapter V**, the results of a simulation study have been presented, which addressed the effects of different sampling intensity in space and time on study results. I showed that all sampling features, i.e. sample size, study length and observation frequency, interactively affected the quality of study results. Long-term studies required a lower sample size to capture the same amount of information than simulated short-term studies. A high sample size in space did to some degree compensate for a short-term study perspective. Nevertheless, the most important sampling feature was study length. Thus, our findings highlighted the importance of long-term studies not only for model building, but also for model evaluation and adjustment.

Discussion

When I started my analyses I did not expect to find such a high variability of vegetation patterns in time and space as was finally encountered. Looking only at the average composition of the system I had the impression that the grassland system changed only slightly between years. Unsurprisingly, the amount of bare soil tended to decrease and shrubs and trees slowly but steadily increased. All other vegetation types did not show any obvious directional trend. More than 30 years after the start of the succession, the study area was still largely covered by acidic dry grassland communities, indicating that sandy, acidic and nutrient-deficient successional sites in former mining areas offer long-term habitats for competitively inferior species and plant communities. Thus, the preservation of suitable sites for such rare communities should be an important goal in restoration schemes for mining areas (see also Schulz & Wiegand 2000, Tischew & Kirmer 2007, Kirmer et al. 2008).

However, what appeared to be a stable or just fluctuating system, rather turned out to be a shifting mosaic of different sandy dry grassland stages. Analyses on temporal vegetation patterns revealed a considerable amount of replacement events, although the net change in the area covered by vegetation types was comparably small (Table III.2 and Table III.3). Trajectories can be best described as a network, in which several stages can develop in two or more other stages and both progressive and retrogressive pathways are possible. However, the major achievement was to obtain the estimated probability of transition events and thus to reveal that some of the trajectories are more likely than others (Fig. III.3).

Shifts in vegetation patterns were by no means absolutely random, even though stochastic dispersal related processes certainly have played a decisive role in succession (see also del Moral et al. 1995,

Prach & Řehouňková 2006). Both, rates and pathways were to some degree determined by environmental site factors (Table III.5, Fig. IV.2) and temporal changes often led to a higher confinement of spatial vegetation patterns to a specific environment (Fig. II.3, Fig. II.4). Thus, the network can be conceived as interplay of stochastic dispersal, site heterogeneity and species interactions (see also e.g. Bliss & Gold 1994, del Moral 2007). Within this interplay, a shift from stochastic processes to more deterministic control took place as dispersal limitations became less important and species interactions more intense.

There are a few studies that detected either dominant dispersal effects (e.g. Wood & del Moral 1987, del Moral et al. 1995, Prach & Řehouňková 2006, Řehouňková & Prach 2008, Vojtěch & Lepš 2009) or greater deterministic control in succession (e.g. Hodkinson et al. 2003, Shiels et al. 2008). This study disclosed that both processes can dominate a system at the same location but at different times. Thus, this finding points to a trade-off between both types of processes. Recently, del Moral (2009) published an interesting paper, in which he demonstrated that deterministic control of vegetation development also increased during primary succession on Mount St. Helens over 16 years (1993-2008). The shift from spatial to environmental factors was revealed by covariance analysis. In the first years (1993, 1997, 2001) only spatial effects were significant, while later these effects were no longer significant and soil factors became prominent predictors (del Moral 2009). Thus, the shift from stochastic dispersal related processes to those more related to environmental filtering as a result of stronger biotic interactions seems to be similar in both studies, but the causes might be different. On Mount St. Helens, the development of deterministic effects was associated with a decline of ephemeral species and increasing dominance of persistent species with strong vegetative growth and greater longevity. This development might conform to some aspects of the gradient-in-time model as species were distributed along a temporal gradient based on their biological characteristics (Pickett 1976). In contrast, the average composition of the post-mining grassland system remained more or less constant, and almost the same set of characteristic species was present from the beginning and throughout the study period. This fact, together with more narrow environmental ranges of vegetation types' dominance, argued for some aspects of the competitive-sorting model implying niche width restrictions due to competitive interactions within the same set of species over time (Margalef 1963, 1968).

Unfortunately, successional processes at the study site have not been observed right from the start. Thus, we can not say at which time certain species have actually reached the site and hence, whether relay floristic (Clements 1904, 1916, 1928, Drury and Nisbet 1973) or rather initial floristic composition (Egler 1954) may apply to this succession series. However, as both concepts are idealized representations of extreme conditions, it is most likely that aspects of both concepts have been emerged. No strong evidence was encountered for the idea that well-defined waves of species colonized the site after the habitat conditions had been altered by previous species (relay floristics). However, I found that particularly in stressful sites, bare soil was almost exclusively colonized by pioneer stages

(Fig. III.3 and p. 58). Thus, site alteration by *Corynephorus canescens* and cryptogams might be an important first step (see also Süß et al. 2004, Felinks & Wiegand 2008). Other facilitative processes might also be involved. For example, the preceding legume stages might have facilitated the spread of *Calamagrostis epigejos* by enhanced nutrient supply (Fig. III.3; see also Schmidt & Brübach 1993, Chapin et al. 1994, del Moral & Rozzell 2005). Unfortunately, no data of habitat modification by certain species is available for the study site. Even so, relay floristic will unlikely fully explain the shifting mosaic and trajectory network observed in our study. Several studies stressed the role of small-scale disturbances in creating dynamic mosaics of various successional stages in dry acidic grasslands (e.g. Heinken 1990, Friedrich 2001, Jentsch 2001, Jentsch et al. 2002). Although bare substrate was not often exposed in large amount at later stages of the succession (Table III.3), it might be that disturbance by ants or small mammals might have been important in pattern generation at finer spatial scales. Shifting mosaics can also be caused by internal community processes which lead to cycling trajectories with upgrade and downgrade phases in succession (e.g. Watt 1947, van der Maarel 1996, Herben et al. 2000). A key point in the cycle is environmental change (e.g. resource availability) induced by species occupying the site. By revisiting the main trajectories observed in our study site (Fig. III.3) some indications can be found that those cycles might have occurred at our study site. For example, there is a considerable probability that pioneer stages have been developed into herbaceous stages, which then were replaced by the *Calamagrostis epigejos* type, which in turn showed regressive transitions back to the pioneer stages. However, in the statistical analyses we did not track the individual fate of certain plots. Therefore, it is questionable whether progressive and regressive succession displaced each other at the same place over time, forming a “true” cycle or whether it is a matter of progressive and regressive trajectories occurred at different sites (see also Fig. IV.2). The latter might also appear as a cycle when successional dynamics are summarized and simplified. Hence, tracking individual plot histories will be an important next step to gain further insight.

