Plants in urban brownfields

Modeling the driving factors of site conditions and of plant functional group occurrence in a dynamic environment

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[...] Le petit prince était maintenant tout pâle de colère.

»Il y a des millions d'années que les fleures fabriquent des épines. Il y a des millions d'années que les moutons mangent quand même les fleurs. Et ce n'est pas sérieux de chercher à comprendre pourquoi elles se donnent tant de mal pour se fabriquer des épines qui ne servent jamais à rien? Ce n'est pas important la guerre des moutons et des fleurs? Ce n'est pas sérieux et plus important que les additions d'un gros Monsieur rouge? Et si je connais, moi, une fleur unique au monde, qui n'existe nulle part, sauf dans ma planète, et qu'un petit mouton peut anéantir d'un seul coup, comme ça, un matin, sans se rendre compte de ce qu'il fait, ce n'est pas important ça?!« [...]

(du livre Le Petit Prince, Antoine de Saint-Exupéry)

[...] Der kleine Prinz war jetzt ganz blass vor Zorn.

»Es sind nun Millionen Jahre, dass die Blumen Dornen hervorbringen. Es sind Millionen Jahre, dass die Schafe trotzdem die Blumen fressen. Und du findest es unwichtig, wenn man wissen möchte, warum sie sich so viel Mühe geben, Dornen hervorzubringen, die zu nichts Zweck haben? Dieser Kampf der Schafe mit den Blumen soll unwichtig sein? Weniger ernsthaft als die Additionen eines dicken, roten Mannes? Und wenn ich eine Blume kenne, die es in der ganzen Welt nur ein einziges Mal gibt, nirgends anders als auf meinem kleinen Planeten, und wenn ein kleines Schaf, ohne zu wissen, was es tut, diese Blume eines Morgens so mit einem einzigen Biss auslöschen kann, - das soll nicht wichtig sein?!« [...]

(aus: Der Kleine Prinz, Antoine de Saint-Exupéry)

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General introduction

Chapter 1
General introduction

Background

Plant-environment relationships, habitat models and their generality

What parameters influence plant species survival and species composition in an environment? For centuries, this question has been of broad interest for both plant ecologists and conservationists (e.g. Raunkiær 1934). Today, this topic has gained even more relevance against the background of increasing human environmental impact and declining biodiversity, which evokes a need for predictions concerning the consequences of environmental change. A way of analysing and moreover of quantifying species - environment relationships are habitat models (cf. Guisan & Zimmermann 2000, Pearce & Ferrier 2000b). These models formalize the relationships between a species or a group of species and its respective environment (Morrison *et al.* 1998) and thus are a manner to describe complex systems (Schröder 2000). By habitat models, species - environment relationships are quantified, and therefore provide measures that (i) enable us to predict the consequences of environmental changes and (ii) give an impression of the general relevance of habitat factors for the respective species (Schröder & Richter 1999/2000). However, regression models are based on the principle of equilibrium and thus they are non-dynamic by definition. Thus, their use in modeling species in disequilibrium is problematic (Gibson *et al.* 2004). In addition, the predictive ability of models can be limited by different environmental as well as methodological effects, e.g. by differences in ranges of environmental parameters, in survey techniques, or in regional prevalences of the species (Pearce & Ferrier 2001, Vaughan & Ormerod 2005).

In 1981, so called ‘habitat suitability models’ were used for the first time by the U.S. Fish & Wildlife Service, deriving suitability indices based on expert knowledge and general rules concerning the habitat preferences of species (Schröder 2000). Later on, due to the advanced availability of soft- and hardware sources, there was an increasing use of multivariate statistics (e.g. Morrison *et al.* 1998). In recent years, logistic regression has become a widely used tool throughout ecology and conservation biology (Pearce & Ferrier 2000b, Guisan & Thuiller 2005), providing descriptive statistics that can handle also presence/absence data, which are a widespread type of data in ecology. In nature conservation practice, habitat models derived by logistic regression provide a basis e.g. to predict the effect of certain management strategies in order to create specific management plans (e.g. Lindenmayer *et al.* 1993, Stephenson *et al.* 2006), or to assess biotopes concerning their habitat suitability for certain species (e.g. Gibson *et al.* 2004).

In order to use the predictions made by these models effectively in conservation planning, it is however essential to validate their predictive accuracy and thus their general applicability in space and time (Bonn & Schröder 2001, Pearce *et al.* 2001, Bulluck *et al.* 2006). Despite the widespread application of predictive models, evaluation of model performance is rarely done (Vaughan & Ormerod 2005, Bulluck *et al.* 2006), especially in vegetation ecology. In addition, little attention has been devoted to the development of appropriate evaluation techniques for assessing the predictive performance of habitat models (Pearce & Ferrier 2000a). In general, the predictive performance of logistic regression habitat models should be evaluated in terms of two measures: calibration (the agreement between predicted probabilities and observed occurrence), and discrimination (the ability of a model to correctly distinguish between occupied and unoccupied sites) (Pearce & Ferrier 2000a, Vaughan & Ormerod 2005).

Despite the rare application of model validation in ecology, there is a variety of terms to describe the validity of models in space and time: predictive accuracy (Pearce *et al.* 2001), generality (Bulluck *et al.* 2006), generalizability (Altman & Royston 2000, De Bello *et al.* 2005, Vaughan & Ormerod 2005), transferability (Betrus *et al.* 2005, Schröder & Richter 1999/2000), transportability (Vaughan & Ormerod 2005, Altman & Royston 2000). Recent examples of studies systematically investigating the generalizability of predictive models in animal ecology are those of Fleishman *et al.* (2003), Jensen *et al.* (2005) and Bulluck *et al.* (2006). Strauss & Biedermann (in prep.-a) tested spatial and temporal model generality for phytophagous insects of urban brownfields. However, besides these studies, hardly any attention has been paid to the validation of plant ecological models. De Bello *et al.* (2005) explored the predictive value of plant traits' response to grazing along a climatic gradient in the Mediterranean. This study, however, rather compared whether a common set of plant functional traits would provide consistent predictions of species responses to grazing in different regions, than performing a direct spatial validation of models of plant functional groups. Kleyer (2002) gave an example for a model transfer in plant functional ecology. He investigated the transferability of models of plant functional types between the urban and the agricultural landscape by comparing observations and modeled predictions, finding recurrent patterns of several functional types in both contrasting landscapes.

Plant traits and plant functional groups

In the beginning, plant community ecology was closely related to plant geography and, in the middle of the 20th century, shifted towards a more dynamic view of understanding processes that produce patterns of plant communities observed in nature. A more recently established field of plant ecology aims at understanding the evolution of species traits and behaviors that lead to observed patterns (Bazzaz 1996, Diaz *et al.* 2001, Lavorel & Garnier 2002, Kahmen & Poschlod 2004, Gondard & Deconchat 2004, Kleyer & Knevel 2005). All plants that are part of succession – not only in urban brownfields - must occupy certain morphological and physiological traits (the so called 'functional traits', Gitay & Noble 1997, Lavorel *et al.* 1997) to cope with and to exploit the changing site conditions. To get a general understanding of those biological processes it is crucial to investigate the pivotal plant traits (Rebele 1994, Bazzaz 1996, Müller & Rosenthal 1998, but see Lindborg & Eriksson 2005). Since plant traits show a wide variety of trade-offs and correlations, functional abilities of species can often be characterized by a small set of traits (Weiher *et al.* 1999).

Moreover, to derive generalizable principles of succession and ecosystem recovery, a grouping of species is essential (Bazzaz 1996, Diaz *et al.* 2001, Kahmen & Poschlod 2004). Plant functional groups (PFGs) are non-phylogenetic groupings of species which perform similarly in an ecosystem based on a set of common biological attributes (Gitay & Noble 1997) and which allow ecosystems to maintain their function even in the face of an extinction of particular species (Shugart 1997, Walker *et al.* 1999). Even if plants within the same community differ in their response to the environment, they share common features from which generalizations can be made. Thus, species can be grouped by similar function or similar response to environmental factors (i.e. by 'functional traits') in order to obtain information about the *group*, rather than about *each member* of the group. This is often sufficient to identify general rules which allow predictions (Bazzaz 1996, Diaz *et al.* 1999, Keddy & Weiher 1999, Kleyer 1999, McIntyre *et al.* 1999a, but see Lindborg & Eriksson 2005). In this regard, statistical tests and habitat modeling are crucial instruments to investigate, whether the observed patterns differ from chance expectation (Weiher & Keddy 1999). A critical point in this regard is the tension between simplicity of models for prediction and complexity to include all relevant parameters. A way to bridge the gap between simplicity and satisfactory precision is the use of known correlations among environmental factors and among plant responses to reduce the number of parameters needed for modeling and predictions (Bazzaz 1996, Westoby 1998, McIntyre *et al.* 1999b, Weiher *et al.* 1999, Lavorel & Garnier 2002).

Urban brownfields

Up to the 1980s, brownfields were seen as an ecological problem, especially in agricultural areas (Kaule 1991). Today, not only ecologists see the advantages of brownfields, notably in urban areas which normally bear a low proportion of natural habitats. Urban brownfields, sites formed by different types of wasteland within city areas (e.g. previously developed land, abandoned railroads or newly created sites), are valuable sites not only because of their positive functions on urban climate or their social value as natural wildspace (Sukopp & Wittig 1993, London-Wildlife-Trust 2002). In today's static and well-tended cultural landscape they represent the only space where natural procedures may run without direct human influence (Kaule 1991). Moreover, they comprise a spatial and temporal pattern of different abiotic conditions and successional stages (Rebele 1992). Concerning the abiotics, a feature of many urban areas is the wide variety of environmental conditions. Soils in cities are usually considerably influenced by human activities and thus can be everything from nutrient poor to highly enriched. These environments are also characterized by high variances in light, moisture and microclimate (Rebele 1994). Depending on initial soil conditions and initial floristic composition (e.g. Egler 1954), the vegetation of urban brownfields shows more or less specifiable successional stages, moving from ruderal annuals to short-lived perennial herbs, being replaced by long-lived perennials and, depending on environmental conditions, by shrubs and woody species. The mentioned variety of patterns supplies new habitats for plant and animal species and provides room for the withdrawal of species (Dettmar 1995).

The characteristical spatio-temporal dynamics and transient character of urban brownfields induce a relatively high diversity of species, as was demonstrated by many studies in the last decades (e.g. Walters 1970, Gilbert 1989, Sukopp 1990, Kaule 1991, Rebele 1991, Sukopp & Wittig 1993, Rebele 1994, Rebele & Dettmar 1996, Niemelä 1999, Rebele & Lehmann 2002, Harrison & Davies 2002, Ricketts & Imhoff 2003, Kühn *et al.* 2004). Further scientific research on succession and dynamics of urban brownfields is crucial to form a basis for predictability of and thus for decisions on sustainable development of those areas (Sukopp & Wittig 1993, Niemelä 1999, Wood & Pullin 2002), especially for a reinforced embedding of the ecological function of brownfields in an urban planning context (Harrison & Davies 2002, London Wildlife Trust 2002).

Succession and temporal development of urban brownfields

In a broad view, succession is the recovery process of vegetation following any disturbance (Bazzaz 1996). Many early ecologists considered succession being a community-level phenomenon. More recent views see succession as a multidirectional, probabilistic process which can have more than one endpoint (Bazzaz 1996, Blatt *et al.* 2005). There have been different approaches to cope with the processes and the predictability of ecosystem succession. Numerous measures for succession have been used in ecology, varying from the abundance of focal species (Yao *et al.* 1999) to the inquiry of a turnover in dominance by life-history groups (Leps 1987), community composition, species richness or spatial heterogeneity in species composition and abundance (Legendre & Fortin 1989). Connell & Slatyer (1977) proposed an approach dealing with the interactions of individual plants and the availability of limiting resources (successional pathways defined by ‘facilitation, tolerance and inhibition’). A common distinction is that of primary and secondary succession (Tilman 1988, Rebele 1994). Primary succession starts with a bare substrate lacking organic humus and plant propagules or any diaspore bank. Secondary successions are determined by an organic soil and plant propagules or diaspores being present from the start (the so-called ‘initial floristic composition’, Egler 1954).

The phenomenon of succession and especially the changes of soil parameters in the course of succession have been studied in various types of landscapes like abandoned fields (Knops & Tilman 2000, Wang 2002), meadows (Korzeniak 2005) and forests (Hardtle *et al.* 2003). There are only few studies of succession on urban brownfields (Rebele & Lehmann 2002). Moreover, the aspect of analyzing soil changes and their relationships with vegetation development has been usually neglected in studies of secondary succession (Abadin *et al.* 2002). In urban brownfields there may be both primary, secondary or intermediate types of succession (Vandermaarel *et al.* 1985, Tilman 1988, Rebele 1992). In general, there are three types of man-induced successions in urban brownfields: (i) those induced by mere abandonment of sites, (ii) successions initiated by severe disturbance attending the destruction of existing biomass, and (iii) succession on sites newly created by filling up soil material (Rebele & Dettmar 1996).

Time since initiation is stated as a general trajectory for succession (Cook *et al.* 2005). One of the main driving factors of the successional course over time is the type of substrate (Gilbert 1989, Chapin *et al.* 2002).

Soil parameters change during the course of succession. Several studies show an increasing acidification, a small increase in soil cation exchange capacity and increasing loads of nitrogen while phosphorus contents of soil may decrease over time (e.g. Richter *et al.* 1994, Chapin *et al.* 2002, De Deyn *et al.* 2004). In addition, vegetation structure may influence soil parameters directly (Isermann 2005). The successional sequence of vegetation development is dominated by annuals in the first year, monocarpic perennials in the second, and perennial herbs and grasses from the third (Rebele & Lehmann 2002). The arising of woody plants is contingent on nutrient conditions and vegetation structure. Along a gradient of decreasing nutrient status, the individuality of successional stages decreases whereas the development towards a stage dominated by woody plants increases (Bornkamm & Hennig 1982, Rebele 1992, Müller & Rosenthal 1998). However, the floristic development of a site seems to be influenced not only by abiotical factors. Those factors give a general framework within which different successional pathways are possible whereas species biological traits and the dynamic behavior of involved species (allocations/allometries, Westoby *et al.* 2002, Malausa *et al.* 2005) are additional driving forces of succession (Bazzaz 1996, Müller & Rosenthal 1998).

In general, the highest biodiversity of ecosystems was found at both mid-stages of the successional sere and an intermediate level of soil conditions (Wang 2002, Cook *et al.* 2005). Moreover, plant species richness and occurrence of insect species depend on vegetation structure (Gough *et al.* 2000, Schaffers 2002, Strauss & Biedermann in prep.-b). In summary, time, soil parameters, and vegetation structure seem to be the main driving factors of succession in urban brownfields. The fact that soil and vegetation structure are both dependent and independent parameters complicates the predictability of site development. This leads to the question which factor influences vegetation structure and thus species richness in urban brownfields most, a question that may be important both for predictions and management of urban brownfields in order to sustain their high biodiversity.

Hypotheses and objectives

Urban brownfields are habitats of high spatio-temporal dynamics and thus form a challenging environment for species occurring under these conditions. The response of species in terms of functional traits can shed light on mechanisms underlying species survival in urban brownfield habitats by the detection of plant - environment as well as of trait - environment relations. In this context, on the one hand, it is crucial to get information about the driving factors of the environmental conditions that form the basis for the development of urban brownfields and thus for the demands on species ocurring in these habitats. On the other hand, the detected rules of plant - environment as well as of trait - environment relations must be formalized, e.g. by means of habitat models. These models enable us to estimate the influence of environmental factors on species or species groups and to make predictions based on the derived general principles. However, the generality of the models is a highly relevant factor for the application in nature conservation practice. It must be assessed by a validation of the models in space and/or time, i.e. by assessing their transferability.

It is assumed that:

- Plant traits show a functional response to the changing conditions of urban brownfields. Traits that are associated with the spatio-temporal dynamics of the environment are most crucial for species survival in urban brownfields. This can be expressed by means of a set of functional traits representing plant functional groups (PFGs) along the environmental gradient.
- Habitat models of PFGs of urban brownfields show similarities across regions. Under certain conditions, they are transferable in space.
- Soil parameters of urban brownfields change during the development of sites over time. The temporal development of the sites' vegetation structure is contingent on these changes but moreover on site age, representing time for settlement and growth of species.

The detection of relevant strategies for species survival in the dynamic environment of urban brownfields was done by clustering and modeling plant functional groups according to species traits and environmental conditions (Chapter 3). Instead of including all available plant traits in our analysis, we preselected a set of candidate traits comprising major attributes of the life cycle of a plant.

The derived results are of considerable relevance for the planning practice in order to sustain the biodiversity of urban brownfields. To verify the regional applicability of the results, the transferability of the habitat models of the PFGs was tested across three cities (Chapter 4).

To contribute to a general understanding of urban soil processes, the temporal development of abiotic parameters over time was evaluated and linked with the development of vegetation structure (Chapter 5), providing useful insights for site management.

Outline of the thesis

This thesis is part of the project 'TEMPO - temporal biodiversity and building' funded by the German Federal Ministry of Education and Research under FKZN 01 LM 0210. The aim of the project is to investigate the feasibility of a sustainable use of industrial and commercial areas. Open space and development are seen as two states of a spatio-temporal cycle, a concept that enables both conservation and development. TEMPO evaluates the idea of 'temporary conservation' in urban brownfields by bringing together research facts and the ideas of architects, socio-economists, planners, and landscape ecologists.

The present thesis considers plant - environment and trait - environment relationships and evaluates strategies of plants to survive in the changing environment of urban brownfields. In Chapter 3, plants are grouped together to plant functional groups (PFGs) by similar trait responses. Habitat models of the derived PFGs provide information about their relationship with the environmental factors and give ideas of traits which are crucial for species survival in urban brownfields. Chapter 4 evaluates the transferability of PFG models across three cities and thus gives hints on the regional generality of the derived models. This is relevant for an assessment of their application in conservation planning and management. Chapter 5 investigates the temporal development of soil parameters of urban brownfields and their relationships with vegetation structure, particularly concentrating on the differences in relevance of abiotic parameters and time for vegetation structure. Box 1 focuses on the question whether field measurements of soil water tension correctly reflect plant availabe field capacity derived from the 'Bodenkundliche Kartieranleitung', which is relevant to assess the international acceptance of values derived from this national manual of soil mapping. Box 2 gives an example for the habitat model transfer of an invasive plant, *Senecio inaequidens* DC., from Bremen to Berlin. *S. inaequidens* is widespread in Bremen and other regions of (north-)western Germany but, up to now, does not widely occurr in eastern Germany. The habitat model transfer evaluates the occurrence probability of the plant in brownfields of the 'non-invaded' city Berlin.

In the articles (Chapters) and short communications (Boxes) the design and all parts of the fieldwork were carried out by myself (but to some extend with the dedicated help of students). An exception is the data of vegetation structure used in Chapter 5, for which the fieldwork and further calculations were done by Barbara Strauß, Landscape Ecology Group, University of Oldenburg, Germany. I am responsible for the data analyses and the writing of the manuscript drafts. Chapter 3 to 5 were carried out together with the co-author. The SAS-macro to identify the PFGs and to conduct stepwise logistic regression was written by Prof. Dr. Michael Kleyer, Landscape Ecology Group, University of Oldenburg, Germany, and was partly transformed by myself.

Chapter 2

Introduction to study sites and experimental design

Chapter 2

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Study sites

In order to be able to work with a broad data base covering sites of different history and size as well as from different climate conditions, and moreover to test the transferability of habitat models across regions, we chose to carry out research on urban brownfields of two study areas: the cities of Bremen, north-western Germany, and Berlin, eastern Germany (Figure 2. 1).

Figure 2. 1: The studied urban brownfields were located in Bremen, and Berlin, Germany.

Bremen

One part of the research was carried out on urban brownfields situated in Bremen, north-western Germany (53°05' N, 8°44' E). The Free Hanseatic City of Bremen (327 km², 550.000 inhabitants) is the second largest city in northern Germany, its economy and industry are largely characterized by foreign trade. The study sites were located to the west and the north-west of the city center within an area of 100 km² (Figure 2. 4). They comprised brownfields of different age, size, and moisture status in varied types of industrial areas, i.e.

previously developed land as well as abandoned railroads, and newly created commercial (mainly freight service) sites.

Most of the investigated sites lie in the landscape unit ‘Bremer Wesermarsch’, which is characterized by fluviatile accumulations of different variations, forming silty and clayey soils (SUS 1991). Some sites near the city center are located in the landscape unit ‘Bremer Düne’, which is characterized by sandy material. The hydrology of Bremen is, amongst other influences, defined by high precipitations and retaining layers in the upper ground. Due to its lowland location, being bordered by moraine tracts of the glacial drift, the Bremen basin is an area of an extensive groundwater surplus (SUS 1991). However, the soil genesis of the investigated sites is based on the mainly man-introduced technical, maily sandy substrates. On most of the sites, these substrates stem from suctions out of the Weser river bed. The fillings often reach an amount of 2 to 3 m above the original soil level, thus, there is hardly any influence of groundwater on soil development and soil conditions of the investigated sites.

Since all study sites are located in industrial, highly anthropogenically influenced areas, the soils of the study area differ to a great extent from the loamy marsh and sandy podsol soils that normally characterize the Bremen area (Nagler & Cordes 1993). Predominant on all study sites are sandy anthrosols (Arbeitsgruppe Boden 2005), in old industrial areas often with a high amount of building rubble. In the majority of cases, newly created sites are former humid grasslands which have been filled up with sandy material. For a more detailed description of the soils found on the Bremen study sites see Chapter 3.

The macroclimate of Bremen is characterized by a maritime climate. Typical are cool summers of high precipitation and relatively mild winters with predominant westerly to south-westerly winds (SUS 1991). Mean annual precipitation amounts to 694 mm, the mean annual temperature is 8.8 °C (Nagler & Cordes 1993). As typical for urban areas, microclimate conditions of the anthropogenically used sites are often different from the general macroclimate (Sukopp & Wittig 1993), notably in terms of an increased mean temperature and thus an increased aridity.

All of the investigated sites were abandoned during the whole study period. Site use was limited to leisure (walking dogs, sometimes biking, golfing, or kite surfing) and occasional storage of material or equipment (Figure 2. 2). The age of the study sites (i.e. time since initiation of succession after severe disturbance or new creation of site) ranged from 0 to 33 years, as detected by a time series of aerial pictures.

Figure 2. 2: Occasional storage of material was one of the disturbances found on the investigated brownfield sites.

The vegetation of the investigated brownfield sites ranged from open conditions with a very low vegetation density of mostly annual plants to rather dense sites covered by grasses and perennial forbs. There were also older sites which are dominated by woody shrubs and pioneer forests comprised of birch (*Betula pendula*), maple (*Acer spec.*) and oak (*Quercus robur*) trees, mainly with a grassy understorey (Figure 2. 3).

Figure 2. 3: The vegetation of the investigated study sites in Bremen and Berlin ranged from very open sites sparsely covered mostly by annual herbs through stages characterized by grasses and forbs to pioneer forests sites of an older age (Photos taken by S. Melisch, B. Strauß and M.Kleyer).

I found a total of 231 vascular plant species on the investigated plots. The mean number of species found on a plot was 17, the maximum number being 40 while the minimum number was 0. A total of 11 red list species was found on the investigated plots; 4 of which are classified as 'critically endangered' (*Stachys germanica, Veronica verna, Arabis hirsuta, Sanguisorba minor*) and 7 as 'endangered' (*Alchemilla vulgaris, Crepis biennis, Echium vulgare, Filago minima, Lepidium campestre, Myosotis ramosissima, Tragopogon dubius*) (Garve 1993).

The sampling on Bremen sites included 133 plots (Figure 2. 4).

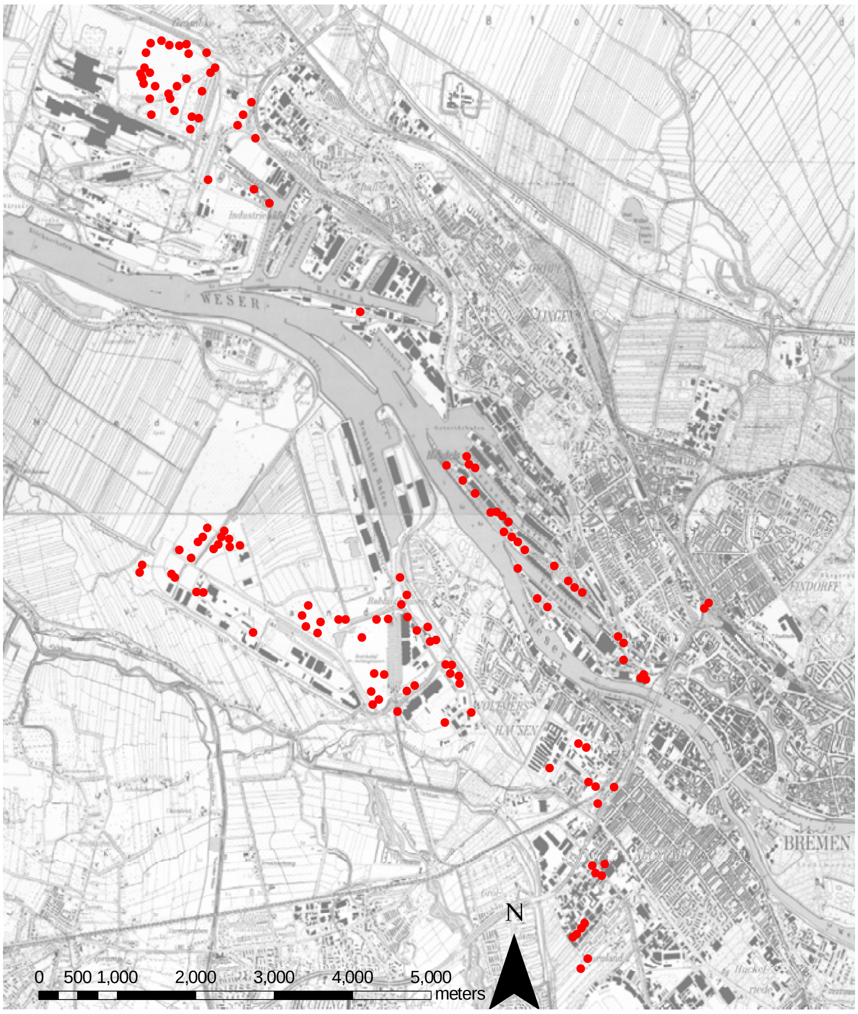

Figure 2. 4: The investigation on Bremen brownfield areas included 133 sampling plots (basic map: modified section of TK25 of Bremen, sheets no. 2818 and 2918, Geoinformation Bremen).

Berlin

The second part of the investigations was carried out on urban brownfields spread over the city of Berlin, eastern Germany (52°30’ N, 13°28’E). The German capital Berlin (892 km², 3.4 Mio. inhabitants) is the largest German city. Berlin has always been an important junction of European traffic which has determined its economics to a great extent. A great impact on the development of Berlin was its separation by the so called Berlin Wall which separated the city in an eastern and western part from 1961 to 1989, the whole wall being accompagnied by strips of idle land. The study sites were located within an area of 370 km² and comprised former areas of the Berlin Wall, abandoned railroads and depots, abandoned housing lots in the city center and previously developed land as well as newly created commercial sites in the open countryside.

The geology of Berlin is characterized by glacial depositions with 20 – 100 m thickness that cover tertiary clay and sand layers (Sukopp 1990). Parent materials are boulder clays and sands with an admixture of blowing sand. Characteristical are deep groundwater layers lying in a depth of more than 10 – 30 m (Sukopp 1990). However, the parent material of the investigated Berlin brownfield sites is highly anthropogenically influenced and to a large extend determined by the insertion of brick rubble due to the destruction of buildings in World War II (see also Runge 1975, Blume & Runge 1978).

These contents of brick rubble are characteristical to the man-influenced soils of the study sites. Originally characterized by cambisols and luvisol, today, the investigated Berlin brownfield sites are sandy anthrosols, resembling natural loose lithosols and (humic-calcaric or calcaric) regosols (Arbeitsgruppe Boden 2005). For a more detailed description of the soils found on the Berlin study sites see Chapter 5.

In general, Berlin is characterized by a continental climate. The mean temperature is 9.7° C, mean annual precipitation amounts to 560 mm (DWD 2006). However, climate parameters such as air temperature, atmospheric moisture, excessive humidity and wind conditions are modified by urban structures and utilization patterns, such as topological profiles, and vegetation structures (Sukopp 1990). From the city's edge to the very compact inner city areas, there is a decrease in nocturnal cooling and frost-day frequency as well as a general reduction in daytime and nighttime wind-speeds, leading to insufficient aeration, which to a high extent contributes to growing impact of emissions (SDUD 2006).

All of the investigated sites remained abandoned during the whole study period. However, the closer the sites are located with respect to the city center, the more intensively was the use of the sites by pedestrians and for leisure activities like dog walking, various sports, and playing children. Sites lying in industrial areas at the city's edge, were occasionally used for storage purposes. The age of the Berlin study sites (i.e. time since initiation of succession after severe disturbance or new creation of site) ranged from 0 to 40 years (evaluated by a time series of aerial pictures).

Figure 2. 5: Berlin sites located in the city center were intensively used by leisure activities and pedestrians (Photos taken by B. Strauß and K. Thielker/taz).

The vegetation of the investigated Berlin brownfield sites resembled the range of conditions in Bremen from very open sites with herbaceous vegetation to old sites dominated by woody plants of different height and density (Figure 2. 3). Pioneer forests found on Berlin sites were characterized by birch (*Betula pendula*), maple (*Acer spec.*), and robinia (*Robinia pseudoacacia*). A total of 184 vascular plant species was found on the investigated Berlin plots. The species number of a plot averaged 21, with a maximum of 38 and a minimum of 10 species found on the plots. A sum of 6 red list species was found on the investigated plots; 2 of these species are 'critically endangered' (*Anthyllis vulneraria, Myosotis discolor*) while *Papaver argemone, P. rhoeas* , *Saxifraga tridactylites* and *Veronica hederifolia ssp. hederifolia* are categorized as 'endangered' species (SDUD 2001).

The sampling on Berlin sites included 91 plots (Figure 2. 6).

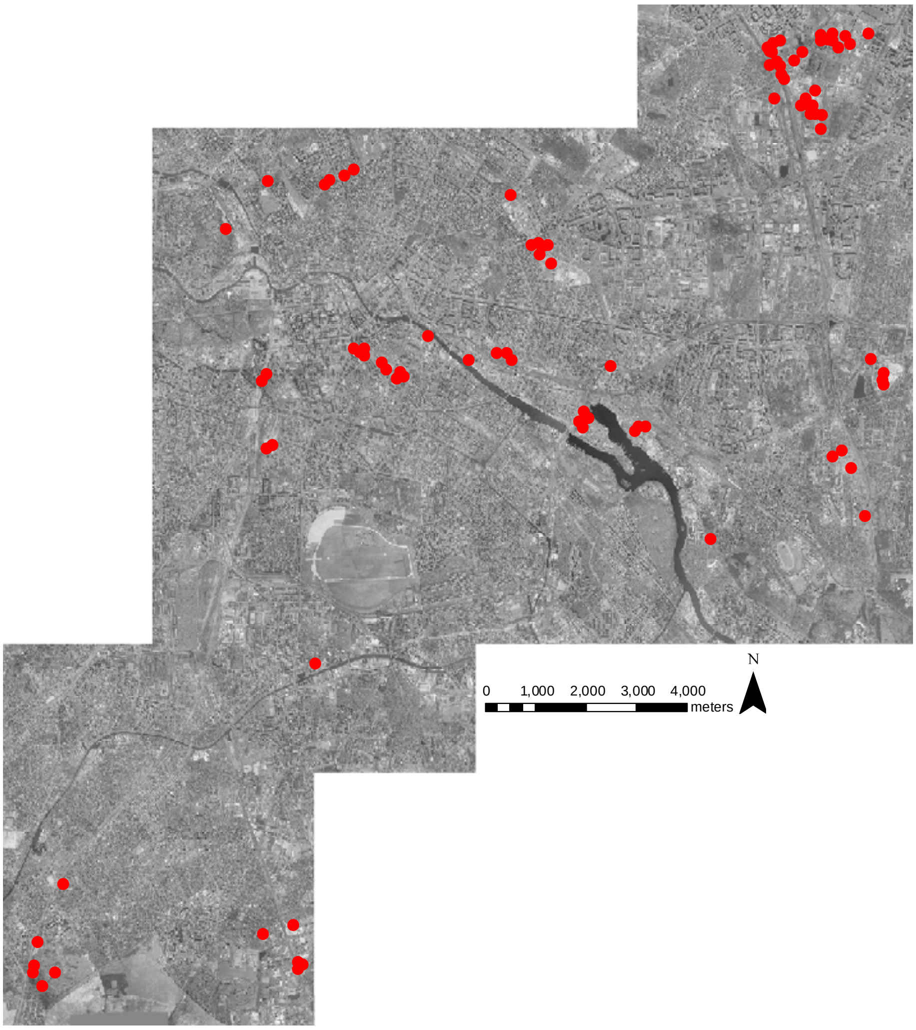

Figure 2. 6: The investigation on Berlin brownfield areas included 91 sampling plots (basic map: aerial photos of Berlin, March 2002, original scale 1 : 10,000, Senatsverwaltung für Stadtentwicklung Berlin).

Experimental design

In the following chapter, I describe the experimental design of the present study (further details in Chapter 3 to 5). The experimental design was applied in the same way in both Bremen and Berlin.

Sampling design

The field sampling of the present study was conducted in a chronosequence (Pickett 1989, Knops & Tilman 2000) of sites along a stratification gradient (Hirzel & Guisan 2002) of site age (time since initiation of vegetation development detected by a time series of aerial pictures), site size (classes separated by the median of all site sizes), and moisture status. The distribution of survey plots on the respective sites was done using ArcGIS 8.2 (ESRI Inc. 2003). Plots were assigned randomly (Hirzel & Guisan 2002) in a minimum distance of 80 m to each other and of 20 m to the edge of the site, where possible. Plots on smaller sites and on linear structures were assigned with greatest possible distance to the edge of the sites.

Table 2. 1: Distribution of study plots on a gradient of site age (time since initiation of succession), site size (ha), and moisture status. Abbreviations: HB= Bremen, BE=Berlin.

	site size <0.76ha* / 1.5ha**				site size >0.76ha* / 1.5ha**			
	HB*	BE**	HB*	BE**	HB*	BE**	HB*	BE**
site age [y]	dry		moist		dry		moist	
0-2	7	1	2	2	19	14	3	2
3-5	6	9	4	1	21	10	10	6
6-10	1	5	4	3	9	11	8	6
>10	11	9	5	3	20	6	3	3

* Bremen: n=133, the median size of sites was 0.76 ha

** Berlin: n=91, the median size of sites was 1.5 ha

Vegetation relevés

The occurrence of vascular plant species was recorded as presence/absence data on a vegetation relevé quadrat of 4 m x 4 m on each plot (Figure 2. 7). Recording in Bremen was done twice, once in April for the early flowering species and once in June for the summer species set. In Berlin, recording was done in May and covered the early as well as the later flowering species.

All plant names are in accordance with the nomenclature of Rothmaler (1994).

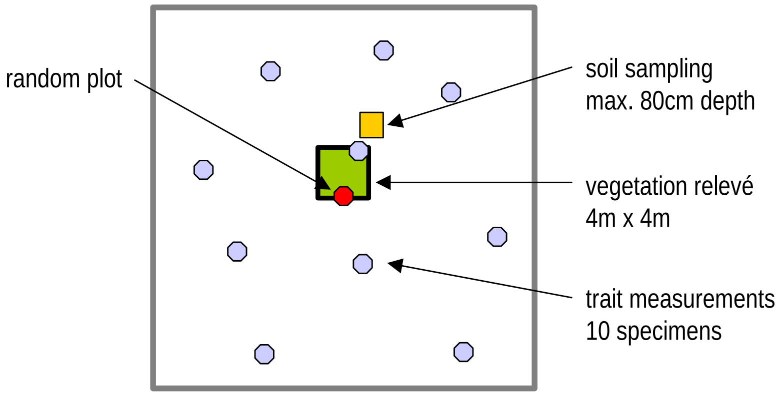

Figure 2. 7: Layout of soil sampling, vegetation relevé and trait measurements on a site. Soil sampling was done in a maximum depth of 80 cm in direct vicinity to the vegetation reléve quadrat. Trait measurements were conducted on plant specimens growing within the whole site.

Measurements of plant traits

After recording the occurrence of plant species, certain plant species were chosen for the analysis of their biological traits. Species selection was done by species' prevalence (i.e. a species occurred on at least 10 of all plots) and in particular cases by the red list status of a respective species. For the list of species chosen for measurements in Bremen (n=66) and Berlin (n=57) see Table A – 9 and Table A – 10.

Recording of traits in the field (Figure 2. 7) and measurements in the laboratory were done according to Cornelissen *et al.* (2003) and Knevel *et al.* (2005) and comprised the following parameters:

- sprout-related traits, measured on 10 specimens of each species:
  canopy height and releasing height, measured on fresh mature plants in the field,
  weight of supporting tissue (stem and petioles), weighed on oven dry material in the laboratory.
- leaf-related traits, measured on 10 specimens of each species:
  leaf size (area, width, length), measured on 2 fresh leaves of each of the 10 respective specimen by means of a usual flat bed scanner providing grey scale images in *.tif-format which were afterwards processed using the software LAFORE (Lehsten 2005),
  leaf weight (single leaf and all leaves of a single plant), weighed on oven dry leaves in the laboratory.
- seed-related traits, measured on 5 specimens of each species:
  seed number per individual, counted in the laboratory,
  seed weight per individual (of a single seed and all inflorenscences together), weighed on oven dry seeds in the laboratory,
  terminal velocity, measured on intact seeds in the laboratory by K. Thompson, University of Sheffield.

The trait measurements and the sampling of plant material were done on specimen growing on different sites chosen randomly from the presences recorded in the plot x species matrix.

For further analysis, I used means of all respective parameters.

The traits mentioned above were either used directly for analysis or for the calculation of further trait parameters. A few other traits were determined by means of literature. For an overview of all traits used within the analyses see Table 3. 3, Chapter 3.

Soil sampling

Soil samples were taken on each of the respective sites in direct vicinity to the vegetation relevé quadrat (Figure 2. 7) from every soil layer found within an 80 cm depth maximum. For an overview of all soil parameters determined on site and in the laboratory or by calculation as well as the respective methods applied see Table 2. 2.

Table 2. 2: Soil parameters were determined on site, in the laboratory by analyzing the soil samples or by calculation from previously determined values.

determination type	soil parameter	method / according to
on site	layer thickness	
	oxidative/reductive signs	Arbeitsgruppe Boden (1994)
	root fraction	
	stone fraction	
	texture of stone fraction	
	soil texture	
laboratory	apparent density	Schlichting *et al.* *(* 1995)
	pH ($CaCl_2$)	
	calcium carbonate ($CaCO_3$)	Scheibler in Schlichting *et al.* (1995)
	plant available phosphorus (P)	ammonia-lactate solution (Egner & Riehm in Schlichting *et al.* 1995)
	plant available potassium (K)	
	organic matter of top soil layer	Arbeitsgruppe Boden (1994)
	water permeability in saturated soil (kf)	
calculation	air porosity (AP)	Arbeitsgruppe Boden (1994)
	plant available field capacity (PAFC)	
	effective cation exchange capacity (ECEC)	
	plant available water (PAW)	Wendling *et al.* (1984) in DVWK (ed.) (1996), Schröder *et al.* (2004)

Degree of current disturbance

The degree of current disturbance was calculated by means of the number, severity and extent of disturbance events on a site:

$$D_c = \frac{x}{365} * b^3 * a$$ Equation 1

which included the number of disturbance events per year (*x*) on a daily level, the proportion of biomass removed or destroyed (*b*) and the proportion of site surface affected (*a*) by the disturbance event. The *b* - value was cubed because destruction of biomass has the most severe effect on vegetation survival and thus has to be emphasized compared to the other parameters.

The values for all parameters were estimated in field. The proportion of removed or destroyed biomass (*b*) was estimated on the basis of the disturbance type as shown in (Table 2. 3).

Table 2. 3: Proportion of removed biomass [%] as a factor for calculating the degree of current disturbance was estimated on the basis of the disturbance type.

type of disturbance	proportion of removed or destroyed biomass [%]
heaping up of material	100
ploughing / removal of upper soil layers	100
storage of material	70
mowing	50
vehicular cruising (loose underground)	40
vehicular cruising (dense underground)	10
biking	5
pedestrian traffic	0.1

Chapter 3

Plant functional groups in urban brownfields – strategies of plants to survive in a dynamic environment

Chapter 3

Plant functional groups in urban brownfields – strategies of plants to survive in a dynamic environment

with Michael Kleyer

Abstract

Plant-environment relationships form the basis for the understanding of vegetation change under dynamic environmental conditions. Species' traits respond differentially to these changes. Species can be assigned to plant functional groups (PFGs) according to similar responses to environmental factors and, from this, general relationships can be detected. In this study, we present plant functional groups for urban brownfields as well as crucial traits for species survival. In a procedure of stepwise logistic regression and cluster analysis, 39 responsive brownfield species were grouped into PFGs by means of iterative combination of a set of five candidate traits chosen a priori. The respective traits are leaf area ratio (LAR), seed longevity index (SLI), terminal velocity (TV), reproductive effort (RE) and plant life span (PLS), which comprise all major attributes of the plant's life cycle. The combination of LAR, SLI and TV gained the highest Nagelkerke values and formed eight plant functional groups comprising species of different successional stages and dispersal modes. The three aforementioned traits are related to environmental conditions, e.g. LAR and SLI to nutrients and moisture and TV to site age and disturbance. Our results show that dispersal in space and time as well as vegetative persistence are crucial traits for species survival in urban brownfields. The high relevance of dispersal aspects is emphasized by two results: (i) generally low R^2_N values of PFGs' models (species predicted but not present because of dispersal limitation) and (ii) the fact that deviance of models' predictions are highest at lowest abilities to disperse in space (high TV). The use of static models for predicting urban habitats is challenged by these results. The higher the influence of dispersal, the higher the need for a spatio-temporal approach in urban ecology.

Introduction

What parameters influence plant species survival and species composition in an environment? For centuries, this question has been of broad interest for both plant ecologists and conservationists (e.g. Raunkiær 1934). Today, this topic has gained even more relevance against the background of increasing human environmental impact and declining biodiversity, which evokes a need for predictions concerning the consequences of environmental change.

Traditionally, plant community ecology was closely related to plant geography. In the middle of the 20th century, plant community ecology shifted towards a more dynamic view of understanding processes that produce patterns of plant communities observed in natural systems. The more recently developed field of plant ecology aims at understanding the evolution of species' traits and behaviors that lead to observed patterns (e.g. Bazzaz 1996, Diaz *et al.* 2001, Lavorel & Garnier 2002, Kahmen & Poschlod 2004). Plant functional groups are a way of describing those patterns (Gitay & Noble 1997). Species are grouped together by similar function or similar response to environmental factors (i.e. 'functional traits', Diaz *et al.* 1999). The aim is to obtain information about the group rather than about each of its members, which allows general rules to be identified and predictions to be reached (Bazzaz 1996, Keddy & Weiher 1999, Diaz *et al.* 1999, McIntyre *et al.* 1999a, Kleyer 1999, but see Lindborg & Eriksson 2005). However, a critical point is the conflict between the simplicity of models needed to allow predictions and their complexity arising from the necessity to include all relevant parameters. Therefore we observe a continous search for the core traits that capture the essential ecological functions of plants (Weiher *et al.* 1999, Westoby 1998, Lindborg & Eriksson 2005).

In fast-changing environments that shape different successional stages of vegetation development, plants must notably hold certain morphological and physiological traits to cope with and to exploit changing site conditions. Relating land use change to species' traits has been a subject of recent studies, often with a focus on grasslands and rural areas (e.g. Lavorel *et al.* 1997, Cousins & Lindborg 2004, Lindborg & Eriksson 2005). In this context, only a few studies deal with urban habitats (Kühn *et al.* 2004, Niemelä 1999). Most of these studies describe ecological conditions and vegetation composition in an urban context and give very little specific information about functional relationships between species composition, plant traits and enviromental conditions (Rebele 1992, Sukopp & Wittig 1993, Zerbe *et al.* 2003).

In the present study we focused on urban brownfields formed by different types of wasteland within city areas (e.g. previously developed land, abandoned railroads or newly created sites). Urban brownfields are exemplary ecosystems to gain knowledge about relations between plant traits and a (changing) environment because of their spatial and temporal pattern of different abiotic conditions and successional stages (Rebele 1992, Pysek *et al.* 2004). Above all, urban brownfields are of high ecological value concerning biodiversity and nature conservation. They form a unique space in our mostly static and well-tended cultural landscape since natural processes still operate without direct human interference (Kaule 1991). Their spatiotemporal dynamics and transient character provide a relatively high diversity of species and ecological functions, as shown by many recent studies (e.g. Gilbert 1989, Sukopp & Wittig 1993, Rebele 1994, Niemelä 1999, Ricketts & Imhoff 2003, Kühn *et al.* 2004).

The focus of our study was to detect plant – enviroment as well as trait – environment relations. Instead of including many available plant traits in our analysis (e.g. Skarpe 1996), we preselected a set of candidate traits comprising major attributes of the plants' life cycle (Bazzaz 1996, Pillar 1999). By clustering and modeling plant functional groups according to species' traits and environmental conditions, we thus identified relevant strategies for species survival in urban brownfields. For our study, the following questions were of interest:

- How many traits are necessary to gain significant models of plant functional groups and which traits should be included?
- Which parts of the life cycle are crucial for species survival in urban brownfields?
- Resources or plant traits: What are the main driving factors for species composition in different successional stages of urban brownfields?

Methods

Study area

The present study took place in the city of Bremen in Northwestern Germany (53°05' N, 8°44' E). The study sites were located on urban brownfields in an area of about 100 km^2 in the western and northwestern part of the city. In the present study we included sites of different age, size and moisture status in varied types of industrial areas, i.e. previously developed land as well as abandoned railroads, and newly created commercial (mainly freight service) sites. During the study period, all sites were abandoned and site use was limited to leisure (walking dogs, sometimes biking, golfing, or kite surfing) and occasional storage of material or equipment.

The macroclimate is characterized as a maritime climate. Characteristic are cool summers with high precipitation and relatively mild winters (Nagler & Cordes 1993) with a mean annual precipitation of 694 mm and a mean annual temperature of 8.8 °C.

Predominant in the whole study area are sandy soils, in old industrial areas often with a high amount of building rubble. Newly created sites are in the majority of cases formerly humid grasslands which have been filled up with sandy material.

Sampling design

The sampling included 133 random plots (Hirzel & Guisan 2002) along a gradient of site age (time since initiation of succession), site size, and moisture status. Table 3. 1 shows the distribution of plots in the stratification matrix.

Table 3. 1: Distribution of study plots on a gradient of site age (time since initiation of succession), size (ha), and moisture status.

	site size <0.76ha		site size >0.76ha	
site age [y]	dry	moist	dry	moist
0-2	7	2	19	3
3-5	6	4	21	10
6-10	1	4	9	8
>10	11	5	20	3

Explanatory data

Soil samples were taken at each of the 133 plots from every soil layer found within an 80 cm depth maximum. The soil parameters determined are listed in Table 3. 2

Table 3. 2: Soil parameters were determined on site, in the laboratory by analyzing the soil samples, or by calculation from previously determined values.

determination type	soil parameter	method / according to
on site	layer thickness	
	oxidative/reductive signs	Arbeitsgruppe Boden (1994)
	root fraction	
	stone fraction	
	texture of stone fraction	
	soil texture	
laboratory	apparent density	Schlichting *et al. (* 1995)
	pH ($CaCl_2$)	
	calcium carbonate ($CaCO_3$)	Scheibler in Schlichting *et al.* (1995)
	plant available phosphorus (P)	ammonia-lactate solution (Egner & Riehm in Schlichting *et al.* 1995)
	plant available potassium (K)	
	organic matter of top soil layer	Arbeitsgruppe Boden (1994)
	water permeability in saturated soil (kf)	
calculation	air porosity (AP)	Arbeitsgruppe Boden (1994)
	plant available field capacity (PAFC)	
	effective cation exchange capacity (ECEC)	
	plant available water (PAW)	Wendling *et al.* (1984) in DVWK (ed.) (1996), Schröder *et al.* (2004)

Other explanatory variables included in the analysis are site size, percentage of moss cover of vegetation survey sites, general age of surveyed city quarter (established around the Second World War, around 1970, or newly established areas), degree of current disturbance and site age, i.e. time since initiation of succession after severe disturbance or new creation of site (detected by aerial pictures).

The degree of current disturbance was calculated by means of the number, severity and extent of disturbance events on a site:

$$D_c = \frac{x}{365} * b^3 * a \qquad \text{Equation 1}$$

which included the number of disturbance events per year (*x*) on a daily level (therefore divided by 365), the proportion of biomass removed or destroyed (*b*) and the proportion of site surface affected (*a*) by the disturbance event. The *b* -value was cubed because destruction of biomass is the most severe effect for vegetation survival and thus has to be emphasized compared to number and area of disturbance.

Response data

Presence/absence of all vascular plant species was recorded at each of the 133 plots in an area of 4m x 4m.

Measures of plant traits were taken on 10 specimens of each of the species selected by prevalence, i.e. they occurred on at least 10 of all plots. Table 3. 3 shows the traits that were determined.

Table 3. 3: Traits and trait features determined by analyzing plant material on site (a), in the laboratory (b), or by calculation from previously determined values (c). The grey marked traits were used in cluster analysis, the white marked traits were used for determination of grey ones.

determination type	trait	parameter measured according to	data type	source of values	definition [unit]
(a)	plant life span (PLS)	Knevel *et al.* (2005)	categorical	Rothmaler (1994)	1 - annual
					2 - biennial
					3 - perennial
(b)	terminal velocity (TV)	Knevel *et al.* (2005)	numerical	field measurements and Kleyer *et al.* (in prep.)	$[m*sec^{-1}]$
	seed weight (single seed)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	[mg]
	seed number (whole plant)	Knevel *et al.* (2005)	numerical	field measurements and Kleyer *et al.* (in prep.)	[no unit]
	leaf size (single leaf)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	$[mm^2]$
	leaf weight (single leaf)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	[mg]
	shoot weight (stem and leaves of whole plant)	Cornelissen *et al.* (2003)	numerical	field measurements	[mg]
(c)	leaf area ratio (LAR)	Anten & Hirose (1999)	ratio	field measurements and Kleyer *et al.* (in prep.)	LMR * SLA $[mm^2/mg]$
	reproductive effort (above ground) (RE)	Poorter & Nagel (2000)	ratio	field measurements and Kleyer *et al.* (in prep.)	seed weight*seed number/shoot weight+seed weight*seed number [no unit]
	seed longevity index (SLI)	Thompson *et al.* (1997)	index	Kleyer *et al.* (in prep.), Schütz (2000)	< 0.3 - transient
					0.3 - 0.55 - short term persistent
					> 0.55 - long term persistent
	specific leaf area (SLA)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	leaf size/leaf weight $[mm^2/mg]$
	leaf mass ratio (above ground) (LMR)	Anten & Ackerly (2001)	ratio	field measurements and Kleyer *et al.* (in prep.)	leaf weight/shootweight [no unit]

Statistical analyses

To achieve the aim of acquiring plant functional groups (PFGs) (Gondard & Deconchat 2004, Lavorel *et al.* 1997) from the sampled data, we used stepwise logistic regression and iterative clustering (see Figure 3. 1). The statistical procedure was implemented in a SAS-macro using the functions PROC LOGISTIC and PROC CLUSTER (SAS-Institute 1989).