It might be that many of the species have arrived at the site quite early. For example, *Pinus sylvestris* had already established the first individuals in the early eighties (1981/82, Kommraus 2008) but has been expanding rapidly only in the last decade, after the first of the established individuals had set fruit. Thus, succession also might be partly a result of differential longevity of species, which all arrived at the beginning but then grew at different rates (initial floristic composition, Egler 1954). Interestingly, the final stage dominated by shrubs and trees did often follow directly the pioneer stages instead of displacing the herbaceous stages. However, as predicted by the time-variable Markov model, the composition of the system will become increasingly dominated by *Pinus sylvestris* (Fig. III.1). Individually trajectories probably will converge to resemble one vegetation type, and convergence is a distinct characteristic of determinism (see also Glenn-Lewin & van der Maarel 1992, Walker & del Moral 2003). In the next years, woody vegetation will become more and more evenly distributed over the site and *Pinus sylvestris* is likely to become the all-dominant player in the system. It is worth thinking about some consequences of this process for the predictability of vegetation pat-

terns, i.e. the match between vegetation type's occurrence and particular site conditions. In our study period, areas dominated by shrubs and trees seemed to occur rather independently of the soil acidity but showed increasing neighbourhood effects due to patch growth around mature trees (e.g. Fig. II.2). This dispersal related process will increasingly form a mosaic of woody patches and gaps, whereby the latter provides refuges for acidic dry grassland communities but the resulting spatial pattern will probably be unpredictable by environmental soil factors. From this point of view, it seems that the system will return to be dominated by chance and dispersal related processes rather than by deterministic factors. Therefore, the ratio between stochastic and deterministic factors (and also endogenous and exogenous processes) may shift once or several times during succession, and thus depends on the time frame considered but also on the research focus (e.g. convergence in community assembly vs. the degree of vegetation-environmental linkages; see also Hobbs et al. 2007a, Woods 2007).

It should be pointed out clearly that the inferences about the future development of the system are usually worse than those about previous processes. Unexpected future events are a general drawback of any predictions (Fig. III.1 and pp. 72-76). Therefore, the field observations have to continue to allow for evaluating model predictions and keeping the models updated. This thesis showed that temporal comparisons of spatially explicit habitat models can provide valuable insights into changing biotic community processes in ecological systems that are not at equilibrium with their environmental drivers (chapter II). Working with sigma-relevés turned out to be a reasonable approach. The results of this thesis show that methodological approaches that have been used so far for small-scale investigations at the level of individuals are also applicable to sigma-relevés, and thus still provide sufficient information for model building and hypothesis testing. However, the approach did not only have the advantage of a reduced mapping effort. Some patterns might have not been observable at a finer scale. What turned out to be a shifting mosaic would most likely have appeared to be a fluctuation at the scale of small-scale relevés or mapping of individual plants (unpubl. data, see also Tischew & Baasch 2004). However, such a systematic comparison across scales has not been accomplished yet, but would be worth doing in future.

Of course, there are also some disadvantages of sigma-relevés. A crucial point is the *a priori* state definition, since a continuum is divided into a finite number of classes. The choice and the number of defined states have to be subjective to some degree, regardless which method is used for definition (e.g. Usher 1992, Lepš & Šmilauer 2003). The sandy dry grassland stages were defined in terms of dominance of occurring species. However, other assemblages also occurred, which did not fit in *a priori* defined states. With time such "other/undefined communities" will become more frequent challenging us to redefine states. Modifications will also be required to answer new arising questions. For example, woody stages dominated by different tree species may play an important role in future, thus should be separately mapped.

Although the results suggest an attractive solution of reducing the mapping effort by a further reduction of sample sizes (Fig. V.2), the future monitoring of the site should adhere to the entire grid, and in addition, continue to record relevés at fine scales as long as possible. The more time and effort will be invested in the ongoing monitoring, the more precisely we will understand the pathways and mechanism of community or ecosystem changes. The ratio between sampling effort and ecological information gained to achieve a specific objective (e.g. monitoring successional pathways, chapter III) might become disproportionate with increasing sampling effort, but with any reduction we have to accept also the limitation of additional scientifically options (e.g. spatial analyses, chapter II). I am convinced that studies that provide many replicates both in time and space are the best basis for the development and testing of ecological theories. However, if forced to decide about a future reduction of effort, the decision should be made in favour of the long-term perspective.

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Publikationsliste

Publikationen in Fachzeitschriften und Büchern

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig und ohne fremde Hilfe verfasst habe. Es wurden keine anderen als die angegebenen Quellen und Hilfsmittel benutzt und diese auch als solche kenntlich gemacht.

Ferner erkläre ich, dass diese Arbeit bisher weder der Naturwissenschaftlichen Fakultät der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde. Ich habe mich bisher noch nie um den Doktorgrad beworben.

Halle/Saale, den

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