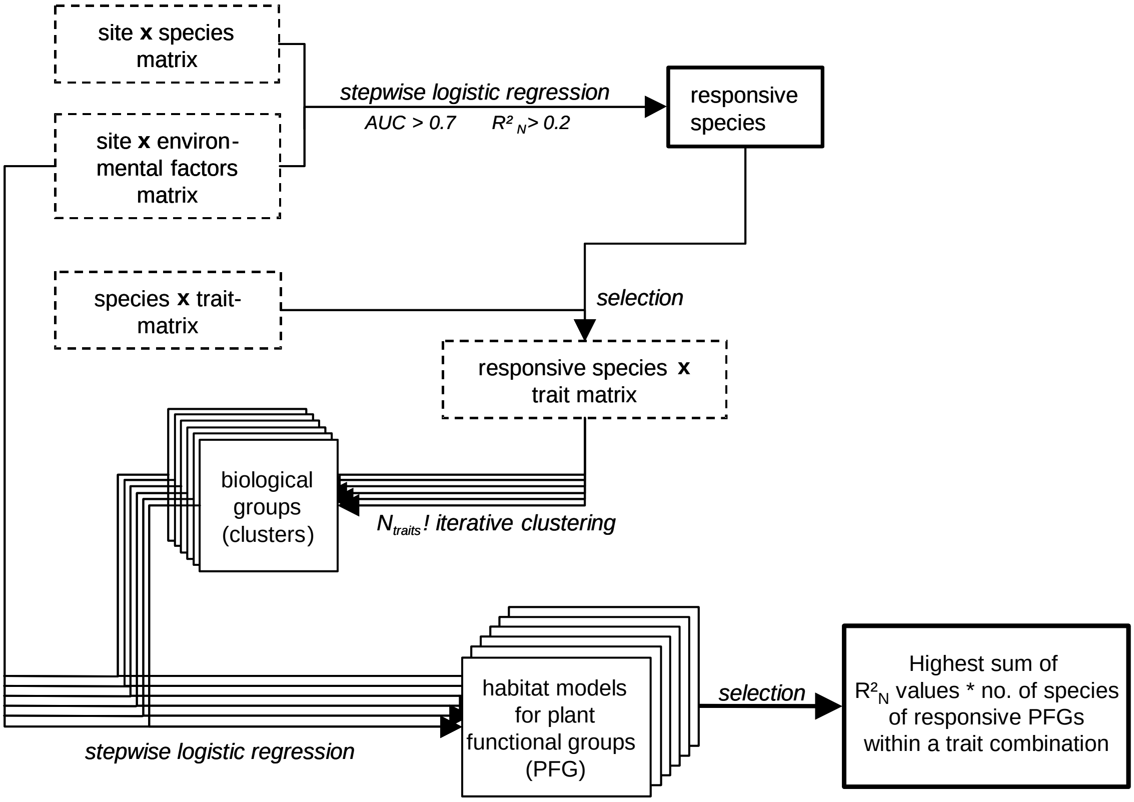

Figure 3. 1: Procedure of generating plant functional groups by habitat modeling and clustering.

Single species habitat models

To get habitat models for single responsive species we generated a site x species and a site x environmental factors matrix. After having checked for multicollinearity (and ensuing exclusion of variables in case of Spearman rho ≥0.5, see Table A - 1), the following explanatory variables and their squares have been included:

- pH-value of soil,
- site age,
- degree of current disturbance,
- site size,
- ratio of moss dominance per plot,
- general age of surveyed city quarter,
- available water per year,
- nutrient conditions (formed by principal component analysis of K,P and ECEC),
- soil atmosphere (formed by principal component analysis of kf and AP).

Due to a wide range of values, K, P, and degree of current disturbance were ln-transformed prior to analysis.

The species chosen by prevalence were implemented in a stepwise forward logistic regression during which those explanatory parameters are selected that significantly improve the single species habitat models (Hosmer & Lemeshow 2000, Bonn & Schröder 2001). At the end of the stepwise logistic regression, using thresholds of AUC 0.7 and R^2_N 0.2, we received cross-validated predicted occurrences for responsive species and therewith habitat models for single species modeling the incidence per plot for one species (Figure 3. 1). Thresholds were used to cull those species from the whole species pool that show a response to environmental factors and thus can be used to gain responsive species groups in the next steps.

Clustering and habitat modeling of plant functional groups (PFGs)

Based on the responsive species and their trait attributes, we formed biological groups by iteratively clustering traits into a maximum of nine different clusters per trait combination. Aiming at integrating the major attributes of the plants' life cycle (Bazzaz 1996, Walker 1997, Pillar 1999, Diaz *et al.* 1999), we chose the following candidate traits for analysis:

- Leaf Area Ratio [LAR] (with regard to vegetative plant persistence on sites),
- Reproductive Effort [RE] (with regard to reproduction),
- Terminal Velocity [TV] (with regard to dispersal),
- Seed Longevity Index [SLI] (with regard to generative persistence on sites),
- Plant Life Span [PLS] (with regard to vegetative plant persistence on sites).

All aforementioned traits were not highly correlated (Spearman rho ≥ 0.5, see Table A - 2).

After having clustered the species according to their trait attributes, another habitat modeling was done, this time of the clusters themselves (Figure 3. 1). The threshold of this second stepwise logistic regression was AUC 0.7. We did not use a threshold of R^2_N in this step, because all clusters should be included into the following selection irrespective of their calibration quality. The clusters' model fitting is based on the presence or absence of species belonging to a cluster. The procedure models the probability that all species of a cluster co-occur.

To select the best set of functional traits out of the whole set of combinations and models we achieved, we decided to focus on the values of the cluster's models R^2_N within each set of functional traits as a measure for the quality of calibration and refinement of the respective model. Within each set of functional traits, we summed up the Nagelkerke values for the models multiplied with their respective number of species. The set of functional traits with the highest sum was selected as best. Multiplying with the number of species was done to equalize the effect that clusters with a low species number usually get higher values for R^2_N since there is a greater possibility that the clusters' maximum number of species will in reality be fulfilled.

Nagelkerke values of all clusters with significant models were implemented into the sum irrespective of their level.

Reasons for low calibration quality of models

To get an idea of the reasons for strikingly low R^2_N-values of PFGs' models, we plotted the proportion of observed species number divided by maximum species number (hereafter named 'occurrence level') within PFGs against the PFGs' predicted probabilities for each site. Thus, it was possible on the one hand to detect the proportions of well predicted as well as poorly predicted probabilities. On the other hand, it became possible to see on which side of and how far from the bisecting line the plotted values are situated. Thus, we got an idea if low Nagelkerke values are due to omission or to commission errors (Guisan & Thuiller 2005), i.e. high predicted probabilites where in fact occurrence level is low or vice versa (which, in the case of binary data, would be expressed by the level of sensitivity and specificity of models).

To find out more about the cases where PFGs' predicted probabilities are high with real occurrence level being low, we divided occurrence level by predicted probability, results < 1 indicating a lower occurrence than predicted. Afterwards, we summed up the values < 1 for each PFG. The lower the sum, the higher the general deviance from the bisecting line. Comparing those sums with the mean terminal velocity of PFGs, we were able to find out if there is an effect of dispersal on the calibration quality of models.

To be able to exclude, in this context, that there is an eventual influence of the proportion of brownfield sites on the occurrence rate, for each PFG, we calculated the mean proportion of brownfield area around sites where the occurrence of the respective PFG was lower than predicted. That is, we summed up all proportions of surrounding brownfield area (within 50 m and 125 m) around those sites having values < 1 and divided them afterwards by the number of the respective plots.

Results

The environment

The study sites' resources and other site characteristics form a gradient within the surveyed landscape (see Table 3. 4).

The pH ranges from very high acidic values, mainly on sites lying in the vicinity of a steel mill and on those of old successional and already forested areas, to alkalescent conditions, which we found either in old railyards, in areas with a high amount of rubble in the soil or in newly sites heaped up mainly with sandy marine material. In 55 sites we found no measurable inorganic carbonate, the highest amounts of $CaCO_3$ were found in old industrial areas with soils containing lots of construction waste. Moisture conditions are constrained by several factors, altogether the most humid sites are those with a retaining layer or very dense soils. Sites with sandy material or gravel layers (newly created sites, old railyards) are mostly arid. The highest nutrient supplies were found in older industrial zones or on sites intensely used for dog walking, while newly created sites in most cases are nutrient depleted. 37 plots were not liable to current disturbance and on a further 67 sites, the intensity of current disturbance was very low. The most disturbed plots were subject either to moving construction site equipment or to intensive leisure activities.

Table 3. 4: Explanatory variables and their statistical values. Variables in grey rows were implemented into principal component analyses. The last two variables were not taken into account for the regression analysis due to their high correlation with other variables (see Appendix 1). Abbreviations used: min. = minimum, max. = maximum, std.dev. = standard deviation, age_site = site age, size_site = size of site belonging to a plot, age_quarter = general age of surveyed city quarter, moss cover = ratio of moss dominance per plot, PAW = plant available water, disturb_curr = degree of current disturbance, P = phosphorus, K = potassium, ECEC = effective cation exchange capacity, kf = water permeability in saturated soil, AP = air porosity, PAFC = plant available field capacity, $CaCO_3$ = calcium carbonate.

	min.	max.	mean	std.dev.
pH	3.4	7.7	6	1.2
age_site [y]	0	33	10	11
size_site [ha]	0.04	27	3.6	5.7
age_quarter	1 (young)	3 (old)	-	-
moss cover [prop]	0	0.8	0.12	0.17
PAW [mm]	2.4	69	25	13.5
disturb_curr	0	$4*10^{-2}$	$7*10^{-4}$	$4*10^{-3}$
P [$kg*ha^{-1}$]	23	4490	510	612
K [$kg*ha^{-1}$]	39	3744	448	457
ECEC [$cmol_c*kg^{-1}$]	0.08	1.6	0.4	0.26
kf [$cm*d^{-1}$]	10	653	268	227
AP [mm]	2.5	211	130	62
PAFC [mm]	4	193	91	42
$CaCO_3$ [$kg*ha^{-1}$]	0	$4.9*10^{6}$	$1.04*10^{5}$	$4.6*10^{5}$

The vegetation

A total of 231 vascular plant species were found on the study sites, of which 66 species were chosen for statistical analysis according to their prevalence (see Table A - 3). A number of 39 responsive species out of the 66 species matched the performance criteria and thus got sufficient quality models.

Plant functional groups

We achieved 31 different combinations of traits that formed a total of 266 plant functional groups (PFGs). The best set of functional traits was the combination of leaf area ratio (LAR), terminal velocity (TV) and seed longevity index (SLI). This trait combination formed 8 PFGs that comprised, in total, 37 species (see Table 3. 5).

Table 3. 5: Plant functional groups (PFGs) formed by leaf area ratio (LAR), terminal velocity (TV), and seed longevity index (SLI). One PFG not mentioned within the table did not match the performance criteria.

Trait combination	no. of species in PFGs	PFG	species (prevalence)	no. of species	AUC	R^2_N
LAR+TV+SLI	37	1	*Poa trivialis* (48), *Arenaria serpyllifolia* (43), *Trifolium arvense* (26), *Artemisia vulgaris* (29)	4	0.82	0.32
		2	*Achillea millefolium* (20), *Cirsium arvense* (18), *Cirsium vulgare* (36), *Deschampsia cespitosa* (25), *Holcus lanatus* (75), *Poa palustris* (11), *Poa pratensis* (23)	7	0.75	0.18
		3	*Dactylis glomerata* (18), *Lolium perenne* (18), *Tanacetum vulgare* (41), *Trifolium pratense* (22), *Arrhenatherum elatius* (15)	5	0.81	0.23
		4	*Carex arenaria* (19), *Chenopodium album* (14), *Corynephorus canescens* (19), *Festuca rubra* (54), *Hypericum perforatum* (34), *Matricaria maritima* (23), *Melilotus officinalis* (15), *Rumex acetosella* (45)	8	0.76	0.16
		5	*Plantago lanceolata* (23), *Trifolium repens* (34), *Vicia hirsuta* (28)	3	0.74	0.21
		6	*Hypochoeris radicata* (40), *Picris hieracioides* (11), *Saxifraga tridactylites* (13), *Senecio inaequidens* (76), *Taraxacum officinale* (55)	5	0.71	0.17
		7	*Plantago major* (18), *Arabidopsis thaliana* (12), *Poa annua* (28), *Bromus tectorum* (6)	4	0.92	0.45
		8	*Vicia angustifolia* (26)	1	0.982	0.73

One part of PFGs (1-4) consists of species with low to medium values for LAR (Figure 3. 2). Those species are rather late colonizers, growing up slowly with a high investment in the supporting structure of sprout and leaves to be able, once grown up, to live on a site for a longer time. In addition to this high investment in vegetative persistence on sites, dispersal and generative persistence play a role: Plants of PFG 1 invest in having long-term persistent seeds. This is a trait that enables plants to endure unfavorable conditions and to grow on a site afterwards. In addition to not being able to be widespread, seeds of PFG 2 species are rather short-term persistent. This fact gives a hint of the focus of the PFG 2 life cycle being more on vegetative persistence than on dispersal or generative persistence. Likewise are the strategies of PFG 3 and 4, i.e. rather high investment in vegetative persistence. However, investment in reaction to disturbance by being able to disperse (both PFGs) and by having very long-term persistent seeds in the case of PFG 4 is also evident.

Species of PFGs 5 – 8 are more or less early colonizers. Having medium to high values for LAR, their investment in supporting structure is rather low. These plants come up fast on recently disturbed sites, investing energy in photosynthetical structure and seeds rather than in strong sprouts (Westoby 1998, Anten & Hirose 1999). Allocation patterns (Poorter & Nagel 2000, Westoby *et al.* 2002) are obvious in the cases of PFG 6 and 7: There is investment in seeds as well as investing biomass either in dispersal or in generative persistence. While seeds of PFG 6's species are able to be widespread and combined with short longevity in soil, species of PFG 7 produce seeds with a higher TV but a higher longevity. The strategy of PFG 8 (consisting of only one species, *Vicia angustifolia)* to endure unfavorable conditions is investment in very long-term persistent seeds rather than in escape (TV value is high) or persistence by strong sprouts.

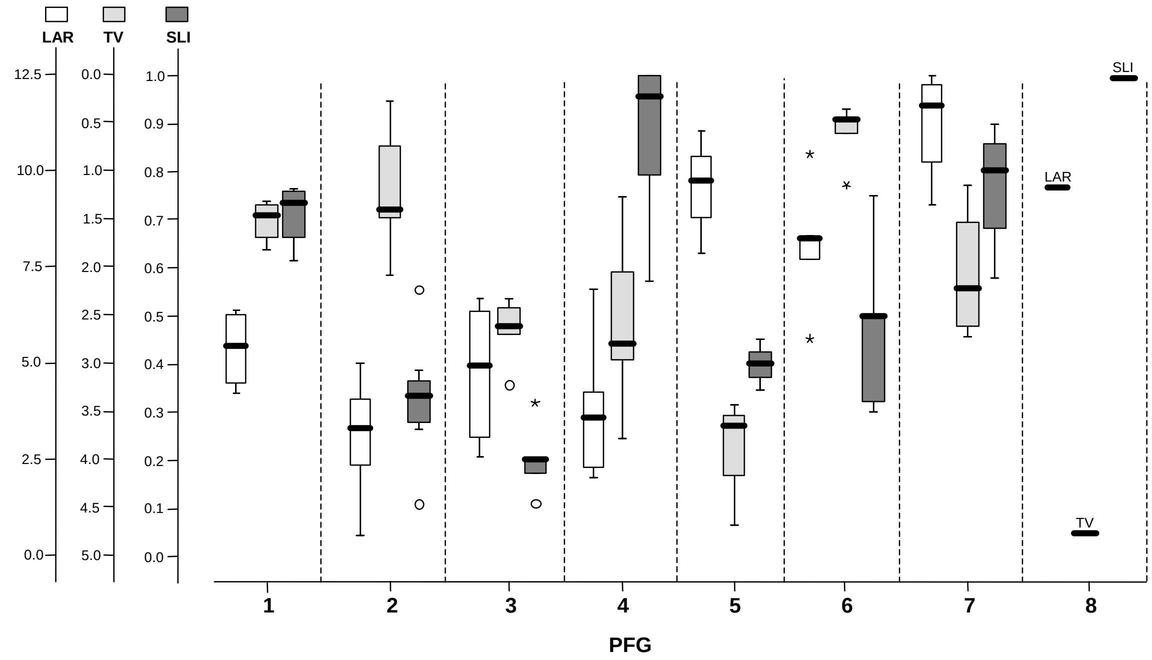

Figure 3. 2: Medians, interquartil ranges and extreme values (marked by * or º) of leaf area ratio (LAR), terminal velocity (TV, y-axis inversed), and seed longevity index (SLI) of responsive species within the different PFGs. For units see Table 3. 3.

The eight PFGs depend differently on the site characteristics (Figure 3. 3; for regression coefficients see Table A - 4): PFG 1 and PFG 2 respond to pH, ratio of moss dominance, age of surveyed city quarter and soil atmosphere (whereas PFG 1 depends additionally on PAW and PFG 2 on site size), and nutrient conditions. PFG 3‘s probability of occurrence depends on pH, site size, and nutrient and soil atmosphere status, while PFG 4 increases with site age, site size, ratio of moss cover and degree of current disturbance. Such as PFG 3, PFG 5 responds in an unimodal way to soil atmosphere, increasing at lower and decreasing at higher levels, and has a positive response to pH and site age. PFG 6 and 7‘s probability of occurrence increases with increasing pH and age of surveyed city quarter, while site age has a negative effect on both. Above all, PFG 6 depends on moss cover, PFG 7 on site size and nutrient status. PFG 8 (consisting of only one species, *Vicia angustifolia*) depends positively on site size and plant available water.

Altogether, pH, and site size are the most often used explanatory site characteristics within the habitat models of PFGs derived by LAR, TV, and SLI.

PFG	pH	age_site	size_site	moss cover	PAW	disturb_curr	age_quarter	nutrients	atmosphere
1	↗			∩	∪		↘		↘
2	∩		∪	↘			↘	↗	↘
3	↘		∪					↘	∩
4		↗	↗	↗		↗			
5	↗	↗							∩
6	↗	↘		∩			↗		
7	↗	↘	↗				↗	↗	
8			↗		↗				

Figure 3. 3: Response of plant functional groups (PFGs) to site characteristics. An arrow pointing downwards indicates a negative, an arrow pointing upwards a positive response to the respective parameter. The bends indicate an unimodal response. Abbreviations: age_site = site age, size_site = size of site belonging to a plot, age_quarter = general age of surveyed city quarter, moss cover = ratio of moss dominance per plot, PAW = plant available water, disturb_curr = degree of current disturbance, atmosphere = soil atmosphere (value generated from principal component analysis), nutrients = nutrient conditions (value generated from principal component analysis)).

Most PFGs have rather low values for R^2_N (see Table 3. 5). The highest number of values deviant from the bisecting line as well as the highest amount of deviance of PFGs' observations vs. predictions is seen on the upper left side of the diagram (Figure 3. 4). This means that predicted probabilities are predominantly lower than corresponding observations. However, there are also many cases where predicted probabilities are higher than corresponding observations (values on diagram's lower right side in Figure 3. 4).

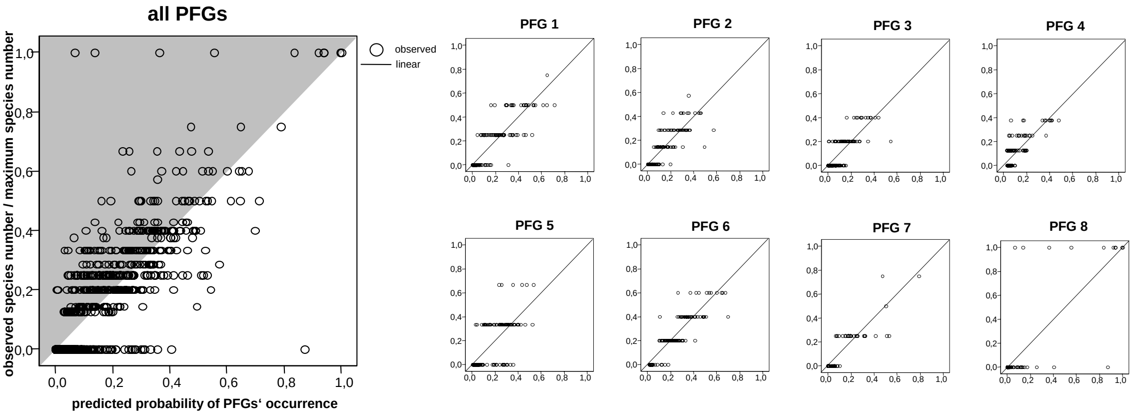

Figure 3. 4: Proportion of observed species number divided by maximum species number within plant functional groups (PFGs) vs. predicted probabilities of PFGs. On the left side observations of all PFGs are shown; Points in the grey triangle indicate that predicted probabilities are lower, points in the white triangle indicate that predicted probabilities are higher than observed proportion. The graphs of each single PFG diagram of observations vs. predictions are presented on the right. The crossing lines show bisectors of the respective diagrams.

Sums of those deviances that lie on the lower right side of the bisecting line in diagrams of Figure 3. 4 are, apart from PFG 7, lowest at medium to high terminal velocities. Thus, the higher the rate of predicted but not observed presences, the higher the mean TV value of the respective PFG (Figure 3. 5A). Mean proportions of brownfield area within 50 m and 125 m from corresponding plots do not show a great variance between the different PFGs (Figure 3. 5B).

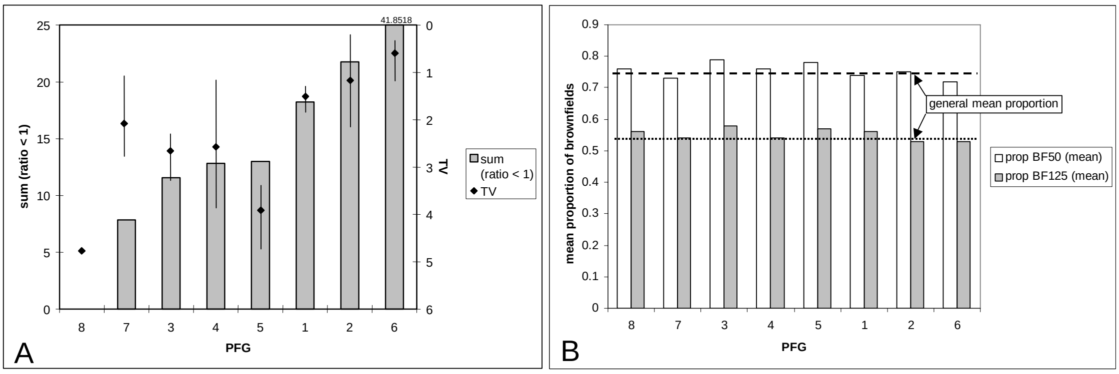

Figure 3. 5: PFGs' sum of ratios < 1 (observed occurrence level divided by predicted probabilities, i.e. values of lower right side of bisecting line in Figure 3. 4) and mean, minimum and maximum values of terminal velocity (A) and the mean proportion of brownfield area within 50 m and 125 m (B).

Discussion

Modeling and clustering of PFGs – a glance at methods

How many traits are necessary to obtain well-fitted PFGs and which should be included? In our view, the *number of traits* is negligible as long as the trait set chosen incorporates all parts of the plants' life cycle (McIntyre & Lavorel 2001). With regard to straightforwardness, it is nevertheless desirable to include as few (uncorrelated) traits as possible (McIntyre *et al.* 1999b), although a satisfactory classification of PFGs based on one single trait is unlikely (Diaz *et al.* 1999). Composed traits like LAR or RE can be a feasible way to include different parts of plant traits into one value. However, attention should be paid to their interpretability and to the fact that in some cases surrogation of traits can lead to a loss of information unique to particular traits (Lavorel & Garnier 2002). The question *which traits* should be included is strongly case and habitat dependent (Wang & Ni 2005). However, again, incorporation of all parts of the plants' life cycle is strongly recommended.

Deriving PFGs by cluster analysis has become an acknowledged technique in recent scientific studies (Kleyer 2002, Pillar & Sosinski 2003). Instead of including all available plant traits in the process of clustering, we selected a set of uncorrelated candidate traits a priori that included all possible parts of a plant life cycle (Bazzaz 1996). We consider this to be a good way to minimize the complexity of models that in the meantime saves the interpretability of results. But even with this preselection of plant traits, the amount of possible trait combinations and especially of PFGs gained by clustering is very high – in our case 266. Thus, there must be other techniques beyond clustering and preselection of traits to select the aspired PFGs (Semenova & van der Maarel 2000). Instead of selection by mere parsimony (Westoby & Leishman 1997), we decided to focus on selection by means of R^2_N-values of clusters formed by a combination of responsive traits. This approach allows for detecting the trait combination forming PFGs whose models draw nearest to actual conditions.

Why do almost half of all significant PFG models (namely 121 out of 266) not match the performance criteria of R^2_N 0.2? Nagelkerke values may be low due to poorly predicted absences as well as to poorly predicted presences.

1) The case ‘present but not predicted’ (omission errors): A bad model can be the reason for data points with a high ratio of occurring species within respective PFGs while predicted values are low. It is possible that not all relevant environmental factors were actually included into the model. In our case, these variables may have been more exact soil water data or wind as a driving factor of dispersal.
2) The case ‘predicted but not present’ (commission errors): Besides a bad model, a reason for high predicted values where in fact occurrence level is low may be that observations of absences in the field are never as certain as observations of presences. An ecologically driven reason for prediction without presence may be that species of a PFG could not reach the habitat because of high distance and/or low ability of dispersal (high terminal velocity) (Guisan & Thuiller 2005). Thus, they do not occur even if environmental conditions of a site are benign.

The latter assumption was confirmed by relating the ratio of predicted but not present occurrences to mean terminal velocity of PFGs’ species and to the proportion of brownfield area around corresponding sites. While the proportion of surrounding brownfields does not vary evidently between cases, terminal velocity seems to have an influence: the higher the rate of predicted but not observed presences, the higher tends to be the mean TV value of the respective PFG and thus the lower its potential to disperse in space.

Ozinga *et al.* (2005) found out that dispersal filters may play a major role for the predictability of species and that a large percentage of unexplained variance in predictive models was not only due to noise but to dispersal limitation, a fact that is reflected by our results. Urban brownfields are basically characterized by stochastic processes and a state of disequilibrium. Static regression models are based on the principle of equilibrium, which is why their use in modeling species in disequilibrium is problematic (Gibson *et al.* 2004). Thus, the more that dispersal in time and space gains influence in brownfield habitats, the greater the challenge of their predictability by static regression models.

PFGs in urban brownfields – environmental linkages and strategies of survival

In urban brownfields like in other habitats, environmental factors give a general framework within which different successional pathways are possible, whereas species’ biological traits and the dynamical behavior of involved species are the driving forces of succession (Bazzaz 1996, Müller & Rosenthal 1998).

We found apparent relations of leaf area ratio (LAR), terminal velocity (TV) and seed longevity index (SLI) to environmental factors: LAR (low values at slow growth and high proportion of supporting tissue) decreases with increasing resource supply by water and nutrients. For example, the possibility of occurrence of PFG 1 and 2, which both are characterized by a low LAR depends positively on nutrient supply and plant available water. In addition, there seems to be a relationship between SLI (high values at long term persistence) and measures of successional stage such as site age and degree of current disturbance. This is most visible in the case of PFG 4 (very high SLI, positive reaction to increasing site age and increasing degree of current disturbance) and PFG 6 and 7 (low SLI, ocurrence increasing with decreasing site age). In contrast to LAR and SLI, TV (high values for fast falling seeds) does not seem to be related strongly to resource supply. PFG 6 (low TV) shows a negative dependency on increasing site age. This hints at TV being related positively to younger successional stages.

As in other habitats, occurrence of species in urban brownfields is determined by means of environment, dispersal, and disturbance filters. Niche division (Grime 1979, Anten & Hirose 1999) is determined by assembly rules in the context of the given environment and resource base (Temperton *et al.* 2004). Deviations from the niche-based occurrence of plants can be driven partly by stochastic processes or by dispersal limitation (Ozinga *et al.* 2005, Cook *et al.* 2005). Our results show that resources (local, niche-based processes) are driving factors of PFGs’ occurrence. However, dispersal limitation (expressed by terminal velocity) also plays an important role for the distribution of PFGs. Thus, concerns of successional stage and disturbance are relevant, too. Apparently, in urban brownfields, the niche-based and the dispersal-based approach reinforce each other (Ozinga *et al.* 2005).

Overall, our results show that dispersal in space (terminal velocity) and in time (seed longevity index) as well as vegetative persistence on sites (leaf area ratio) are the most crucial traits for plant survival in urban brownfields. These results are confirmed by many authors (e.g. Westoby 1998, Lavorel & Garnier 2002) who stated persistence and dispersal as being crucial plant strategies.

Dispersal in time is a very crucial trait for species to survive under unfavorable environmental conditions (Piessens *et al.* 2005, see also Grime 1979 (‘ruderal strategy’)). Concerning fast changing environments, Schippers *et al.* (2001) concluded escape in time as being a better strategy than escape in space. This conclusion confirms our results concerning the relevance of dispersal in time. However, in the case of urban brownfields, escape in space seems to play a major role for species’ survival as well. The basis for species composition is environmental conditions. But beyond this, dispersal limitation affects occurrence of species in urban brownfields (Ozinga *et al.* 2005, Cook *et al.* 2005).

Besides dispersal in time and space, vegetative persistence (in our case expressed by leaf area ratio (LAR)) is a crucial trait for species’ survival. If once reestablished by dint of dispersal, plants need to persist on sites (Westoby 1998 and Weiher *et al.* 1999). In addition to resprouting, traits of plant height and architecture are characterised as being decisive for response to disturbance (Lavorel & Garnier 2002). However, we rather see LAR as a measure for vegetative persistence than for competitive ability (Kleyer 1999), because it seems to play a crucial role for species survival not only in denser vegetation but in initial states as well as in older states of brownfields' succession.

Reproductive effort (RE) and plant life span (PLS) play a more minor role in this case. A high RE can be expressed both by few heavy seeds as well as numerous light ones. Both strategies may increase local growth within an already colonized site. A high number of seeds in addition increases the probability of reaching empty sites prior to other colonizers (Ronce *et al.* 2000). The lower relevance of reproductive effort compared to terminal velocity shows the high importance of the ability to disperse and reach colonizable sites. This ability seems to be better expressed by a trait like TV that only deals with widespread rather than dealing with proportion of seed mass itself. PLS on the other hand was pointed out as being the most basic trait for species persistence by Weiher *et al.* (1999), in that case for remnant populations where recruitment is a secondary process. 'Immortality is good': This statement made for plant life span does not seem to apply to fast changing environments like urban brownfields. For these habitats, the most relevant trait is not immortality of a plant itself on a certain site but immortality of a population or functional group by dispersal and resprouting within a fast changing mosaic of convenient sites.

High relevance of dispersal aspects shows that there is a need in urban ecology for a spatio-temporal approach, especially when it comes to predictions (Weiher & Keddy 1999, Diaz *et al.* 1999). A not plot- but space-related study design could help to find out more about dispersal topics as well as metapopulation and spatial connectivity within urban landscapes (see also Pysek *et al.* 2004).

Chapter 4

The transferability of plant functional group models across urban brownfields of three German cities

Chapter 4

The transferability of plant functional group models across urban brownfields of three German cities

with Michael Kleyer

Abstract

In the face of large-scale environmental changes, a regional or even global generality of patterns and processes provides useful instruments for predicting their consequences. To effectively use the predictions derived from habitat models in conservation planning, it is essential to validate their predictive accuracy and thus their general applicability in space and time. In the present study, we investigated the transferability of urban brownfields' plant functional group models across three German cities (Stuttgart, Berlin and Bremen) and thus concentrated on assessing the spatial transferability of models. Since we used predictions as an absolute estimate of the probability of PFGs' occurrence at a site, knowledge of model calibration was essential for interpreting the predicted values. We derived a common set of PFGs for all three cities using iterative clustering of plant traits. For the resulting PFGs, city-specific logistic regression models were made, which afterwards were applied to the respective other cities. This was done in order to answer the following questions: (i) do data from different regions lead to similar models of urban brownfields' plant functional groups, if the same modeling techniques are applied, and (ii) can plant functional groups' models be successfully applied to urban brownfields of other cities? Our results showed (i) that despite many landscape specific reactions that are not commonly relevant for all regions, in a broader view and assuming similar ranges of environmental variables for all included regions, models of urban brownfields' PFGs were of a certain similarity and (ii) that model transferability was highly contingent on the environmental comparability of the regarded cities. Dissimilarity of relevant model parameters lowered the transferability of models. In addition, for urban habitats, the inclusion of site history parameters turned out to be essential to covering the city-specific effects, especially regarding species dispersal, which turned out to be a major trait that induced a transferability of PFG models.

Introduction

The analysis of species - environment relationships has always been a central issue in ecology, their quantification being the core of predictive modeling (Guisan & Zimmermann 2000). In recent years, the predictive modeling of species distribution has become a widely used tool throughout ecology and conservation biology (Guisan & Thuiller 2005, Vaughan & Ormerod 2005). To effectively use the predictions made by these models in conservation planning, it is essential to validate their predictive accuracy and thus their general applicability in space and time (Bonn & Schröder 2001, Pearce *et al.* 2001, Bulluck *et al.* 2006). However, despite the widespread application of predictive models, evaluation of model performance is rarely done (Vaughan & Ormerod 2005, Bulluck *et al.* 2006), especially in vegetation ecology. In addition, little attention has been devoted to the development of appropriate evaluation techniques for assessing the predictive performance of habitat models (Pearce & Ferrier 2000a).

Recent examples of studies systematically investigating the generalizability of predictive models in animal ecology are those of Fleishman *et al.* (2003), Jensen *et al.* (2005) and Bulluck *et al.* (2006). Strauss & Biedermann (in prep.-a) tested spatial and temporal model generality for phytophagous insects of urban brownfields. However, with the exception of these studies, hardly any attention has been paid to the validation of plant ecological models. De Bello *et al.* (2005) explored the predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. This study, however, rather than performing a direct spatial validation of plant functional groups' models, instead compared whether a common set of plant functional traits would provide consistent predictions of species' responses to grazing in different regions. Kleyer (2002) gave an example for a model transfer in plant functional ecology. He investigated the transferability of plant functional type models between the urban and the agricultural landscape by comparing observations and modeled predictions, finding recurrent patterns of several functional types in both contrasting landscapes.

In general, the predictive performance of logistic regression habitat models should be evaluated in terms of two measures: calibration (the agreement between predicted probabilities and observed occurrence), and discrimination (the ability of a model to correctly distinguish between occupied and unoccupied sites) (Pearce & Ferrier 2000a, Vaughan & Ormerod 2005). Since in the present study we used predictions 'face value', i.e. as an absolute estimate of the probability of PFGs' species occurring at a site, knowledge of model calibration was essential to interpret the predicted values, whereas evaluating the models' discriminatory power could be neglected (Pearce & Ferrier 2000a). Low calibrative power can be attributed to two systematic sources: bias and spread. Bias describes a consistent over- or underestimate of the probability of occurrence, typically appearing when a species' prevalence differs from the training data (Pearce & Ferrier 2000a). Spread describes predicted values that are too extreme, i.e. too low at unoccupied and too high at occupied sites, typically deriving from model overfitting due to e.g. a high number of variables included in the regression or to a lower amount of available training data (Vaughan & Ormerod 2005).

In the face of large-scale environmental changes, a regional or even global generality of patterns and processes provides useful instruments to predict their consequences (Nygaard & Ejrnaes 2004, De Bello *et al.* 2005, Guisan & Thuiller 2005). Plant functional groups (PFGs) are a way of describing vegetation patterns in terms of species' traits response to environmental factors (Gitay & Noble 1997, Nygaard & Ejrnaes 2004). Assessing PFGs' spatial transferability from the landscape specific to a regional scale is the aim of the present study. We investigate the transferability of models of urban brownfields' plant functional groups (PFGs) of one habitat type (urban brownfields) across different regions. Investigating PFGs' transferability in the context of urban brownfields gave us the opportunity to test models in an environment characterized by high spatiotemporal dynamics and a transient character (Walker 1997), providing a relatively high diversity of species and ecological functions (Rebele 1992, Pysek *et al.* 2004). Urban brownfields of different regions are ideal habitats for verifying the transferability of models, since they have both comparable and dissimilar characteristics. On the one hand, they can share a lot of features such as the type of utilization, the degree of spatial complexity, site history and the mostly man-made uniformity of the soil (Gilbert 1989, Sukopp 1990). On the other hand, regional specifics such as climatic conditions and different turn-over rates of utilization and abandonment (Scheele *et al.* 2005, Empter 2006) induce a dissimilarity. That gave us the opportunity to ascertain relevant and non-relevant parameters for the transferability of urban vegetation patterns across landscapes.

In the context of the present study, the following questions were of interest:

- Do data from different regions lead to similar models of urban brownfields' plant functional groups, if the same modeling techniques are applied?
- Can plant functional groups' models be successfully applied to urban brownfields of other cities?

To obtain a better understanding of these questions, we derived a common set of PFGs for all three cities using iterative clustering of plant traits. For the resulting PFGs, city-specific logistic regression models were made, which afterwards were applied to the respective other cities. Calibration of models, i.e. comparison of occurrence rate and predicted probabilities, was measured by means of the squared Pearson correlation coefficient r^2 (Mittlböck & Schemper 1996, Hosmer & Lemeshow 2000).

Methods

Study sites

The study areas of the present investigation were located in urban brownfield sites in the cities of Bremen (northwestern Germany, 53°05' N, 8°44' E), Berlin (eastern Germany, 52°30' N, 13°28'E) and Stuttgart (southwestern Germany, 48°46' N, 9°10' E). Included were sites of different age, size and moisture status in varied types of industrial areas, i.e. previously developed land as well as abandoned railroads, and newly created commercial sites. A few of the Stuttgart sites were located in housing areas. In general, the Stuttgart site mosaic was more dense and more small-scale compared to the Berlin and Bremen sites. Notably in Bremen, a high proportion of urban brownfields lay in newly established areas in the open countryside. During the study period, all sites were abandoned and site use was limited to leisure (walking dogs, sometimes biking, golfing or kite surfing) and occasional storage of material or equipment. Berlin (mean temperature 9.7° C, mean annual precipitation 560 mm) has a more continental climate than Bremen, whose climate is rather maritime (mean temperature 8.8 °C, mean annual precipitation 694 mm). Stuttgart (mean temperature 9.7-11° C, mean annual precipitation 675 mm) is situated in a basin-shaped valley of the southern German upper Triassic mountains, the valley of the Neckar river adjoining this basin. Predominant in the Bremen and Berlin investigation areas were sandy soils, often containing a high portion of building rubble. Newly created sites, which were found mostly in Bremen, were in the majority of cases former humid grasslands which have been filled up with sandy material. The Stuttgart soils were divided up into three different parts: basin soils consist of deep fills, mainly with the local Gypsiferous Keuper Marl. Soils of the slopes consist of various parent substrates from the Keuper formation and were deeply developed during former periods of vine cultivation. Sites in the extensive industrial areas of the Neckar valley mostly consist of land fills, partly containing building rubble resulting from the destruction of World War II.

Sampling design

A total number of 303 investigation plots were included into the analysis over all three cities. The data sampling of Bremen (HB) and Berlin (BE) included chronosequences (Pickett 1989, Knops & Tilman 2000) of 133 (HB) and 91 (BE) plots which were randomly stratified (Hirzel & Guisan 2002) along a gradient of site age (time since initiation of vegetation development), site size, and moisture status. For the 79 Stuttgart (ST) sampling sites, selection was based on vegetation maps of public areas. From these, a random number of five sampling sites was chosen from the patches of each given urban brownfield vegetation type (for further explanation of the Stuttgart method see Kleyer 2002 and Kleyer 1999).

Soil samples were taken at each of the 224 HB and BE plots from every soil layer found within an 80 cm depth maximum. Table 4. 1 shows the soil parameters determined in Bremen and Berlin. Soil samples in

Stuttgart were taken from a 100 cm depth and analyzed in the laboratory. For a more exact description of methods and parameters analyzed see Kleyer (2002) and Kleyer (1999).

Table 4. 1: Soil parameters were determined on site, in the laboratory by analyzing the soil samples, or by calculation from previously determined values.

determination type	soil parameter	method / according to
on site	layer thickness	
	oxidative/reductive signs	Arbeitsgruppe Boden (1994)
	root fraction	
	stone fraction	
	texture of stone fraction	
	soil texture	
laboratory	apparent density	Schlichting *et al. (* 1995)
	pH ($CaCl_2$)	
	calcium carbonate ($CaCO_3$)	Scheibler in Schlichting *et al.* (1995)
	plant available phosphorus (P)	ammonia-lactate solution (Egner & Riehm in Schlichting *et al.* 1995)
	plant available potassium (K)	
	organic matter of top soil layer	Arbeitsgruppe Boden (1994)
	water permeability in saturated soil (kf)	
calculation	air porosity (AP)	Arbeitsgruppe Boden (1994)
	plant available field capacity (PAFC)	
	effective cation exchange capacity (ECEC)	
	plant available water (PAW)	Wendling *et al.* (1984) in DVWK (ed.) (1996), Schröder *et al.* (2004)

Other explanatory variables included in the analysis were site location (ST, HB or BE) to identify possible mere location effects. Also included were site age, i.e. time since initiation of succession after severe disturbance or new creation of site (detected by aerial pictures) and the degree of current disturbance. The degree of current disturbance was calculated by means of the number, severity and extent of disturbance events (*D*) of a site:

$$D_c = \frac{x}{365} * b^3 * a$$ Equation 1

which included the number of disturbance events per year (*x*) on a daily level (therefore divided by 365), the proportion of biomass removed or destroyed (*b*) and the proportion of site surface affected (*a*) by the disturbance event. The *b* -value was cubed because destruction of biomass is the most severe effect for vegetation survival and thus has to be emphasized compared to the number and area of disturbance.

Presence/absence of all vascular plant species was recorded at each of the 224 HB and BE plots in an area of 4m x 4m. For Stuttgart, vegetation relevés were carried out at 79 plots in 5 m² quadrates (see also Kleyer 2002).

Measures of plant traits for most of the species were taken from 10 specimens of each of the species selected by prevalence, i.e. they occurred in at least 10 of the plots. Table 4. 2 shows the traits that were determined. Trait values for the remaining species that were not analyzed in field were taken from Kleyer *et al.* (in prep.).

Table 4. 2: Traits and trait features determined by analyzing plant material on site (a), in the laboratory (b), or by calculation from previously determined values (c). The grey marked traits were used in cluster analysis, the white marked traits were used for determination of the grey on.

determination type	trait	parameter measured according to	data type	source of values	definition [unit]
(a)	plant life span (PLS)	Knevel *et al.* (2005)	categorical	Rothmaler (1994)	1 - annual 2 - biennial 3 - perennial
(b)	terminal velocity (TV)	Knevel *et al.* (2005)	numerical	field measurements and Kleyer *et al.* (in prep.)	[m*sec^{-1}]
	seed weight (single seed)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	[mg]
	seed number (whole plant)	Knevel *et al.* (2005)	numerical	field measurements and Kleyer *et al.* (in prep.)	[no unit]
	leaf size (single leaf)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	[mm^2]
	leaf weight (single leaf)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	[mg]
	shoot weight (stem and leaves of whole plant)	Cornelissen *et al.* (2003)	numerical	field measurements	[mg]
(c)	leaf area ratio (LAR)	Anten & Hirose (1999)	ratio	field measurements and Kleyer *et al.* (in prep.)	LMR * SLA [mm^2/mg]
	reproductive effort (above ground) (RE)	Poorter & Nagel (2000)	ratio	field measurements and Kleyer *et al.* (in prep.)	seed weight*seed number/shoot weight+seed weight*seed number [no unit]
	seed longevity index (SLI)	Thompson *et al.* (1997)	index	Kleyer *et al.* (in prep.), Schütz (2000)	< 0.3 - transient 0.3 - 0.55 - short term persistent > 0.55 - long term persistent
	specific leaf area (SLA)	Cornelissen *et al.* (2003)	numerical	field measurements and Kleyer *et al.* (in prep.)	leaf size/leaf weight [mm^2/mg]
	leaf mass ratio (above ground) (LMR)	Anten & Ackerly (2001)	ratio	field measurements and Kleyer *et al.* (in prep.)	leaf weight/shootweight [no unit]

Statistical analysis

To acquire the plant functional groups (PFGs), a stepwise logistic regression and iterative clustering as described in Schadek & Kleyer in prep. were carried out, using a SAS-macro including the functions PROC LOGISTIC and PROC CLUSTER (SAS-Institute 1989).

After a multicollinearity check (and ensuing exclusion of variables in case of Spearman rho $\geq$0.7; for correlation coefficients see Table A - 5), the following explanatory variables and their squares were included into the regression analysis: study location, site age, degree of current disturbance, pH-value of soil, available water per year and nutrient conditions (formed by principal component analysis of K, P and ECEC). Due to a wide range of values, K, P, and degree of current disturbance were ln-transformed prior to analysis.

For the trait based cluster analysis, we chose the following candidate traits, which represent different aspects of survival strategies of plants:

- specific leaf area [SLA] (with regard to vegetative plant persistence on sites),
- plant life span [PLS] (with regard to vegetative plant persistence on sites),
- canopy height (with regard to veget. plant persistence on sites and dispersal),
- seed number/terminal velocity[2] (with regard to dispersal),
- clonality (with regard to vegetative persistence and dispersal),
- seed weight of single seed (with regard to reproduction),
- seed longevity index [SLI] (with regard to generative persistence on sites).

All aforementioned traits were not highly correlated (Spearman rho ≥0.7; for correlation coefficients see Table A - 6).

To test the transferability of the PFG habitat models across the three mentioned cities, and to be able to make statements about their spatial generality, we separated the general site x PFG factor matrix as well as the site x environmental factor matrix into city specific matrices (Figure 4. 1). Thus, city specific stepwise logistic regression models for each PFG could be generated. In the next step, we applied the derived logistic regression habitat models to the environmental conditions of the respective two other cities in order to get predictions for each PFG on each plot based on the respective two 'foreign' models. For the comparing of competing models' fit to the same set of data, i.e. the comparison of the observed to the generated predicted values from the fitted models (model calibration), R^2 measures can provide useful statistics (Hosmer & Lemeshow 2000). In our analysis, we used the squared Pearson correlation coefficient r^2 recommended by Mittlböck & Schemper (1996) (see also Backhaus *et al.* 2003). To examine the calibration components bias and spread, we used calibration plots as recommended by Vaughan & Ormerod (2005).

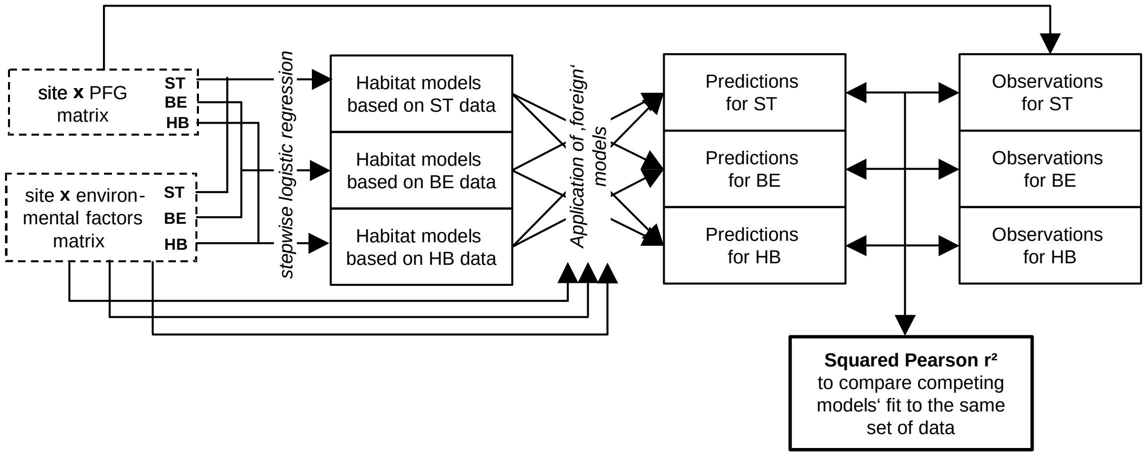

Figure 4. 1: Procedure of testing the transferability of PFG habitat models across cities.

Results

The environment

The pH ranged in general from very high acidic values to alkalescent conditions (Figure 4. 2). While the Stuttgart plots had neutral conditions, the median of the pH in Berlin plots was slightly higher, all Berlin values ranging from alkalescent to medium acidic. The Bremen plots showed a remarkably lower pH, the median lying near neutral, with a number of values ranging into very high acidic conditions. Plant available water per year (PAW) ranged from over 100 mm to almost 0 mm. The PAW of all three cities spanned resembling ranges, the Stuttgart sites having the highest values of all three cities. Also, the range of site age was comparable among the mentioned cities, however, Stuttgart had a higher contingent of older sites compared to Berlin and Bremen. The same holds true for the current disturbance, being generally low in all three cities with the exception of some Stuttgart sites. The highest nutrient supplies generally were found Berlin, where soil phosphorus contents are higher than in the soils of the two other cities. Contents of potassium in Stuttgart were comparable to those of Berlin, Stuttgart having by far the highest effective cation exchange capacity of all three cities (Figure 4. 2) due to the less sandy conditions compared to Berlin and Bremen (data not shown).

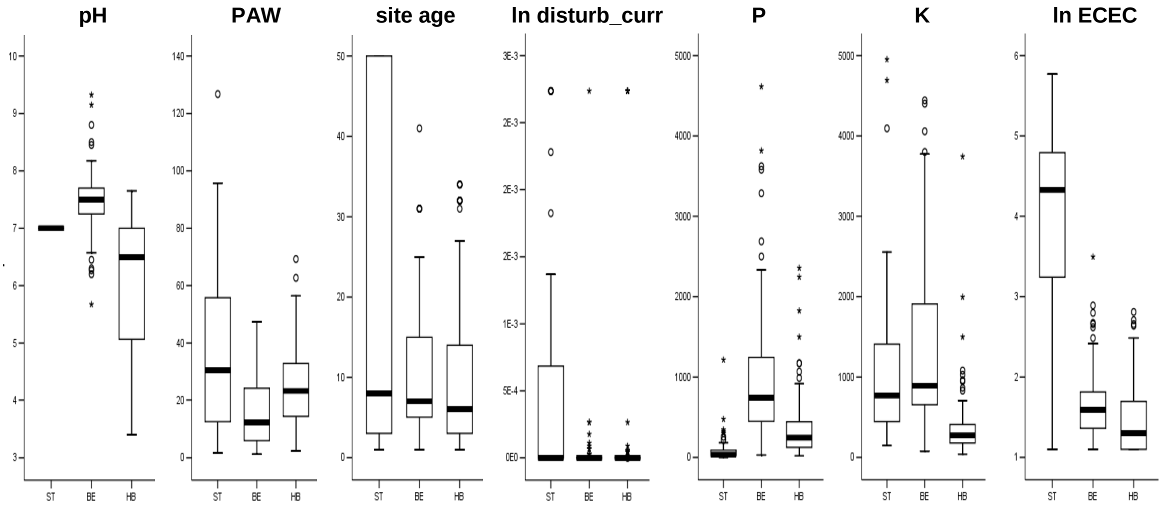

Figure 4. 2: Medians, interquartil ranges and extreme values (marked by * and °) of explanatory variables measured on the investigation sites of Stuttgart, Berlin and Bremen. Abbreviations: pH=pH-value (measured in a $CaCl_2$ solution), PAW = plant available water [mm], site age = time since initiation [y], ln disturb_curr: degree of current disturbance (ln–transformed), P = phosphorus [$kg*ha^{-1}$], K = potassium [$kg*ha^{-1}$], ln ECEC = effective cation exchange capacity (ln-transformed) [$cmol_c*kg^{-1}$].

Plant functional groups

From iterative trait clustering a sum of 9 PFGs containing 42 species was derived (Table 4. 3 and Table A - 7). PFG 1 consists of species characteristic of middle aged grassland-like brownfields with a relatively high nutrient and moisture status. PFG 2, on the one hand, is composed of species that rather belong to older sites and are able to occur under a wide range of environmental conditions. On the other hand, species with rather narrow habitat requirements such as *Corynephorus canescens* and *Rumex acetosella* (both not occurring in the city of Stuttgart), are also assigned to this PFG. PFG 3, 5 and 6 are characterized by annuals; the PFGs are separated by different moisture and nutrient requirements of their species. The PFGs 4 and 7 group biennial and perennial species, the species of PFG 4 having higher demands on nutrients and moisture than those of PFG 7. PFG 8 as well as PFG 9 consist of only one species (*Bromus sterilis/Lactuca serriola*).

Table 4. 3: Plant functional groups (PFGs) formed by plant life span (PLS), seed number divided by terminal velocity² (seed number/TV²), seed longevity index (SLI), and clonality. The prevalence numbers show counts of PFGs on the investigated plots. A count was taken each time a PFG was represented on a plot by at least one of its containing species. Abbreviations: ST=Stuttgart, BE=Berlin, HB=Bremen.

Trait combination	PFG	species (prevalence)	no. of species	R^2_N	PFG represented by at least one species (no. of events)			
					sum	ST	BE	HB
PLS + seed number/TV² + SLI + clonality	1	*Linaria vulgaris* (32, not HB), *Lolium perenne* (48), *Elymus repens* (90), *Plantago lanceolata* (59), *Poa angustifolia* (31), *Poa compressa* (107), *Rumex acetosa* (15, not BE), *Rumex obtusifolius* (11, not BE), T*araxacum officinale* (156), *Trifolium repens* (59), *Arrhenatherum elatius* (44)	11	0.0789	176	66	66	44
	2	*Corynephorus canescens* (22, not ST), *Dactylis glomerata* (57), *Festuca rubra* (80), *Hypericum perforatum* (76), *Picris hieracioides* (31, not BE), *Plantago major* (51), *Poa trivialis* (85), *Rumex acetosella* (52, not ST), *Artemisia vulgaris* (115)	9	0.1431	196	0	74	122
	3	*Saxifraga tridactylites* (22), *Sonchus oleraceus* (10, not BE/HB), *Veronica arvensis* (55), *Vicia hirsuta* (47, not ST)	4	0.4896	25	1	0	24
	4	*Achillea millefolium* (65), *Agrostis capillaris* (24, not ST), *Poa pratensis* (54), *Calystegia sepium* (18, not BE)	4	0.3794	53	5	38	10
	5	*Conyza canadensis* (109), *Daucus carota* (101), *Medicago lupulina* (134), *Poa annua* (58), *Cerastium semidecandrum* (70)	5	0.4201	130	47	73	10
	6	*Chenopodium album* (50), *Polygonum aviculare* (27), *Vicia angustifolia* (65)	3	0.3026	67	12	42	13
	7	*Matricaria maritima* (60), *Melilotus officinalis* (23), *Oenothera biennis* (61, not ST), *Arenaria serpyllilfolia* (100)	4	0.3736	101	14	63	24
	8	*Bromus sterilis* (88)	1	0.7902	61	0	61	0
	9	*Lactuca serriola* (56)	1	0.9901	35	0	35	0

Besides abiotic demands, the different PFGs are dividable by their species' traits and as such by species' survival strategies (Table 4. 4): Dispersal in space and/or time (represented by seed number/TV² and SLI) is high for PFG 6, 7, and 9 species, while PFG 2 and 4 are characterized by species with a high potential of vegetative persistence on sites and a high ability of clonal dispersal. The other PFGs, however, show medium to low values for all mentioned traits. Model fit of most of the PFGs' models based on the whole 'three-city' dataset of explanatory variables is good to very good. Exceptions are the models of PFG 1 and 2 which show values below 0.2.

Table 4. 4: Traits used for clustering the resulting plant functional groups and their statistical values. Abbreviations used: min. = minimum, max. = maximum, std.dev. = standard deviation, PFG = plant functional group, PLS = plant life span, TV = terminal velocity, SLI = seed longevity index. For units see Table 4. 2.

	PFG	PLS	seed number/TV^2	SLI	clonality
min.	1	3.0	2.95	0.00	0.00
	2	3.0	11.10	0.52	0.50
	3	1.0	5.42	0.45	0.00
	4	3.0	19.92	0.11	1.00
	5	1.0	7.87	0.44	0.50
	6	2.0	2.74	0.71	0.00
	7	2.0	19.49	0.57	0.00
	8	1.0	4.83	0.00	0.00
	9	2.0	5.08E+05	0.12	0.00
max.	1	3.0	1605.97	0.43	0.50
	2	3.0	4856.12	1.00	1.00
	3	1.0	3.03E+04	0.55	0.00
	4	3.0	446.96	0.39	1.00
	5	2.0	114.65	0.90	0.50
	6	1.0	56.35	1.00	0.00
	7	2.0	1629.98	1.00	0.00
	8	1.0	4.83	0.00	0.00
	9	2.0	5.08E+05	0.12	0.00
mean	1	3.0	350.81	0.27	0.45
	2	3.0	1224.80	0.75	0.56
	3	1.0	7671.44	0.50	0.00
	4	3.0	133.33	0.26	1.00
	5	1.4	57.32	0.64	0.50
	6	1.0	20.70	0.84	0.00
	7	2.0	625.61	0.79	0.00
	8	1.0	4.83	0.00	0.00
	9	2.0	5.08E+05	0.12	0.00
std.dev.	1	0.0	507.43	0.13	0.14
	2	0.0	1918.47	0.13	0.16
	3	0.0	1.31E+04	0.03	0.00
	4	0.0	181.21	0.11	0.00
	5	0.5	41.86	0.15	0.00
	6	0.0	25.20	0.12	0.00
	7	0.0	621.38	0.16	0.00
	8	0.0	0.00	0.00	0.00
	9	0.0	0.00	0.00	0.00

Modeled based on specific data of the respective cities, the different PFGs showed varying responses to the respective explanatory variables (Table 4. 5, for regression coefficients see Table A - 8). Most of the PFGs reacted to site age, pH and plant available water. Only three of the nine PFGs showed responses to the degree of current disturbance and nutrients. The origin of the included data (location) did not determine the occurrence of PFGs in any of the models (Table 4. 5). In addition to the variations in PFGs' reactions to the variables, there were cases where one and the same PFG, modeled based on data of different cities, was explained by different variables or showed differently directed responses to the same variable. PFGs 2, 5 and 7 all responded to PAW, but each in a different way (Table 4. 5).

Model fit of the city-specific models broadly reflected the results of the 'three-city' models (Table 4. 3): the models for PFG 3 to 9 showed values of R^2_N which are above the acceptable level of $R^2_N > 0.2$, whereas PFG 1 and 2 model fits lay below this level. For a few PFGs, there was no significant model at all for one or more city (ST: PFGs 1-4 and 8+9, BE: PFG 3, HB: PFGs 8+9).

Table 4. 5: Response of plant functional groups (PFGs) to site characteristics. An arrow pointing downwards indicates a negative, an arrow pointing upwards a positive response to the respective parameter. The bends indicate an unimodal response. Grey rows show that there was no model for this PFG based on data of the respective city. Abbreviations: PFG = plant functional group, ST=Stuttgart, BE=Berlin, HB=Bremen, location = city the data are measured in, disturb_curr: degree of current disturbance, site age = time since initiation [y], pH=pH-value (measured in a $CaCl_2$ solution), PAW = plant available water [mm], nutrients = nutrient content (formed by principal component analysis of K, P and ECEC).

PFG	model based on data of	R^2N	location	disturb_curr	site age	pH	PAW	nutrients
1	ST							
	BE	0.08		↘		↗		
	HB	0.1			∪		↗	
2	ST							
	BE	0.05					↘	
	HB	0.09			∩	↗	↗	↗
3	ST							
	BE							
	HB	0.39			∩	↗	↗	
4	ST							
	BE	0.31			∩			
	HB	0.42				↘		
5	ST	0.21		↗			↘	
	BE	0.27			↘		∩	
	HB	0.39				↗	↘	
6	ST	0.55		↗				↗
	BE	0.16		∩	∩			
	HB	0.41			∩		↗	
7	ST	0.23						∪
	BE	0.33			↘		↘	
	HB	0.36				↗	∪	
8	ST							
	BE	0.94			↘		↘	
	HB							
9	ST							
	BE	0.78			↘	↘		
	HB							

Transferability of PFG models

In general, the transferability of the urban brownfields' PFG models measured by the squared Pearson correlation coefficient r^2 was rather low. Compared to the r^2 values of those cases where the models were applied to the respective city itself, the 'foreign' models mostly did not explain half of the variance explained by the original model (Table 4. 6).

Models based on the Stuttgart data in general had high values of r^2 for the city itself (Table 4. 6). However, the r^2 values for the Stuttgart model transfer to Bremen and Berlin were low except for the case of PFG 5 model transfer to Berlin. In the case of most PFGs, Berlin data based models showed low to medium r^2 values when being transferred to the other cities. However, for PFG 6 and 7, the transfer of the Berlin model resulted in very low r² values for Stuttgart, the values for Bremen being remarkably higher. Bremen models were in general of a lower quality than those of Stuttgart and Berlin, but the transferability to the other two cities was in most cases higher than that of the Stuttgart and Berlin based models. However, Bremen models were mainly transferable to Berlin conditions. The r² values for Bremen based models transferred to Stuttgart were in most cases rather low.

In summary, the transferability of the mentioned models was low. It must be pointed out that, in the case of the models with higher values for r² (PFG 6 and 7), Bremen and Berlin models were more transferable to each other than those of Stuttgart to the other cities and vice versa.

Table 4. 6: Transferability of the PFG models expressed by the squared Pearson correlation coefficient r² for models applied to the data of the respective two other cities. Bold letters indicate r² values from which the within city specific model. Abbreviations: ST=Stuttgart, BE=Berlin, HB=Bremen.

		squared Pearson correlation coefficient r²		
		model based on data of		
	model applied to	ST	BE	HB
PFG 1	ST	-	0.012	0.171
	BE		**0.660**	0.155
	HB		0.104	**0.292**
PFG 2	ST	-	--	--
	BE		**0.520**	0.078
	HB		0.022	**0.688**
PFG 3	ST	-	-	0.230
	BE			--
	HB			**0.688**
PFG 4	ST	-	0.011	---
	BE		**0.800**	0.004
	HB		0.001	**0.680**
PFG 5	ST	**0.791**	0.058	0.548
	BE	0.338	**0.826**	0.301
	HB	0.045	0.075	**0.541**
PFG 6	ST	**0.851**	0.002	<0.001
	BE	0.013	**0.505**	0.237
	HB	0.005	0.194	**0.546**
PFG 7	ST	**0.657**	0.002	<0.001
	BE	0.012	**0.894**	0.349
	HB	0.010	0.259	**0.613**
PFG 8	ST	-	--	-
	BE		**0.906**	
	HB		--	
PFG 9	ST	-	--	-
	BE		**0.749**	
	HB		--	

- = no model

-- = no observations of PFG species in the study area the model is applied to

--- = included variable is constant within the whole study area the model is applied to

Discussion

The results of the present study show that the spatial transferability of plant functional groups' models is contingent on basic model conditions, on the implemented environmental conditions of the considered cities, as well as on the implemented species' traits. In the following, we exhibit the basic conditions of the PFG models. After that, we discuss the models' transferability with regard to these basic conditions as well as to the environment specific influences of the incorporated cities. In addition, we present how model transferability reflects species' traits.

Basic model conditions

To get an idea of the predictive performance and thus of the transferability of habitat models, evaluation is best undertaken with independent, external data (Guisan & Zimmermann 2000, Pearce *et al.* 2001, Nygaard & Ejrnaes 2004). Nonetheless, a detailed examination of the basic model conditions cannot be neglected in preparation for the external evaluation (Pearce & Ferrier 2000a).

In the present study, most of the PFGs' models showed, when modeled over the explanatory data of all three cities, values for R^2_N (Table 4. 3) which lie above the acceptable quality level of 0.2 (Backhaus *et al.* 2003). This indicated that they should thus be applicable for predictions, however, the models for PFG 1 and 2 range below the quality level. A possible reason for PFG 1 and 2 models explaining such a low proportion of observed variance may be the number of species grouped in these PFGs; the higher the amount of species in a PFG, the higher the possibility that species traits show different responses not only within a study area but especially, as the case with our three cities, across regions (Dyer *et al.* 2001). Habitat models of PFGs can be of good quality solely under the assumption that shared trait attributes result in similar behavior if the environment is changing (Kleyer 2002). When modeling with a composed data set of different regions, the use of different ranges in the explanatory data can lead to region specific responses of species (Dyer *et al.* 2001, De Bello *et al.* 2005) and thus lead to a low model quality. Another explanation for the low model quality may be that some of the species grouped within the mentioned PFGs were not present in at least one of the study areas; this is a fact that can additionally influence model quality negatively (Pearce & Ferrier 2000b). Regarding PFG 2, the mentioned effects become most obvious: First, PFG 2 has different species occurrence rates for the different three cities, a fact that influences model quality directly due to the different representation of data points over the whole data range. Second, this PFG consists on the one hand of species that are rather generalists and are able to exist under a wide range of environmental conditions, but on the other hand of species like *Corynephorus canescens* and *Rumex acetosella*, which have very special habitat requirements, especially in the case of soil pH and nitrogen (Ellenberg *et al.* 1992). Thus, even if all species of this PFG share similar trait attributes, their differences in habitat requirements and occurrence range lead to an insufficient model quality.

The quality of the city specific PFG models broadly reflects that of the PFG models mentioned before which were derived from pooled environmental data of all three cities. We assume models of low internal quality to be poorly transferable and thus, in order to get general conclusions about similarity and transferability of models, we focus on models with an acceptable internal validation quality.

Similarity of PFG models derived from region-specific data

Do data from different regions lead to similar PFG models concerning the implemented parameters and PFGs' reaction on them? The differences in PFGs' reactions (Table 4. 5) are mostly due to different environmental ranges within the three cities and, considering this, the apparent general similarities outweigh the differences. For example, the reaction of PFG 5 to plant available water (PAW) is not similar for all three cities. However, this may be due to a wider range of PAW values found in Berlin. Thus, negative response to PAW in the upper range of values is common for all three cities while the unimodal relationship of Berlin is visible only when regarding the lower end of the PAW range. Berlin soils are sandy and often include a high amount of brick rubble, both resulting in a low water holding capacity and as such in low PAW values.

The reaction of PFGs to environmental factors can be either landscape specific or general, i.e. valid for different landscapes (Kleyer 2002). Factors whose ranges are generally comparable across regions induce general responses (Dyer *et al.* 2001, De Bello *et al.* 2005), which again induce similarity of the PFG models. However, in cases of parameters whose ranges are specific for each region and which in addition have a high influence on PFG occurrence, landscape specific reactions of PFGs lower or even impede the similarity of our models (De Bello *et al.* 2005). In the present study, this becomes most obvious for the factors PAW and site age in the cases of PFG 5 and 6. All three PFG 5 models respond to PAW, which we assume to be due to the fact that the three cities share a wide range of PAW values. All other response factors in the case of PFG 5 have different ranges for the three cities and do not induce a similarity of the PFG's response. PFG 6 responds to site age modeled with Berlin and with Bremen data but not in the case of Stuttgart. We expect this to be due to the more similar range of site ages of Berlin and Bremen compared to Stuttgart, which has a lot more older sites. In general, particularly PAW induces similarity to the PFG models whereas site age, degree of current disturbance and soil pH are impeding factors in this case.

In summary, responding to the initial question if data from different regions lead to similar models, we conclude that in a broader view, and assuming similar ranges of environmental variables for all included regions, models of urban brownfields' PFGs are of a certain similarity. A closer look at the models and the implemented factors reveals many landscape specific reactions that are not commonly relevant for all regions. The influence of this on the transferability of the PFG models is high and can be directly related to the environmental demands and traits of the respective species, as will be discussed in the following.

Transferability of PFG models

As a consequence of PFGs showing similar responses when ranges of parameter values are more or less similar across the regions, we found that models were better transferable when (i) using similar parameters for model building and (ii) covering similar parameter ranges across cities. For example, in the cases of PFGs 5, 6 and 7, where two cities share at least one model parameter, transferability is remarkably higher than in other cases where different parameters are used for the city specific models. Similar environmental ranges of the used parameters additionally increase the level of transferability (Vaughan & Ormerod 2005). The Bremen PFG 5 model transfers better to Stuttgart than to Berlin, which may be due to the fact that the shared range of PAW as the common parameter is wider between Bremen and Stuttgart than between Bremen and Berlin.

Another hint at the relevance of regional peculiarities inhibiting the generalizability of models is that, in the majority of cases, the transferability of Stuttgart models to Bremen and Berlin and vice versa is low. In general, a low transferability can be due to different environmental as well as methodological effects (Pearce & Ferrier 2001, Vaughan & Ormerod 2005). General methodological reasons might be the use of different survey techniques, seasonal variation in survey period, and a different regional prevalence of PFG species in the different cities (Pearce & Ferrier 2000a). Calibration plots can give useful hints regarding the reasons for a low transferability of models (Vaughan & Ormerod 2005). In the case of PFG 6 and 7, where the mentioned effect was most obvious, plots of observed vs. predicted values (data not shown) do not show a clear direction of calibration error in terms of bias and spread which would allow a direct interpretation. Transferring Bremen and Berlin models of these PFGs to Stuttgart, there is spread as well as positive and negative bias. Problems with transferability often cannot be diagnosed directly by the type of calibration error (Vaughan & Ormerod 2005), which is also obvious in the present study. Calibration error derived from different prevalences and seasonal variation as a methodological reason for low transferability can be excluded since, for PFG 6 and 7, prevalences of Bremen sites were not remarkably lower than those of Stuttgart and there was no noticeable seasonal variation in the survey period. In general, we suppose environmental conditions to have the greatest inhibiting effect on model transferability in our case. There are environmental differences between Stuttgart and Bremen/Berlin regarding several parameters. Stuttgart soils, for example, are far more clayey than the sandy soils of Bremen and Berlin and mostly have a higher soil pH. The climate of Stuttgart is greatly influenced by its location in a river valley and thus cannot be directly compared to the rather open situation in Bremen and Berlin. This leads to special habitat conditions in Stuttgart, which are amplified by the more small-scale and dense site mosaic, which in turn induces a higher degree of current disturbance. The situation of Berlin and especially of the Bremen sites differs from Stuttgart by climate as well as by habitat size, fragmentation, and degree of current disturbance due to a high proportion of urban brownfields which are situated in newly established areas in the open countryside.

These differences find expression in the transferability of the models and can directly be related to the environmental demands and the trait features of the respective PFGs. In general, the PFGs clustering annual plants have a higher transferability, notably from Bremen to Berlin and vice versa than those containing biennial or perennial species. In addition, a high ability to disperse in space and time as well as low nutrient and moisture demands favor a high transferability. On the other hand, PFGs containing species with special environmental demands or those characterized by a high potential for vegetative persistence and a high ability of clonal dispersal are in general of a lower transferability. General and flexible responses of species obviously induce generality to urban brownfields' PFG models, i.e. in terms of the CSR-scheme of Grime 1979, ruderals favor whereas competitors and stress-tolerators inhibit model transferablity.

In summary, besides a slight influence of the different stratification of survey plots, we assume that the low model transferability of and to Stuttgart is especially due to important, landscape specific explanatory variables missing from the respective 'foreign' models (Pearce & Ferrier 2000a). The presence of novel factors influencing distribution and the ecotypic variation between the regions lead to a failure of model transport (Oostermeijer & van Swaay 1998, Vaughan & Ormerod 2005). Concerning the present study, in our view, the site history was the main factor which remained unincluded by our models and thus may lead to their low transferability. Different site histories of urban brownfields may lead to different parent material of soil as well as to differences in space related parameters such as the location of brownfields (city center or open countryside) or the complexity of the site mosaic within the respective industrial area and thus the spatial relation of habitats. By inclusion of site history parameters, the high relevance of dispersal in space and time in case of urban habitats (Ozinga *et al.* 2005, Cook *et al.* 2005, Schadek & Kleyer in prep.) would be covered by the models, which would increase the model transferability.

Conclusions

The predictive power of a common set of traits is marked by its repeatability over a wide range of conditions (McIntyre *et al.* 1999, Rusch *et al.* 2003, De Bello *et al.* 2005). The transferability of urban brownfields' PFG models across regions is highly contingent on the type and the degree of species' and thus PFGs' responses to environmental factors (landscape specific vs. general response; Kleyer 2002). The content of ruderals with a high ability to disperse in space and time as well as of generalists enhances the transferability of urban brownfields' PFG models. Moreover, general responses which provide repeatability can be estimated under similar environmental conditions along with a lack of regional peculiarities (De Bello *et al.* 2005). Thus, when dealing with generalizability of PFG responses and a resulting predictability of environmental changes across regions, managers and conservationists should carefully consider habitat types, survey techniques, climate and seasonal variation, and especially the environmental ranges and site history of the regions being considered (Fleishman *et al.* 2003, Vaughan & Ormerod 2005).

Chapter 5

Vegetation structure and soil of urban brownfields over the course of time

Chapter 5

Vegetation structure and soil of urban brownfields over the course of time

with Michael Kleyer

Abstract

Urban brownfields and abandoned sites in the urban landscape contribute greatly to urban biodiversity due to their characteristically high spatio-temporal dynamics and their transient character. To be able to make predictions and hence sustain species richness, we need to qualify and quantify the relationship between abiotic conditions and vegetation as well as their development over time. Species richness is, among other things, contingent on vegetation structure. Moreover, vegetation structure provides information about habitat suitability and helps predict successional pathways, thus bearing relevant information for a possible management. In the present study, we examined vegetation height, vegetation density and several soil parameters of a chronosequence of 220 urban brownfield sites in Bremen and Berlin, Germany. By linking these parameters to site age using single and multiple linear regression, we got to know more about the development of soil parameters and vegetation structure over time as well as about which factors mostly influence the vegetation structure of urban brownfields. Soil parameters of the sites are in general not clearly linked to site age. Dividing the sites by their soil history, we found pH responding negatively and plant available water responding positively to site age on sites that were in use before abandonment, while on newly created sites widespread conditions inhibited us from seeing clear trends of temporal development. Nutrient conditions in general showed no temporal trend. Vegetation height and density increased significantly over time, being mostly contingent on site age, soil phosphorus content and water permeability of the soil (with height and density) and plant available water (with density). By this, we see that vegetation structure and thus biodiversity of sites is not only contingent on site age, a fact which has to be taken into account for a management to sustain the biodiversity of urban brownfields.

Introduction

Urban brownfields and abandoned sites in the urban landscape are valuable sites, and not only because of their positive influence on urban climate and their social value as natural wildspace (Sukopp & Wittig 1993, London-Wildlife-Trust 2002). Moreover, due to their spatio-temporal dynamics and transient character, the species richness of urban brownfields is generally high (e.g. Gilbert 1989, Sukopp & Wittig 1993, Rebele 1994, Niemelä 1999, Ricketts & Imhoff 2003, Kühn *et al.* 2004). However, there is a general trend towards a declining biodiversity within cities, mostly due to an increasing urbanization (Pysek *et al.* 2004, Pauchard *et al.* 2006). This evokes a need for predictions and management concerning the consequences of environmental change for urban ecosystems in order to sustain urban biodiversity. A crucial base for this is a general knowledge of the quality of habitats and soil conditions and their development over time, as well as a quantitative understanding of the relations between habitats and plant species.

In general, the description and analysis of vegetation's structural dynamics is an important research aspect on the level of ecosystem processes (Zehm *et al.* 2003), especially concerning the relationship of abiotic to biotic conditions. Measures of vegetation structure provide information about, for instance, habitat suitability and can be useful in the prediction of successional pathways (Jones *et al.* 2004, Ruiz-Jaen & Aide 2005). Plant species richness and the occurrence of insect species are contingent, *inter alia*, on vegetation structure (Gough *et al.* 2000, Schaffers 2002, Strauss & Biedermann in prep.), as well as vegetation height and density, all being crucial parameters for the biodiversity of sites. Moreover, changes in vegetation structure are stated to be the most conspicuous and visible indications of a successional sere (Bautista-Cruz & del Castillo 2005), a fact that may be important for site management. This poses the question: Which factors are the main driving force for the succession and development of brownfield sites' vegetation structure? One crucial succession factor stated is 'time since initiation of vegetation development' (Cook *et al.* 2005). Another main driving factor for the successional course is the type of substrate (Gilbert 1989, Chapin *et al.* 2002). Soil parameters often change during the course of site development. Several studies show, for example, an increasing acidification and increasing loads of nitrogen while phosphorus contents of soil decrease over time (e.g. De Deyn *et al.* 2004, Richter *et al*. 1994, Chapin *et al.* 2002). However, the direction of change and the level of variation in these changes often remain unclear. In addition, vegetation structure itself changes over time and may influence soil conditions directly (Fiala *et al.* 2001, Isermann 2005). Thus, we see the factors *time since initiation* and the *various soil conditions* as the main driving factors of vegetation structure development and hence of biodiversity in urban brownfields. This leads to the question: Which of the factors have the highest influence on vegetation structure, and thus on species richness in urban brownfields? This is a fact that is of importance for predictions as well as for management of urban brownfields in order to sustain their high biodiversity (Prach *et al*. 2001a).

The phenomenon of vegetation development and the changes of soil parameters in the successional course have been studied in various types of landscapes, such as abandoned fields (Knops & Tilman 2000, Wang 2002), meadows (Korzeniak 2005) and forests (Härdtle *et al.* 2003). However, the aspect of analyzing soil changes and their relationships with vegetation development has usually been neglected in these studies (Abadin *et al.* 2002, Otto *et al.* 2006). Also, for urban habitats, there are only a few studies of spontaneous vegetation succession (Prach *et al.* 2001b, Rebele & Lehmann 2002) that directly link vegetation dynamics to environmental conditions. In addition, most of the existing studies of urban soils remain on a very general level (e.g. Effland & Pouyat 1997) or focus on the aspect of contaminated soils and heavy metals in the urban area (Jennings *et al.* 2002, Markiewiez-Patkowska *et al.* 2005). Due to the continued growth of human populations and the uncontrolled spread of urban areas worldwide, a general understanding of urban soil processes is becoming increasingly important (Effland & Pouyat 1997).

To enlarge the knowledge base about the development of urban vegetation and soils, especially concerning their behavior over time and their dependencies, we examined the following questions:

1) How do soil parameters of urban brownfields change during development of sites over time?
2) Do the vegetation structure parameters vegetation height and vegetation density increase significantly over time?
3) Which are the main factors affecting vegetation structure of urban brownfields?
4) Which parameters can be determinants of a biodiversity sustaining site management?

To answer these questions, we analyzed the soil parameters and vegetation structure of several urban brownfields in Bremen and Berlin, Germany. By linking these parameters to site age using single and multiple linear regression, we obtained more information about the development of soil parameters over time as well as about which factors mostly influence the vegetation structure of urban brownfields.

Methods

Study sites

The present study took place at brownfield sites in the cities of Bremen, northwestern Germany (53°05’ N, 8°44’ E), and Berlin, eastern Germany (52°30’ N, 13°28’E). Sites of different age, size and moisture status in varied types of industrial areas, i.e. previously developed land as well as abandoned railroads, and newly created commercial sites were included. During the study period, all sites were abandoned and site use was limited to leisure (walking dogs, sometimes biking, golfing or kite surfing) and occasional storage of material or equipment. Berlin (mean temperature 9.7° C, mean annual precipitation 560 mm) has a more continental climate than Bremen, whose climate is rather maritime (mean temperature 8.8 °C, mean annual precipitation 694 mm). Sandy soils are predominant in the study areas, often mixed with a high portion of building rubble in old industrial areas and in areas of Berlin destroyed during the Second World War. Newly created sites, which were found mostly in Bremen, are in general formerly humid grasslands which have been filled up with sandy material.

Sampling design

All the sampling during the present study was conducted in a chronosequence (Pickett 1989, Knops & Tilman 2000) consisting of 213 plots which were randomly chosen along a stratification gradient (Hirzel & Guisan 2002) of site age (time since initiation of vegetation development), site size, and moisture status.

Soil samples were taken at each of the 220 plots from every soil layer found within a maximum depth of 80 cm. Table 5. 1 shows the soil parameters measured, including the abiotical parameters pH-value (measured in a $CaCl_2$-solution), water permeability in saturated soil (kf), air porosity (AP), plant available field capacity (PAFC), plant available water (PAW), content of calcium carbonate ($CaCO_3$), content of plant available phosphorus (P) and potassium (K), and effective cation exchange capacity (ECEC). Due to their wide range of values, the last four parameters were ln-transformed prior to analysis.

Site age (time since initiation) for each plot was determined via a time series of aerial photographs.

Measurements and subsequent calculation of vegetation structure were taken on the herb layer of every plot using a white screen, erected perpendicular to the ground (see Sundermeier 1999) as described in Strauss & Biedermann (2005). In our analyses, we included the weighted vegetation height [cm], which does not describe the absolute maximum height of individual plants but the relative center of vegetation height within a stand, calculated from an average of several measures of maximum plant height. For terms of vegetation density we included horizontal density [%], which is the vegetation cover in top view and describes the amount of bare ground, and vertical density [%], which is the density of vegetation in lateral view.

Table 5. 1: Soil parameters were determined on site, in the laboratory by analyzing the soil samples, or by calculation from previously determined values.

determination type	soil parameter	method / according to
on site	layer thickness	
	oxidative/reductive signs	Arbeitsgruppe Boden (1994)
	root fraction	
	stone fraction	
	texture of stone fraction	
	soil texture	
laboratory	apparent density	Schlichting *et al.* (1995)
	pH ($CaCl_2$)	
	calcium carbonate ($CaCO_3$)	Scheibler in Schlichting *et al.* (1995)
	plant available phosphorus (P)	ammonia-lactate solution (Egner & Riehm in Schlichting *et al.* 1995)
	plant available potassium (K)	
	organic matter of top soil layer	Arbeitsgruppe Boden (1994)
	water permeability in saturated soil (kf)	
calculation	air porosity (AP)	Arbeitsgruppe Boden (1994)
	plant available field capacity (PAFC)	
	effective cation exchange capacity (ECEC)	
	plant available water (PAW)	Wendling *et al.* (1984) in DVWK (ed.) (1996), Schröder *et al.* (2004)

Statistical analysis

To draw near the dependences of the three factors site age, abiotic conditions, and vegetation structure, we used the following statistical methods:

- correlation analysis according to Spearman,
- simple linear regression,
- multiple linear regression (forward stepwise, $p_{in}=0.05$, $p_{out}=0.10$).

Within multiple linear regression, inclusion ranks were used to draw near the statistical relevance of variables influencing vegetation structure (Backhaus *et al.* 2003). The earlier a variable is included into the model, the relatively higher its correlation to the dependent variable. Standardized regression coefficients (B*) are independent from the specific scale of the respective parameter (Backhaus *et al.* 2003) and were used to measure the strength of an independent variable's influence within the model compared to other included variables.

All analyses were done in SPSS 13.0.1 (SPSS Inc. 2004). 3D-response curves were generated using MATLAB 6.1 (The MathWorks, Inc.).

Results

The environment

The study sites' resources and other site characteristics form a gradient within the surveyed landscape (see Table 5. 2). The pH ranges from very high acidic values, mainly on sites lying in the vicinity of a steel mill and on those of old successional and already forested areas, to alkalescent conditions, which we found either in old railyards, in areas with a high amount of rubble in the soil, or in newly created sites mainly filled up with sandy marine material. In 30% of the sites we found no measurable inorganic carbonate. The highest amounts of $CaCO_3$ were found in old industrial areas as well as in areas of Berlin within soils containing lots of construction waste. Moisture conditions are constrained by several factors, altogether the most humid sites are those with a retaining layer or very dense soils. Sites with sandy material or gravel layers (newly created sites, old railyards) are most arid. The highest nutrient supplies were found in older industrial zones with a high amount of brick rubble in soils or on sites intensely used for dog walking, while newly created sites in most cases are nutrient depleted.

Table 5. 2: Parameters of soil and vegetation structure as well as site age and their statistical values for Bremen (n=128), Berlin (n=85) and for both cities (n=213). Abbreviations used: min. = minimum, max. = maximum, std.dev. = standard deviation, pH=pH-value (measured in a $CaCl_2$ solution), PAW = plant available water, P = phosphorus, K = potassium, kf = water permeability in saturated soil, AP = air porosity, PAFC = plant available field capacity, $CaCO_3$ = calcium carbonate, ECEC = effective cation exchange capacity, site age = time since initiation, horizontal density = vegetation cover in top view, vertical density = density of vegetation in lateral view, height = weighted vegetation height. Parameters in grey rows were not taken into regression analysis because of high correlation with other variables.

	min.			max.			mean			std.dev.		
	Bremen	Berlin	all	Bremen	Berlin	all	Bremen	Berlin	all	Bremen	Berlin	all
pH	3.4	5.7	3.4	7.7	9.3	9.3	6.0	7.4	6.6	1.1	0.5	1.2
PAW [mm]	2.4	1.2	1.2	69.3	47.4	69.3	24.8	15.6	20.7	13.5	11.1	13.5
P [kg*ha^{-1}]	23	29	23	4490	6497	6497	510	1339	847	610	1226	999
K [kg*ha^{-1}]	39	77	39	3744	5923	5923	448	1706	959	455	1368	1125
kf [cm*d^{-1}]	10.4	5.6	5.6	653	653	653	262	129	210	224.4	163	213
AP [mm]	2.5	2.6	2.5	210	222	222	128	64	102	62.1	55.5	67.6
PAFC [mm]	4.0	1.1	1.1	193.4	175.4	193.4	90.8	63.8	79.2	41.5	42.3	44.5
$CaCO_3$ [kg*ha^{-1}]	0	0	0	$1.3*10^6$	$4.88*10^6$	$4.88*10^6$	$1.04*10^5$	$3.88*10^5$	$2.2*10^5$	$4.5*10^5$	$3.1*10^5$	$4.3*10^5$
ECEC [cmol$_c$*kg^{-1}]	0.02	0.08	0.02	2.36	1.62	2.36	0.57	0.41	0.47	0.26	0.44	0.36
site age [y]	0	0	0	33	40	40	10.1	10.0	10.0	10.6	8.3	9.8
horizontal density [%]	0	1	0	90	100	100	38.9	48.2	42	26	24	26
vertical density [%]	0	0.07	0	21.5	22.1	22.1	4.1	6.3	4.8	4	4.8	4.4
height [cm]	0	1.05	0	22.3	28.3	28.3	8.9	11.3	9.7	3.8	4.5	4.3

Soil parameters vs. site age

There are no high correlations found of soil parameters to site age (Table 5. 3).

Table 5. 3: Spearman rank correlation coefficients of parameters used in linear regression. Correlations >= 0.5 are marked in bold letters. Abbreviations used: horiz. dens. = vegetation cover in top view, vertical dens. = density of vegetation in lateral view, height = weighted vegetation height, site age = time since initiation, kf = water permeability in saturated soil, pH=pH-value (measured in a $CaCl_2$ solution), PAW = plant available water, P = phosphorus, K = potassium.

	horiz.dens	vertical dens.	height	site age	kf	pH	PAW	P	K
horiz.dens	1								
vertical dens.	0.83	1							
height	0.56	0.77	1						
site age	0.55	0.62	0.35	1					
kf	-0.36	-0.38	-0.29	-0.19	1				
pH	-0.01	0.02	0.16	-0.29	-0.28	1			
PAW	0.23	0.27	0.06	0.21	-0.02	-0.45	1		
P	0.38	0.36	0.35	0.01	-0.48	0.54	-0.03	1	
K	0.24	0.27	0.29	-0.03	-0.57	0.64	-0.19	0.73	1

Linear regression of abiotic factors as dependent and site age as independent variable shows varying responses (Figure 5. 1).

Plant availabe water (PAW) and pH show significant but very weak responses to site age, the first increasing and the latter declining over time (Figure 5. 1a and b). Since we assume soil genesis to be a major factor for the high variance in values, we separately modeled on the one hand all Berlin sites plus those Bremen sites containing brick rubble, and on the other hand, the newly filled up sandy sites in Bremen. Recently created sites in Bremen have different starting conditions than those containing brick rubble. The significance as well as the goodness-of-fit of the ‘brick rubble models’ is strikingly higher than that of the ‘no brick model’ of the Bremen sites (Figure 5. 1c and d). In addition, the r^2 of the separated ‘brick rubble models’ is also higher than that of the general models (upper part of Figure 5. 1). This fact reflects the very low r^2 values of the general models being mainly contingent on the very heterogeneous data of the newly heaped up, sandy ‘no brick’ sites of Bremen.

The nutrient parameters P ($p>0.05$, $r^2=0.001$) and K ($p>0.05$, $r^2=0.010$) do not show any response to site age.

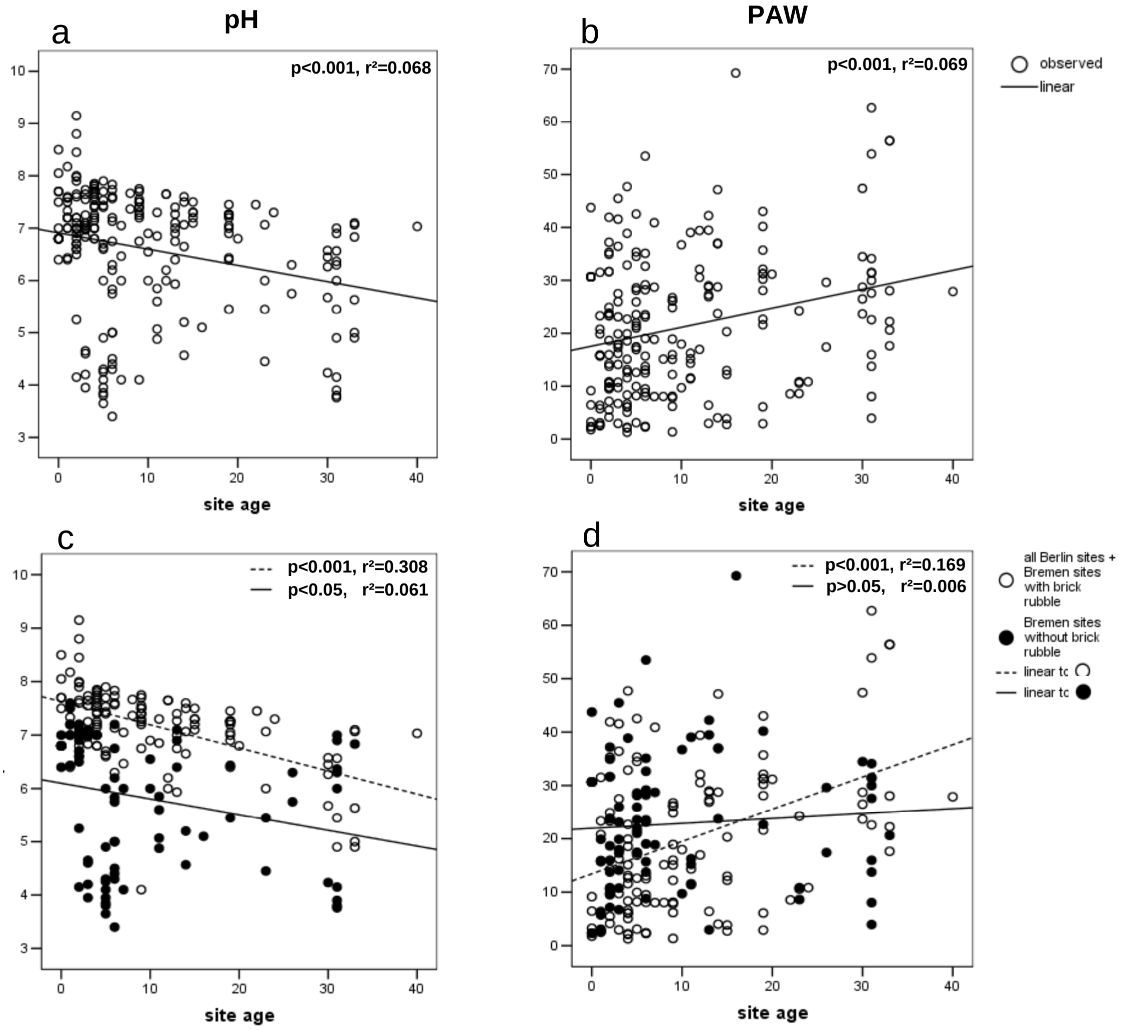

Figure 5. 1: Scatterplots and curve fits of linear regressions of abiotic parameters vs. site age. Figure 5. 1a and b show models of all data points, Figure 5. 1c and d show separated models of all Berlin sites plus Bremen sites containing brick rubble and of Bremen sites without soil containing brick rubble. Abbreviations: see Table 5. 3.

Vegetation structure vs. site age

The vegetation structure parameters horizontal and vertical density are highly correlated to site age (Table 5. 3). Vegetation height in turn does not have a high correlation to time since initiation of vegetation development (Table 5. 3).

According to the single linear regressions, all parameters of vegetation structure respond significantly to site age (Figure 5. 1). Height as well as density parameters increase with increasing site age. However, as it was already the case concerning the abiotic parameters and their relationship to site age, values of vegetation structure are rather widespread around the fitted curve, a fact which is indicated by the low values for the goodness-of-fit (r^2). The linear model for vegetation height especially has a low r^2 value while the two density parameters show slightly higher values for r^2.

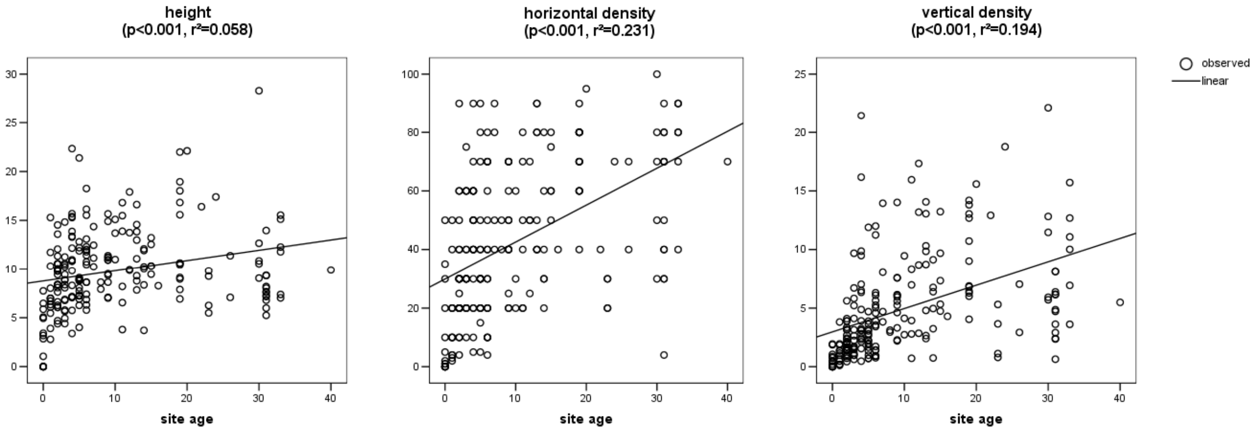

Figure 5. 2: Scatterplots and curve fits of linear regressions of vegetation height, horizontal density and vertical density vs. site age.

Factors influencing vegetation structure

According to the multiple linear regression model, the factors influencing vegetation structure are site age, water permeability of saturated soil (kf), soil phosphorus content, and, in cases of vegetation densities, plant available water (PAW) (Table 5. 4).

Table 5. 4: Results of multiple linear regression of vegetation structure parameters depending on abiotic parameters and site age. Abbreviations: rank=inclusion rank (step at which a parameter is included into the model), B*=standardized regression coefficient. For all other abbreviations see Table 5. 3.

	height $r^2=0.221$		vertical density $r^2=0.380$		horizontal density $r^2=0.423$	
Parameter	rank	B*	rank	B*	rank	B*
site age	2	0.225	1	0.383	1	0.425
kf	3	-0.187	3	-0.209	3	-0.225
PAW			4	0.144	4	0.130
P	1	0.291	2	0.272	2	0.270
pH	not included into the models					
K						

Vegetation vertical and horizontal density as well as height depend positively on site age and soil phosphorus content (P) and respond in a negative manner to increasing water permeability in saturated soil (kf) (Table 5. 4 and Figure 5. 3). In addition, for both vegetation vertical and horizontal density, plant available water (PAW) is a positive influencing factor (Figure 5. 1b). The multiple regression model of vegetation height explains about 20% of the observed variance while the models for both density parameters explain about 40%. In summary, all vegetation structure parameters increase with increasing site age and phosphorus content, vertical and horizontal density generally showing a higher response (Table 5. 4) and thus a stronger increase in the curves' slope (Figure 5. 3) compared to height.

According to the multiple linear regression, soil pH and soil potassium content do not play a role for the vegetation structure of the studied brownfield sites.

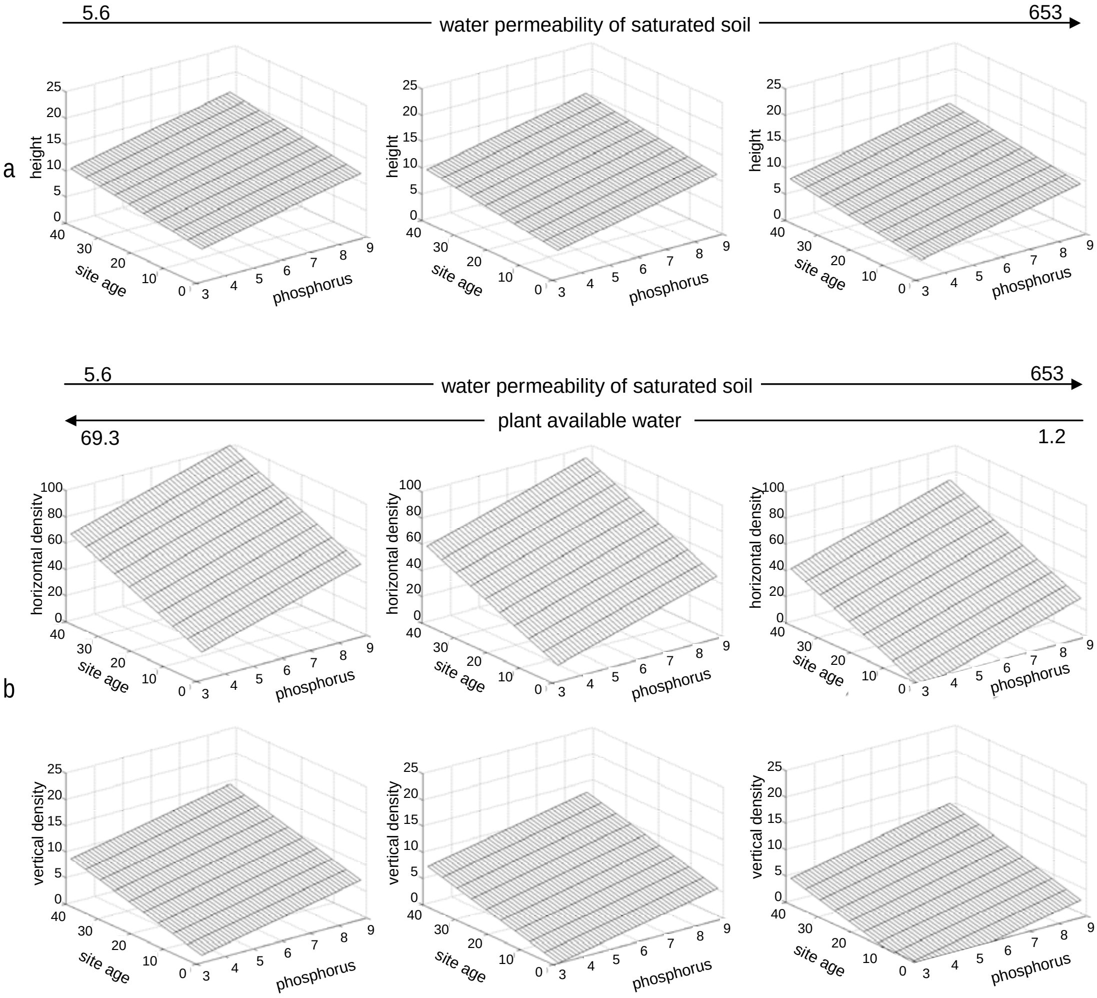

Figure 5. 3: Response curves of multiple linear models of weighted vegetation height [cm] (Figure 5. 3a) depending on site age [y], phosphorus [kg*ha^{-1}, ln-transformed] (within the graphs) and water permeability of saturated soils (kf) [cm*d^{-1}] as parameter for the sequence and of horizontal and vertical vegetation density [%] (Figure 5. 3b) depending on site age [y], phosphorus [kg*ha^{-1}, ln-transformed] (within the graphs) and water permeability of saturated soils (kf) [cm*d^{-1}] and plant available water (PAW) [mm] as parameters for the sequence.

Exceptions of the general coherences: Very low values in vegetation structure at older sites

Scatterplots of vegetation structure vs. site age (Figure 5. 2) show sites of strikingly low vegetation height and especially of very low vegetation densities at older sites. These exceptions of a general increase in height and density with increasing site ages mainly exist on the Bremen sites. As soil phosphorus content (along with site age) is the main explaining variable of vegetation structure, we expect very low values for vegetation structures to be contingent on very low phosphorus contents of sites. But what can be the reason for the existence of sites having very low nutrient contents as well as for those having a medium to high load of soil phosphorus content at the same high site age when the general parameters (e.g. climatic and disturbance /

nutrient deposition effects) are comparable? As mentioned before, sites in Bremen are in general dividable into the history of their soil genesis and thus by the presence or the absence of brick rubble in the soil at the initiation point of vegetation development. A separated modeling of sites containing brick rubble and those which do not shows that sites without rubble generally contain lower soil phosphorus loads and that it is these sites where, according to the linear model, e.g. very low vertical vegetation densities occur at high site ages (Figure 5. 4).

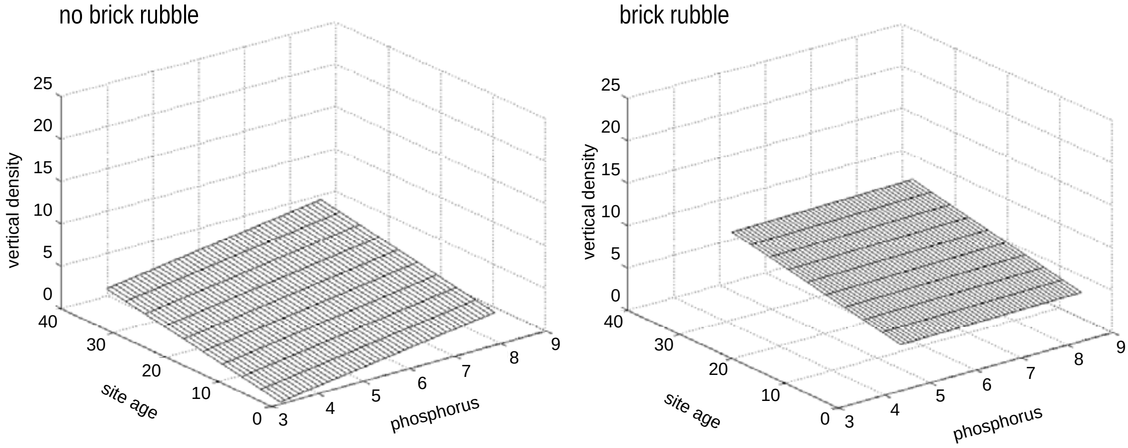

Figure 5. 4: Response curves of vertical vegetation density [%] of sites in Bremen depending on site age [y] and phosphorus [kg*ha^{-1}, ln-transformed]. The left graph shows dependencies on sites with brick rubble content within soil, the right graph illustrates response of vertical density in cases of soil without brick rubble content.

Discussion

Soil parameters of urban brownfields over time

In general, the variance of soil parameter values of the investigated brownfields at different site ages is strikingly high. Temporal trends are rarely visible and models are of low quality if the data of all investigated sites are included into the modeling. Only if we divide the investigation sites by their soil history, which means in this case by the presence or absence of brick rubble in the respective soil, do more significant trends with better fitted models become visible.

On sites containing brick rubble, soil pH shows a significant decline during the temporal development of the investigated brownfields. This result is consistent not only with several studies dealing with other ecosystems (De Deyn *et al.* 2004, Richter *et al.* 1994; but see Gough *et al.* 2000) but also with investigations concerning unused sandy environments (Sykora *et al.* 2004). Moreover, supporting our results, Bornkamm & Hennig 1982 found a temporal decline of pH in urban brownfields' soils of Berlin. The apparent acidification may be due to protons disposed by plant roots absorbing nutrients or because of an accumulation of biomass and an increasing organic layer of soils during the temporal development of the sites' vegetation layer, which was already mentioned for dune slack ecosystems by Sykora *et al.* (2004) (see also Berendse *et al.* 1998). Soil moisture on sites containing brick rubble increases over time, an effect which we assume to be mostly due to an increasing soil humus content. Other reasons can be an increasing above-ground biomass and organic layer and perhaps also an elevated soil density of disturbed sites caused by moving vehicles, trampling, or a general soil settlement of newly filled up areas (Effland & Pouyat 1997, Littlemore & Barker 2001, DeBusk *et al.* 2005). However, not all considered soil parameters of urban brownfields and even of the soils containing brick rubble change significantly over time. In contrast to soil pH and moisture, the amount of available macronutrients P and K do not show a significant response to site age. These results are contrary to the findings of other authors. For instance, in general, site age was stated to have a high influence on soil nutrients (Knops & Tilman 2000). Several studies found a significant decline in soil P contents over time (Bautista-Cruz & del Castillo 2005, Aerts & Chapin 2000, De Deyn *et al.* 2004; but see Wang 2002). Possible explanations for the stable soil nutrient contents in urban brownfields may be an ongoing fertilization due to the deposition of railroad dust, to animal excretions (e.g. dogs and rabbits) or to the existence of weathering brick rubble in the soil acting as a source of nutrients. In summary, a significant change of soil conditions could only be found on sites having been in use before abandonment, whereas starting conditions on sites emerging in the open countryside are too various for general trends of soil development to be visible.

As shown for the presence or absence of brick rubble in the soil, a reason for the strikingly high variance of soil parameters at different site ages may be that soil conditions at the initiation of site development are highly site specific, depending on the site history (Pickett *et al.* 2001). In addition, the fact that vegetation structure influences soil parameters directly (Isermann 2005, Fiala *et al.* 2001), and vice versa, can lead to different pathways of soil conditions' development and thus to a high heterogeneity within site ages. Obviously, for investigations in an urban context, the site and soil history is an important factor that should be included into the stratification matrix used to generate chronosequences. In this regard, brick rubble content may be just one of a few parameters capable of expressing site history. For example, dividing sites by the general age of the investigated industrial area showed results very similar to those gained by taking brick rubble content to split up the data set (data not shown).

Vegetation structure of urban brownfields over time

Changes in vegetation structure are stated to be the most conspicuous and visible indications of a successional sere (Bautista-Cruz & del Castillo 2005). But is there a general and significant temporal trend of increasing vegetation height and density within the herb layer of urban brownfields? The results of our study show a general increase of vegetation height and density during the temporal development of urban brownfields, a fact that supports results of other vegetation structure studies (e.g. Otto *et al.* 2006). However, the range of vegetation structure is very wide for all kinds of site ages.

Both horizontal and vertical vegetation density show a positive response to site age. Again, ranges of density values are remarkably wide in terms of all site ages, especially in the case of horizontal density. There are different possible explanations for this result: Strikingly high densities in the case of very young sites may be due to the fact that the respective sites underlie a secondary succession defined by an organic soil and plant propagules or diaspores being present from the start (Chapin *et al.* 2002). A low density on older sites may be contingent on disturbances causing a high amount of bare ground or on the lack of a limiting resource like the macronutrient phosphorus (e.g. Chadwick *et al.* 1999, Bungard *et al.* 2002) not allowing the development of a dense vegetation (Gilbert 1989). In the case of vegetation height, there is a significant relationship to site age, too, but it is not as strong as in case of vegetation density. Reasons for this may (again) be different site and diaspore conditions at the initiation point of vegetation development or disturbances as well as the lack of a limiting resource (Chadwick *et al.* 1999) inhibiting a higher canopy height of vegetation.

Another general reason for the varying canopy height and density along the whole range of site ages may be that, besides stochastical processes (Tilman 1990, Müller & Rosenthal 1998), the incidence of species growing to different heights and densities and thus the course of vegetation development are to a very high degree ruled by the individual site conditions influencing the course of succession and therefore species turnover. Thus, as mentioned before in the case of soil development, site history (Pickett *et al.* 2001) as well as landscape context of sites (Niemelä 1999, Prach *et al.* 2001b) should be included into the stratification matrix while generating chronosequences for vegetation structure studies.

What are the main driving factors for urban brownfields' vegetation structure?

According to our results, site age and thus time for settlement and growth of species is the main driving factor of urban brownfields' vegetation structure and especially of vegetation density. These findings are in agreement with Cook *et al.* (2005), who stated that time since initiation seems to be a primary determinant of variation in plant community composition. In an early study on ruderal succession of urban brownfields, Bornkamm (1986) found that along with time, soil is also a major factor for vegetation structure of urban brownfields. Nutrients have a key role in succession (Wang 2002), particularly of sandy environments (Hrsak 2004). Consistent with this, our results show that besides time since initiation, nutrient conditions, i.e. soil phosphorus content and water permeability of soil as a measure for nutrient leaching, are also relevant parameters for brownfields' vegetation structure. The exclusion of the macronutrient potassium within our models may be due to its high correlation with phosphorus and is thus not to be seen as having a minor relevance of this nutrient for vegetation structure. For vegetation density of urban brownfields, plant available water is another influencing factor. These findings are in agreement with Blatt *et al.* (2005) and Sykora *et al.* (2004), the latter referring to moisture being crucial for above-ground biomass of dune slack vegetation stands. Thus, as seen in other habitats, besides time for access and growing up, nutrient supply and water as basic needs for the development of biomass are crucial parameters for vegetation height and density of urban brownfields.

Contrary to findings of Gough *et al.* (2000) who studied the Alaskan arctic tundra, pH is not a major influencing factor of vegetation structure. A reason for this may be that under the nutrient poor conditions of the arctic environment, pH plays a major role due to its influence on rock weathering and nutrient availability. By contrast, in urban brownfields which are often nutrient rich, the role of pH is rather subordinate for nutrient supply and vegetation growth.

However, models including site age, nutrients and water conditions do not explain more than half of the variance of the observed vegetation height and density. Obviously, there must be other factors influencing vegetation structure of urban brownfields that were not included into the present model. In this regard, the implementation of the landscape context of sites (Niemelä 1999, Prach *et al.* 2001b) and metapopulation aspects (Niemelä 1999, Wood & Pullin 2002) can be relevant.

Can site age be the only determinant of a biodiversity sustaining site management?

The highest biodiversity of ecosystems can be found at mid-stages of the successional sere (Wang 2002). The biodiversity of the observed brownfields (measured by the mere plant species' number of a site) reflects this result: The highest number of species was found at mid-stages of vegetation height and density (data not shown). Emphasizing the relevance of vegetation structure for urban brownfields' species diversity, the occurrence of insect species on urban brownfield sites highly depends on vegetation structure (Strauss & Biedermann in prep.-b).

Our results show a clear dependency of vegetation structure on site age. So can a management of brownfield sites, in order to sustain biodiversity, be determined by the mere age of the sites? Although there is a significant response of vegetation structure to site age, our findings show wide ranges of vegetation structure present at every site age. Due to these wide ranges, it may prove to be difficult to determine the successional stage of the respective site and thus the state of biodiversity from site age. A strikingly high temporal and spatial heterogeneity and a small scale variance of site conditions are the main characters of urban brownfields (Rebele 1994, Kühn *et al.* 2004). Due to this fact, there are often no clear series of site development (Bornkamm 1986). Our models show that site age is not the only factor affecting vegetation height and density of urban brownfields. As could be shown in the case of the presence or absence of brick rubble in soils, site specific influences such as soil conditions at the initiation of vegetation development impact the vegetation structure of brownfields greatly. In addition to soil conditions, soil seed bank, landscape context, and other influences obviously induce enough heterogeneity to prevent any unified theory (Blatt *et al.* 2005).

In order to conserve urban brownfields' high biodiversity, the site management cannot only be based on site age. Site age can provide hints for management practices, but before these commence, the development of vegetation structure should be ascertained. In cases of persistent 'extreme values' in vegetation structure conditions (e.g. very open sites at higher ages), site management should pay attention to the fact that these sites may bear extreme site conditions that are benign for the existence of rare species. These sites increase habitat variability within a region promising a higher regional biodiversity and should thus not be treated (e.g. by fertilizing) to artificially increase vegetation structure in order to achieve a higher site specific biodiversity.

Box 1

Do field measurements of soil water tension reflect values of plant available field capacity derived from the ‘Bodenkundliche Kartieranleitung’?

Box 1

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Background and aim

Soil water is a relevant for ecosystem functioning as it influences microorganisms and soil fauna, water and gas balance of soils, nutrient flow and plant growth (Schachtschabel *et al.* 1992, Hu & Schmidhalter 2005). In addition, soil moisture influences succession (Bornkamm & Hennig 1982, Blatt *et al.* 2005) and the vegetation structure of urban brownfields (see Chapter 5).

To make allowance for the relevance of soil moisture, I implemented the parameter plant available field capacity (PAFC) into my analyses of urban brownfields' plant - environment relationships (Chapter 3 and 4) and the temporal development of soil conditions (Chapter 5). PAFC is contingent on soil texture and apparent density of the respective soil, which I measured in the field. Its values can be derived from standardized tables in dependendy on these two parameters in the so called 'Bodenkundliche Kartieranleitung" (Arbeitsgruppe Boden 1996). This manual of soil mapping is published by the German Federal Institute for Geosciences and Natural Resources (BGR), which is the central geoscientific authority providing advice to the German Federal Government in all geo-relevant questions. The manual is the main national basis for soil description and is valid and commonly used throughout Germany. It provides advice on soil mapping as well as standardized tables to further analyze and interpret several soil parameters. However, its constricted national validity and the fact that the standardized tables have a more or less 'estimative' character evokes difficulties in publishing the results compared to those derived from measurements whose techniques are commonly applied in the international ecological community.

To verify if the soil moisture parameter PAFC derived from the 'Bodenkundliche Kartieranleitung' (Arbeitsgruppe-Boden 1996) is a valid estimate of the real soil moisture and thus can be used in studies published outside the national application area of the manual, I compared the values of PAFC to field measurements of soil water tension (pF). PAFC is directly related to pF and is defined as the soil water content between pF 4.2 (permanent wilting point) and 2.5 (field capacity) (see Figure B1. 1). Assuming a direct coherence between PAFC and pF values, the derived PAFC values should have a negative correlation to the measured pF values (high PAFC at low pF and vice versa).

In addition to examining the relationship of pF and derived PAFC, I discuss the applied method, since the instruments are newly applied within our working group and my comments may give hints to improve further measurements.

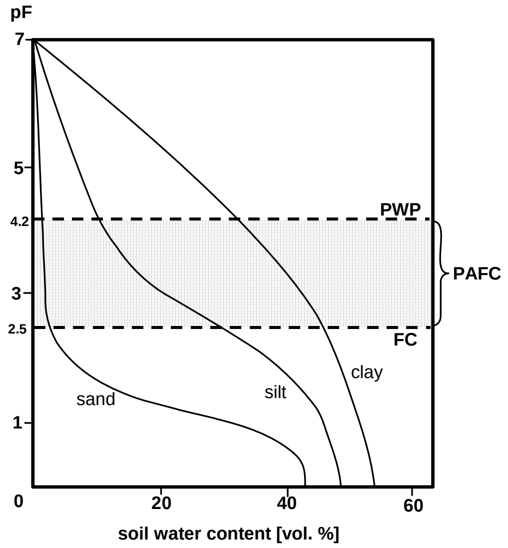

Figure B1. 1: Relationship between soil water content and soil water tension (pF) of sandy, silty and clayey soils. The dotted area indicates the range of pF values with plant available field capacity (PAFC). Abbreviations: pF: soil water tension, PWP: permanent wilting point, FC: field capacity, PAFC: plant available field capacity. From Schachtschabel *et al.* 1992, modified.

Methods

Study area and field measurements

The study was conducted on urban brownfield sites of different age and moisture status in the city of Bremen, Northwestern Germany. During the study period, all sites were continously abandoned. Predominant in the whole study area are sandy soils, in old industrial areas often with a high amount of building rubble.

The measurements were carried out by sensors to register the exact matrix potential, so called ‘pF-meters’ (http://www.geo-precision.com/Produkte/pF-Meter/pf-meter.html). These pF-meters measure the matrix potential within a range of pF 0 to 7. A digital data logger is directly connected to every pF-meter. Power supply is provided by a 12V battery. The instrument is shown in Figure B1. 2A.

The sampling included 24 out of 133 random plots of a previous study. The plots of this previous study were stratified along a gradient of site age (time since initiation of succession), site size, and moisture status (see Chapter 3). The 24 chosen plots covered the whole range of PAFC values measured in the former study.

On the 24 plots, I inserted a total of 28 pF-meters into a depth of 15 cm below ground (Figure B1. 2B). On 20 of the chosen plots I buried one pF-meter each, while on 4 plots, I installed two pF-meters in a distance of 1 m to each other for control measurements. All pF-meters stayed in the soil from the 16th of April 2004 to the 4th of November 2004. Measurements were taken automatically every six hours a day (3 am, 9 am, 3 pm, 9 pm). To minimize the effect of soil temperature on the results, I later decided to include solely the 9 am measurements into my analysis. Unfortunately, the correctness of the measurement turned out to be highly voltage-sensitive. Since the voltage of several batteries became low after a short time period and measurement of the attached pF-meters stopped or became incorrect, I only included data up to the middle of June 2004 into my analysis. In addition, I excluded data of the first two weeks of the measurement period to avoid measurements in disturbed soil condition after burying the instruments. In conclusion, I included all 9 am data from the 1st of May to the 15th of June 2004 into the analysis.

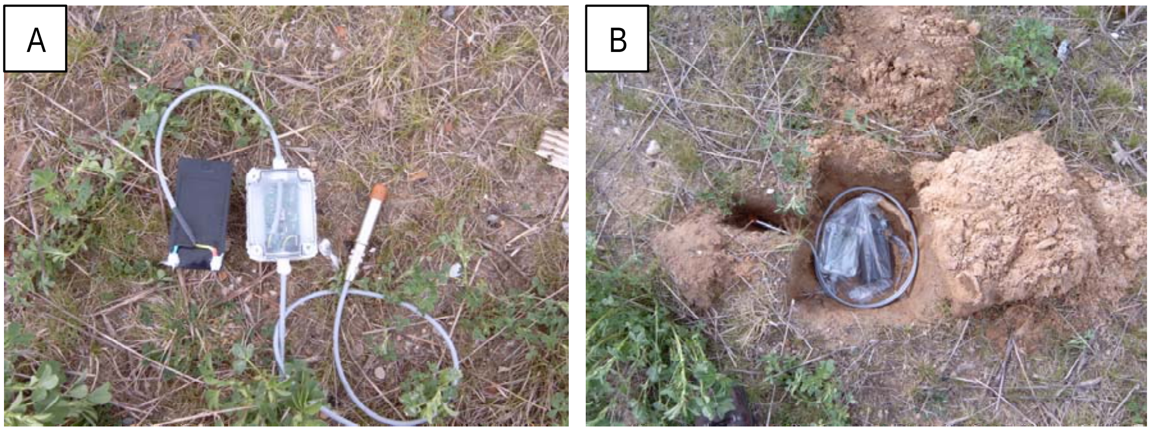

Figure B1. 2: Figure B1. 2A shows the pF-meter (battery, data logger and sensor) before burying. Figure B1. 2B shows the pF-meter before being covered with soil. At every plot, the data logger was placed in a depth of 15 cm.

Analysis of the data

To compare those instruments which were deployed in direct vicinity to each other and to explore the pF response to precipitation and thus get an idea of the correct functioning of the instruments, I plotted the respective pF gradients into one diagram along with data of daily precipitation of the concerning area and the regarded period (Deutscher Wetterdienst 2005).

To analyze the relationship between the means of measured pF-values and the corresponding PAFC values, I used the correlation coefficient according to Pearson, a scatterplot and a linear curve fit. Since the control measurements showed only a medium comparability to each other and thus the correctness of the pF-values measured seemed to be questionable, I additionally checked the mean of pF-values on every individual plot concerning its accordance with the plot's vegetation, using the indicator values of Ellenberg *et al.* (1992). Only those pF-data which showed a medium to high accordance to the vegetation were included into the statistical analysis (n=17). All statistical analysis was done using SPSS 13.0.1 (SPSS Inc. 2004).

Results and discussion

Quality of pF-meter measurements and methodological remarks

The paired pF-values measured in direct vicinity show a general comparability (Figure B1. 3A, B and D). However, the gradients of the pF-meter I and II plotted in Figure B1. 3C have different directions within the last two weeks of measurement. In addition, even if the tendency of the pF gradient is comparable in general, the respective pF-values mainly differ from each other up to a range of 1 unit (Figure B1. 3C). I reason that there is a medium comparability of measured pF-data between the different instruments and thus that measured data has to be regarded carefully before being included into further analyses.

Regarding the accordance of measured pF-data to the precipitation events, slight increases of the inverted pF gradients are visible at most precipitation events >4 mm/day (Figure B1. 3). This result agrees with those of the pF gradients derived from the 22 other pF-meters (data not shown). The generally weak reactions may be explained by the fact that the mainly sandy soils get drained very quickly after a precipitation event. Thus, due to the long measuring interval, the expected strong decrease in soil pF after an event could not be detected. However, in my view, the correct functioning of the used instruments in measuring an increasing and decreasing soil water tension is confirmed by these results.

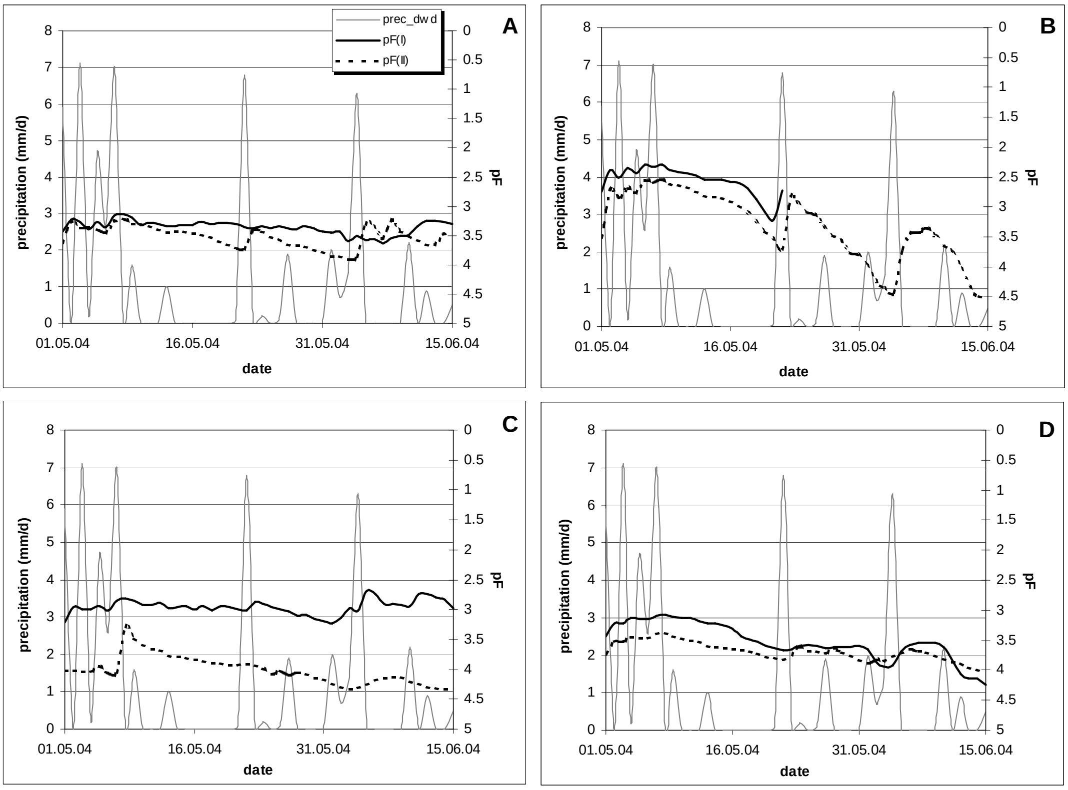

Figure B1. 3: Gradients of pF-measures on four plots where two pF-meters were deployed in direct vicinity and gradients of daily precipitation [mm] (Deutscher-Wetterdienst 2005). Abbreviations: prec_dwd: daily precipitation according to Deutscher-Wetterdienst 2005, pF(I): pF-meter no. 1 at the respective plot, , pF(II): pF-meter no. 2 at the respective plot, installed in a distance of one meter to pF-meter no. 1.

General methodological remarks are as follows:

Only 50 % of all instruments measured correctly for at least half of the measuring period (data not shown). Only 2 out of 28 pF-meters maintained a correct functioning until November. Since the deterioration of measurement quality was always accompanied by a decrease in battery voltage, I regard this as the reason for the incorrect measurements. For further use of the instruments in field I recommend to check battery voltage at regular intervals. This can easily be done in field by transferring data and thus information about the charging status of the battery from the logger with the aid of an infrared interface and a pentop. To avoid repeated disturbance of soil in order to maintain correct measurements, the logger should best be installed above ground and not, as in my case, be buried into the soil. However, a difficulty in letting the logger above ground lies in the resulting susceptibility to sabotage, which must be individually considered before every case of application.

I got the impression that the act of digging the soil to install the sensor, the logger and the battery (Figure B1. 2B) may have disturbed the soil conditions considerably and thus influenced the measured pF-values directly. Perhaps, digging a hole for the logger and battery and drilling a sensor-fitting hole into the side wall in the desired depth could avoid greater soil disturbance and thus improve data quality, even if this technique may on the other hand have a negative influence on the soil conditions around the hole due to compression.

Relationship between pF-values and plant available field capacity (PAFC)

There is a high negative correlation (–0.784 with $p<0.01$) between the mean pF-values and the PAFC of the investigated plots. This confirms my initial assumption. The relationship is shown in the scatterplot (Figure B1. 4). The linear curve fit is highly significant and explains more than 60 % of the data’s variation.

These results indicate that the PAFC values derived from the manual ‘Bodenkundliche Kartieranleitung’ (Arbeitsgruppe Boden 1996) seem to be valid estimates of the real soil moisture, measured in field by means of soil water tension (pF).

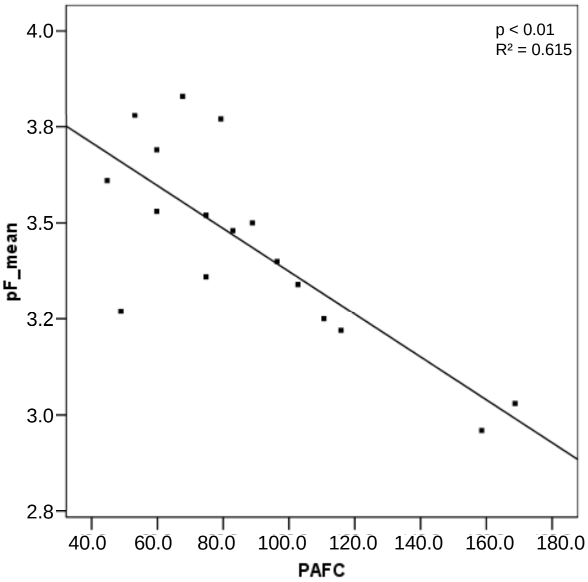

Figure B1. 4: Scatterplot and linear curve fit of mean pF values vs. PAFC values (n=17). Abbreviations: pF_mean: mean pF value, PAFC: plant availabe field capacity [mm].

Conclusions

The results of my study indicate, in the broader sense, that PAFC values derived from the 'Bodenkundliche Kartieranleitung' (Arbeitsgruppe Boden 1996) may be valid estimates of the real soil moisture and thus can be published outside their national application area. Nonetheless, this general result may be subject to restrictions regarding the other study outcomes. The pF-meter measurements turned out to be slightly inconsistent between individual instruments and only 60 % of the data seemed to fit real field conditions concerning the present vegetation. Thus, the general reliability of measurements provided by the pF-meters is only medium. I finally included only a low number of data points into the statistical analysis, which constricts the results' transferability to other study areas and thus their generality (Vaughan & Ormerod 2005). A study with larger data sets could be promising to improve the generalizability of the mentioned results.

Box 2

The potential of the South African wool alien *Senecio inaequidens* DC. to occurr on brownfield sites of Berlin – a model transfer from Bremen to Berlin

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Background and aim

Invasion of alien species can be derogatory to ecosystems (McNeely 2004) as well as to economics (Pimentel *et al.* 2000). Invaders may alter abiotic ecosystem functions (Ehrenfeld 2004) and besides that, they may directly outcompete and displace native species (e.g. Vitousek 1990, Gordon 1998), thereby causing an impact on biodiversity (Chapin *et al.* 2000, Mack *et al.* 2000). In general, especially cities are subject to the invasion of alien species (McKinney 2002, Kühn *et al.* 2004).

The invasive plant *Senecio inaequidens* DC. (Asteraceae) is a native South African perennial and was first described by Harvey in 1865 (Michez 1995 in: Lopez-Garcia & Maillet 2005). *Senecio inaequidens* was brought to Europe via sheep's wool from 1889 onwards. The first occurrences in Europe were recorded in the vicinity of German wool-processing factories near Hanover in 1889 and in Bremen in 1896 (Ernst 1998). Since 1950, *S. inaequidens* expanded rapidly throughout Western, Central and Southern Europe, also to environments outside industrial areas, its rapid dispersal being facilitated by modern transportation, especially along railways (Ernst 1998). *Senecio inaequidens* is nowadays stated as an important invasive species in Europe (Lopez-Garcia & Maillet 2005, Garcia-Serrano *et al.* 2005). In Germany, *S. inaequidens* is spread mainly over the (north)western part of the country while the East and the South of Germany, up to now, are not affected by an area-wide invasion of this plant (Figure B2. 1).

Senecio inaequidens is characterized by several traits that facilitate its invasiveness (Sans *et al.* 2004). The species has a high self-fertility and a long flowering period from May to the end of December (Ernst 1998). Its achenes display different types of dormancy along with the ability to germinate rapidly and under a wide range of temperatures (Lopez-Garcia & Maillet 2005). A low dormancy of the early summer seeds allows the establisment of a second generation in the same year whose seeds have a high dormancy and frost resistance and germinate early in the following spring (Ernst 1998). The terminal velocity of *S. inaequidens* seeds is very low and its seed numbers are in general medium to high (own measurements), resulting in a high ability to disperse in space. In addition, *S. inaequidens* is characterized by a high resistance to herbivory due to its leaf contents of toxic pyrrolizidine alkaloids (Ernst 1998, Scherber *et al.* 2003). Its low to medium specific leaf area (own measurements) indicates a robust but photosynthetically effective leaf architecture. *Senecio inaequidens* exhibits rapid growth under a wide range of environmental conditions (Garcia-Serrano *et al.* 2005, Lopez-Garcia & Maillet 2005).

In contrast to Bremen, where *S. inaequidens* was present on almost 60 % of all study sites, in Berlin, it was found on only 3 out of 85 sites. The aim of my study was to predict the potential occurrence of *S. inaequidens* for several brownfield sites of Berlin and thus to make an assumption about a potential future distribution of this plant within the German capital. To predict the occurrence of *S. inaequidens* in Berlin, I transferred a habitat distribution model of *S. inaequidens* derived from Bremen data to the environmental conditions of Berlin.

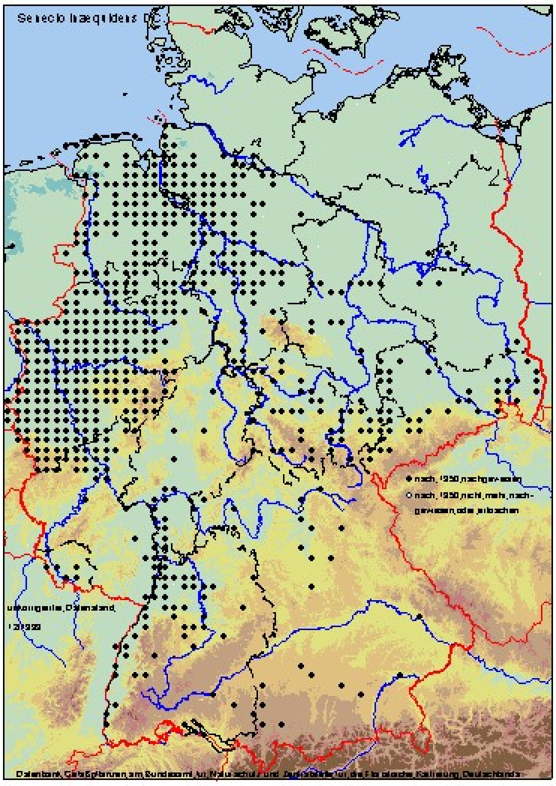

Figure B2. 1: Distribution of *Senecio inaequidens* throughout Germany in 1999 (image source: www.floraweb.de).

Methods

The study was conducted on urban brownfield sites in the city of Bremen, north-western Germany, and Berlin, east Germany. Sites of different age, size and moisture status in varied types of industrial areas, i.e. previously developed land as well as abandoned railroads, and newly created commercial sites were explored. During the study period, all sites were continously abandoned and site use was limited to leisure, mostly walking dogs, and occasional storage of material or equipment. Berlin (mean temperature 9.7° C, mean annual precipitation 560 mm) has a more continental climate than Bremen, whose climate is rather maritime (mean temperature 8.8 °C, mean annual precipitation 694 mm). Predominant are sandy soils, often containing a high portion of building rubble.

Presence/absence of *S. inaequidens* was recorded on 133 plots in Bremen within an area of 4m x 4m each. Statistical analysis was conducted using stepwise logistic regression. The explanatory variables included into the regression analysis were pH-value of soil, site age [y], degree of current disturbance (for measurement of this parameter see Chapter 2), site size [ha], ratio of moss dominance per plot [proportion], general age of surveyed city quarter [categorical], available water per year (PAW) [mm], nutrient conditions (generated by principal component analysis of soil potassium and phosphorus content and effective cation exchange capacity), and soil atmosphere (generated by principal component analysis of soil water permeability and soil air porosity). The resulting model of *S. inaequidens* derived from the Bremen data was applied to the environmental conditions of 85 Berlin sites. Thus, I got predicted probabilities for the occurrence of *S. inaequidens* for every individual site in Berlin. The statistical procedure was implemented in a SAS-macro using the function PROC LOGISTIC (SAS-Institute 1989) (for further description of the method see Chapter 3).

Results

The Senecio inaequidens *model*

The logistic regression model derived by the data of Bremen ($R^2_N = 0.27$, AUC = 0.747) showed a response of *S. inaequidens* to the parameters site age and plant available water (PAW) (Figure B2. 2). *Senecio inaequidens* has the highest probability to occurr at low to medium site ages combined with a low to medium PAW. However, according to the model, the plant generally is able to occur over the whole range of site ages, a medium to high PAW limiting plant’s occurrence especially at the older stages (Figure B2. 2).

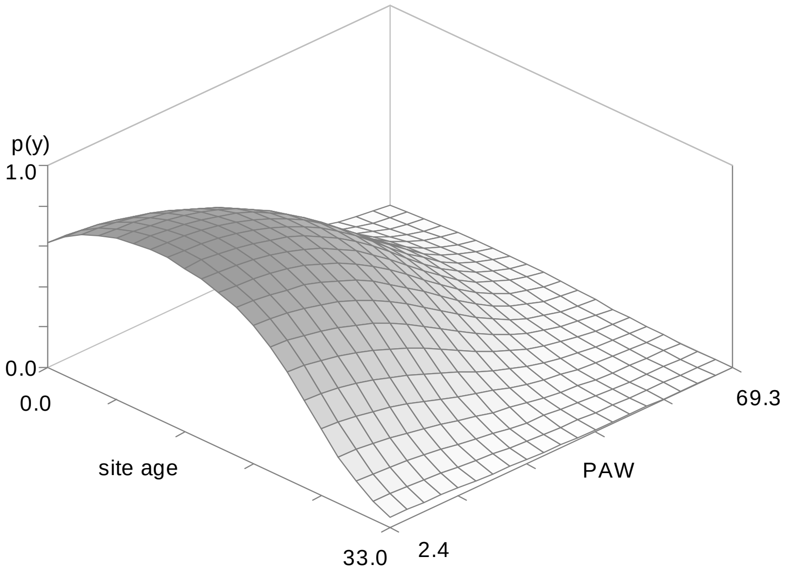

Figure B2. 2: Response curve of *Senecio inaequidens* to site age [y] and plant available water (PAW) [mm]. The y-axis shows the occurrence probability of the species (p) against the two parameters.

PAW and site age broadly have comparable values for Bremen and Berlin (Table B2. 1). Limitations to the model applicability exist only in cases of very dry or very old Berlin sites.

Table B2. 1: Statistical values for plant available water (PAW) and site age in Bremen (n=133) and Berlin (n=85). Abbreviations: min. = minimum, max. = maximum, std.dev. = standard deviation, PAW = plant available water [mm].

	min.		max.		mean		std.dev.	
	Bremen	Berlin	Bremen	Berlin	Bremen	Berlin	Bremen	Berlin
PAW [mm]	2.4	1.2	69.3	47.4	24.8	15.6	13.5	11.1
site age [y]	0	0	33	40	10.1	10.0	10.6	8.3

Transfer of the model

The modeled occurrence probability of *S. inaequidens* on Berlin sites ranges from 0.002 to 0.82 (data not shown). On 43 % of the study sites, the occurrence probability of *S. inaequidens* exceeds 0.75 (Figure B2. 3). On almost 50 % of the sites, the occurrence probability lies between 0.5 and 0.75, while on 7 % it is lower than 0.5.

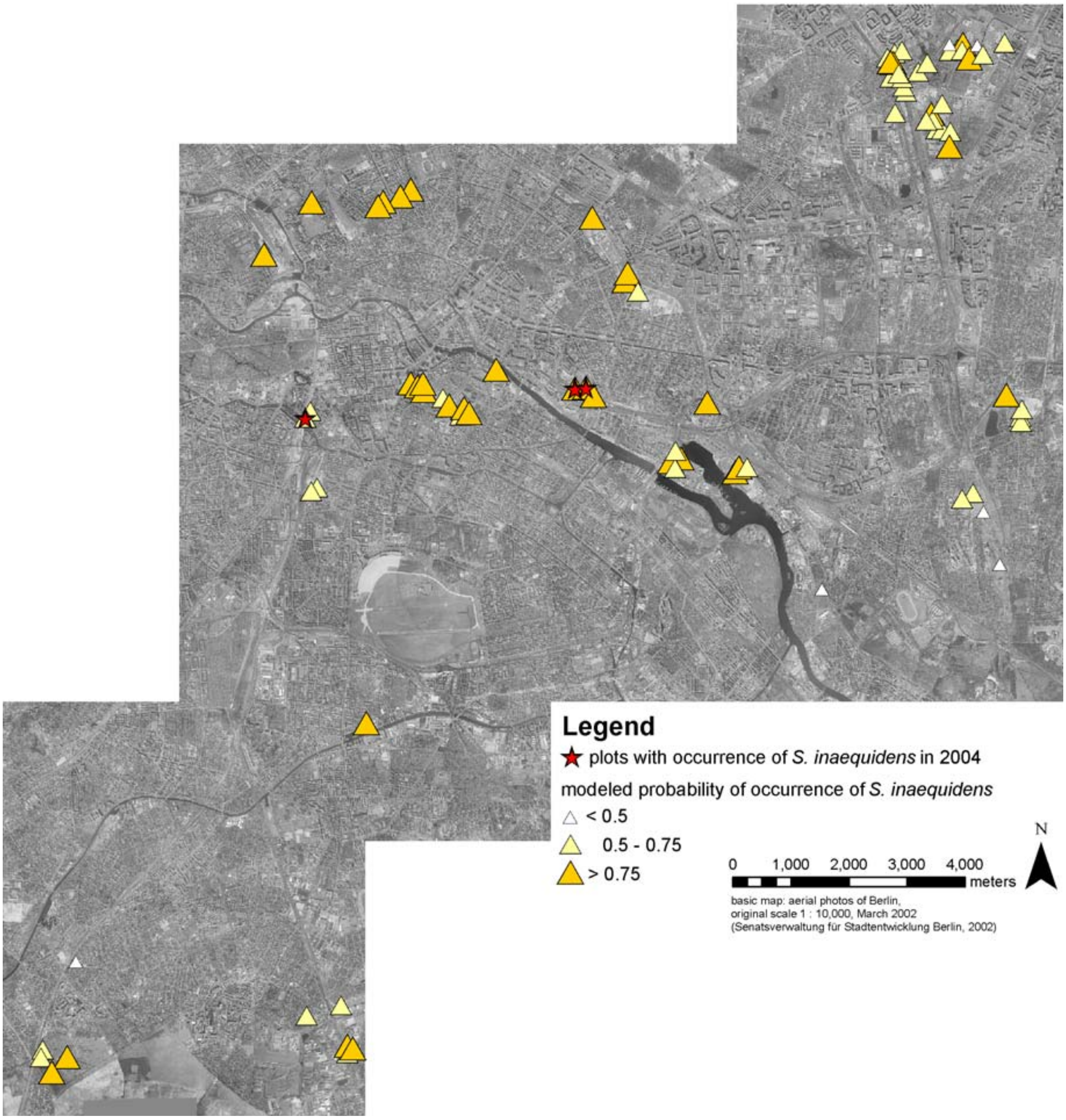

Figure B2. 3: Map of the Berlin study sites and the corresponding occurrence probability of *Senecio inaequidens*.

Discussion

Senecio inaequidens is known for its ability to occur under a wide range of conditions (Ernst 1998, Lopez-Garcia & Maillet 2005). This is confirmed by my results: modeled with Bremen data, *S. inaequidens* solely shows a response to site age and plant available water (PAW), obviously being mainly independent from other environmental conditions such as nutrient status or pH value. My results are in agreement with those of Ernst 1998, who found *S. inaequidens* being typically sensitive to competition for light and water. This explains the tendency of *S. inaequidens* to have a lower occurrence probability at older site ages, since older sites, due to a higher vegetation density (see Chapter 5), generally provide a lower proportion of bare ground for settlement and a lower light availability. Above all, by several authors, these mentioned parameters determining the occurrence of *S. inaequidens* have been stated as being generally relevant for the distribution of invaders (e.g. Thompson *et al.* 2001, Gibson *et al.* 2005).

According to the model transfer and the resulting occurrence probabilities, *S. inaequidens* is able to occur on most of the studied brownfield sites of Berlin. A closer look on Figure 2. 3 shows that the highest occurrence probabilities exist on plots in the city center and along the former Berlin Wall in the north-western part of the city, while in younger industrial areas (mostly located in the north-east), the probability values are lower.

The today's presences of *S. inaequidens* in Berlin were found on abandoned railway yards, all being located in direct vicinity to tracks which are still in use. Since *S. inaequidens* is distributed typically by human traffic and especially along rail- and motorways (Ernst 1998), I assume its future distribution to follow the existing tracks of the Berlin railway system. Assuming further that on intensely used railways situated more into the city center, herbicides may inhibit a wider distribution, *S. inaequidens* may mostly distribute further to the south-eastern as well as to the south-western periphery of the city.

Chapter 6

Main results and overall discussion

Chapter 6

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Brownfields provide fundamental features for the urban environment, such as positive climate function, social value by providing natural wildspace in the urban context and moreover space for withdrawal of plant and animal species (Sukopp & Wittig 1993, Dettmar 1995, London-Wildlife-Trust 2002). In our modern static and well-tended cultural landscape they represent the only space where natural processes may run without direct human influence (Kaule 1991). Due to their complex spatio-temporal pattern of different abiotic conditions and successional stages, urban brownfields provide a relatively high diversity of species (e.g. Rebele 1992, Niemelä 1999, Kühn *et al.* 2004), yet, urban brownfields often contribute strongly to the biodiversity of a city. However, the characteristics of urban biodiversity are not easily tackled by the usual ways of nature conservation which normally comprise a protection of areas by exclusion of human influence ('protection by excluding utilization'). My findings showed that the highest biodiversity of urban brownfields is provided at mid-stages of the successional sere (cf. Wang 2002). Thus, contrary to many other habitats, urban brownfields must be temporarily disturbed in order to sustain their high biodiversity, which claims for conservation under the premise of 'protection by including utilization'. It is crucial to provide an empirical and scientifical basis for such a conservation strategy. The aim of this thesis was thus to detect relevant strategies for species survival in this changing environment and to find general rules for the development and maintenance of urban brownfields.

It was hypothesized that plant traits show a functional response to environmental conditions of urban brownfields and, furthermore, that those traits would be most relevant that are associated with the spatio-temporal dynamics of these habitats. In this context, it was assumed that there is a set of functional traits representing plant functional groups (PFGs) along the environmental gradient of the investigated brownfield sites. To be applicable in the practical context, the detected rules must be ascertained concerning their generality. It was assumed that habitat models of PFGs show similarities across regions and can be successfully transferred to other cities. A general knowledge about the temporal development of soils and vegetation structure of urban brownfields as well as about their relationships provides a further basis for a sustainable site management. In this context, it was hypothesized that soil parameters change over time and that vegetation structure is contingent on these changes as well as on time for settlement and growth. To verify the mentioned hypotheses, I recorded presence/absence data of vascular plant species, abiotic parameters and traits of selected plant species on urban brownfield sites of Bremen and Berlin, Germany. Using stepwise logistic regression, I identified responsive species, i.e. species with a significant response to the environment. By iterative clustering, including a set of candidate traits that represent the whole plant life cycle, I derived plant functional groups comprising the responsive species that were represented by a set of functional traits. This is an approach which helps to generalize ecological rules to a higher level of organisation. The habitat modeling of the derived PFGs quantified their relationships with the environment. The generality of the models was tested by the transfer of city specific PFG – habitat models to other cities.

General information about the temporal development of brownfield sites in terms of soil factors and vegetation structure as well as about their relationships to each other was assessed by single and multiple linear regression.

Plant functional groups as representatives for species survival strategies

The procedure of grouping plants according to their traits showed that dispersal in space and in time as well as vegetative persistence on sites are most crucial factors for plant survival in urban brownfields (Chapter 3). Measured by means of the R^2_N-values of the clusters, the models of those PFGs drew nearest to actual conditions, that were clustered by a combination of leaf area ratio (LAR), terminal velocity (TV), and seed longevity index (SLI). Altogether, the statistical clustering procedure of the mentioned traits yielded 8 PFGs containing 37 out of 39 responsive species. The initial hypothesis that plant traits show a functionality to the changing conditions of urban brownfields was corroborated by the study results. LAR is a trait that describes aspects of vegetative persistence by embodying the leaf area of a plant in proportion to its aboveground biomass and features low values at slow growth and at high proportions of supporting tissue. I found that LAR decreased with increasing resource supply by water and nutrients, which was consistent with findings of Anten & Hirose (1999) and Westoby *et al.* (2002). Furthermore, SLI, an index which measures the ability of a seed to persist in a germinable state, was found to be related to site age and the degree of current disturbance. According to my results, a high SLI seems to be favorable for plants to survive in a disturbed and patchy environment (Cook *et al.* 2005, Piessens *et al.* 2005). Comparable to SLI, TV shows a relationship to site age; low TV values, which correspond with a high ability to disperse in space, were found to be associated to rather young successional stages of urban brownfields. This is a result that highlights the relevance of the ability to disperse in space as a requirement for a rapid colonization of newly emerged, possibly isolated sites (Cook *et al.* 2005). A high ability to disperse in space thus ensures species survival in the highly dynamic mosaic of urban brownfields. The results show, that, on the one hand, resources (local, niche-based processes) are driving factors of PFG occurrence. On the other hand, dispersal limitation (expressed by terminal velocity) plays an important role for the distribution of PFGs. Thus, in addition to resources, successional stage and disturbance are relevant, too. Apparently, in urban brownfields, the niche-based approach, which assumes local processes to be the overriding factor determining local species composition, and the dispersal-based approach reinforce and complement each other (Ozinga *et al.* 2005).

Overall, our results show that dispersal in space (terminal velocity) and in time (seed longevity index) as well as vegetative persistence on sites (leaf area ratio) are the most crucial traits for plant survival in urban brownfields. This is consistent with the initial hypothesis, that those traits are most crucial for species survival in the urban brownfield environment, which are associated with the spatio-temporal dynamics. These results correspond to the findings of many authors (e.g. Westoby 1998, Lavorel & Garnier 2002) who stated persistence and dispersal as crucial plant strategies. Reproductive effort and plant life span, however, seem to play a minor role in habitats that are ruled by high spatio-temporal dynamics. Both traits rather concern the survival of individual plants within a certain site. This concept obviously does not fit the dynamics of the urban brownfield sites. In urban brownfields, the most relevant trait is not persistence of a plant itself on a certain site but persistence of a population or functional group by dispersal and resprouting within a fast changing mosaic of convenient sites. Statements of Weiher *et al.* (1999), who pointed at PLS as being the most basic trait for species persistence, are obviously more suitable for less dynamic environments.

The high relevance of dispersal in space is emphasized by another, rather method-related result of the present study. Almost half of all significant PFG models did not match acceptable performance criteria in terms of Nagelkerke values (R^2_N>0.2, Backhaus *et al.* 2003). In general, Nagelkerke values are low if species within the respective PFGs are predicted but actually not present and vice versa. These two kinds of errors can be due to different reasons (Guisan & Thuiller 2005, Vaughan & Ormerod 2005). Omission errors, i.e. failing to predict a species where it does occur, can be due to a low model quality, which often arises by not including all relevant environmental factors into the model. In our case, these variables could have been more concise data on soil water or wind as a driving factor of dispersal. Commission errors, i.e. predicting a species where it does not occurr, can stem again from a low model quality as well as from the fact that observations of absences in the field are never as certain as observations of presences. Moreover, an ecologically driven reason for prediction without presence may be that species of a PFG could not reach the habitat because of high distance and/or low ability of dispersal (high terminal velocity) (Cook *et al.* 2005, Guisan & Thuiller 2005). Thus, they do not occur even if environmental conditions of a site are benign. The latter assumption, in my view, may be very relevant in case of the patchy, highly dynamic environment of urban brownfields and thus was further inquired. To find out more about a possible relationship of commission errors and the spatial dispersal ability of the respective species, I related the ratio of predicted but not present occurrences (i) to the mean terminal velocity of PFG species and (ii) to the proportion of brownfield area around corresponding sites. While the proportion of surrounding brownfields as sources for species immigration does not vary evidently between cases, terminal velocity seems to have an influence: the higher the rate of predicted but not observed presences, the higher tends to be the mean TV value of the respective PFG. These results confirm studies of Ozinga *et al.* (2005), who found that dispersal filters may play a major role for the predictability of species and that a large percentage of unexplained variance in predictive models was not only due to noise but to dispersal limitation. Urban brownfields are basically characterized by stochastic processes and a state of disequilibrium. Static regression models are based on the principle of equilibrium, which is why their use in modeling species in disequilibrium is problematic (Gibson *et al.* 2004). Thus, the greater the influence of dispersal in time and space in brownfield habitats, the more difficult becomes the predictability of plant - or trait - environment relationships by static regression models.

The similarity and the spatial transferability of urban brownfield PFG models

The dynamical, patchy nature of the habitats and the ability of species to reach sites with benign conditions are highly relevant factors for the similarity of urban brownfield PFG models, too (Chapter 4). Modeled city-specifically with the environmental data of Stuttgart, Berlin and Bremen, almost all PFGs respond to site age, which points at the relevance of the ability of a species to reach new sites with suitable environmental conditions. Other response variables are pH and plant available water (PAW), which points at the relevance of the vegetative persistence ability of species if once reestablished by dint of dispersal (Westoby 1998 and Weiher *et al.* 1999). The principle of a reciprocal reinforcement of the niche-based approach and the dispersal-based approach (Ozinga *et al.* 2005), mentioned above for PFGs in Bremen, obviously holds true for urban brownfield habitats in general, irrespective of their location and the corresponding regional differences, e.g. in climate and soil conditions. Overall, the initial hypothesis that urban brownfield PFG models show similarities across regions is maintained by the results of the present study. The differences in PFG reactions, which are apparent in the cases of PAW and pH, are mostly due to different environmental ranges within the three cities, and, considering this, the apparent general similarities outweigh the differences. The fact that the reaction of PFGs to environmental factors can be either landscape specific or general, i.e. valid for different landscapes (Kleyer 2002), also becomes obvious by regarding the parameters having the most different values between Stuttgart, Berlin and Bremen. There is a different response to the degree of current disturbance, which is higher in Stuttgart than in the other two cities, as well as to nutrients, which are different due to the more clayey soil conditions of Stuttgart compared to the rather sandy soils of Berlin and Bremen. In summary, factors of which ranges are generally comparable across regions induce general responses (Dyer *et al.* 2001, De Bello *et al.* 2005), which again induce similarity of the PFG models. However, in cases of parameters of which ranges are specific for each region and which in addition have a high influence on PFG occurrence, landscape specific reactions of PFGs lower or even impede the similarity of the models (De Bello *et al.* 2005).

There is an apparent influence of the existence of general and landscape specific responses on the transferability of the PFG models. As a consequence of PFGs showing similar responses when ranges of parameter values are more or less similar across the regions, I found that models were better transferable when (i) using similar parameters for model building and (ii) covering similar parameter ranges across cities. In general, the transferability of the urban brownfield PFG models measured by the squared Pearson correlation coefficient r^2 was medium to low. Compared to the r^2 values of those cases where the models were applied to the respective city itself, the ‘foreign' models mainly did not explain half of the variance explained by the original model. Concentrating on those models, which could be transferred reasonably well to one or both of the other cities, Bremen and Berlin models were more transferable to each other than those of Stuttgart to the other cities and vice versa. This is yet another hint at the relevance of regional peculiarities to the generalizability of models. In general, a low transferability can be due to different environmental as well as to methodological effects (Pearce & Ferrier 2001, Vaughan & Ormerod 2005). To draw nearer to the reasons of the low model transferability such as the use of different survey techniques, seasonal variation in survey period or a different regional prevalence of PFG species in the different cities (Pearce & Ferrier 2000), I first used calibration plos. Calibration plots can give useful hints on the reasons for a low transferability of models by categorizing the errors into the systematic sources bias and spread (Vaughan & Ormerod 2005). Bias describes a consistent over- or underestimate of the probability of occurrence, typically appearing when the prevalence of a species differs from the training data (Pearce & Ferrier 2000). Spread describes predicted values that are too extreme, i.e. too low at unoccupied and too high at occupied sites, typically deriving from model overfitting due to e.g. a high number of variables included in the regression or to fewer available training data (Vaughan & Ormerod 2005). Transferring Bremen and Berlin models to Stuttgart, there was spread as well as positive and negative bias, thus, unfortunately, a direct interpretation of the plots in order to detect the error source was impossible. Problems with transferability often cannot be diagnosed directly by the type of calibration error (Vaughan & Ormerod 2005), which became obvious in the present study. However, calibration error derived from different prevalences and seasonal variation as a methodological reason for low transferability can be excluded in the case of the present study. In fact, I suppose environmental conditions to have the greatest inhibiting effect on model transferability in the present study. There are environmental differences between Stuttgart and Bremen/Berlin regarding several parameters. Stuttgart soils, for example, are far more clayey than the sandy soils of Bremen and Berlin and in most cases have a higher soil pH. The climate of Stuttgart is influenced by its location in a river valley and thus cannot be directly compared to the rather open situation in Bremen and Berlin. This leads to special habitat conditions in Stuttgart, which are amplified by the more small-scale and dense site mosaic, which in turn induces a higher degree of current disturbance. The situation of Berlin and especially of the Bremen sites differs from Stuttgart by climate as well as by habitat size, fragmentation and degree of current disturbance, since, in Bremen and Berlin, there is a high proportion of urban brownfields which are situated in newly established areas in the open countryside. Thus, obviously, the presence of novel factors influencing distribution and the ecotypic variation between the regions lead to a failure of model transport (Oostermeijer & van Swaay 1998, Vaughan & Ormerod 2005). In summary, site history is the main factor which remained unincluded by the models and thus may lead to their low transferability. Different site histories of urban brownfields may lead to different parent material of soil as well as to differences in space related parameters such as the location of brownfields (city center or open countryside) or the complexity of the site mosaic within the respective industrial area and thus the spatial context of habitats. By inclusion of site history parameters, the high relevance of dispersal in space and time and of vegetative persistence in case of urban habitats (Ozinga *et al.* 2005, Cook *et al.* 2005, see also Chapter 3) is covered by the models which increases the model transferability.

The high relevance of dispersal in space and time is also reflected by the environmental demands and the trait features of those PFGs that can be transferred reasonably well to other cities. In general, the PFGs clustering annual plants have a higher transferability, notably from Bremen to Berlin and vice versa than those containing biennial or perennial species. In addition, a high ability to disperse in space and time as well as frugal nutrient and moisture demands favor a high transferability. On the other hand, PFGs containing species with special environmental demands or those characterized by a high potential for vegetative on-site persistence and a high ability of clonal dispersal are in general of a lower transferability. General and flexible responses of species obviously induce generality to the models of urban brownfields' PFGs, i.e. in terms of the CSR-scheme of Grime (1979), ruderals favor whereas competitors and stress-tolerators inhibit model transferablity.

In conclusion, urban brownfield PFG models are transferable in space, however, the success in transfer is highly contingent on the type and the degree of species, and thus PFG, responses to environmental factors (landscape specific vs. general response; Kleyer 2002). The content of ruderals with a high ability to disperse in space and time as well as of generalists enhances the transferability of urban brownfield PFG models. General responses which provide repeatability can be estimated under similar environmental conditions along with a lack of regional peculiarities (De Bello *et al*. 2005).

The development of urban brownfields over time

In addition to the spatial dynamics mentioned above, urban brownfields show a temporal variability in terms of environmental conditions as well as of vegetation of sites (e.g. Rebele 1992). To detect general rules in the temporal development of urban brownfields could give additional useful hints for a management of sites in order to know not just how sites should be arranged into the regional mosaic but also to know in which stage of succession sites should be disturbed to sustain a high regional biodiversity.

The single linear regression models of the pooled Bremen and Berlin soil data just partly confirmed my initial hypothesis that soil conditions of urban brownfields change over time. There were soil parameters such as plant availabe water (PAW) and soil pH showing significant but very small responses to site age, the first increasing and the latter declining over time. However, the nutrient parameters soil phosphorus and potassium content did not show any response to site age and in general, there were no high correlations found between soil parameters and site age. However, as mentioned above concerning the transferability of PFG models, site history played a major role to detect significant general rules also in this case. Since I assumed soil genesis to be a major factor for the found high variance in pH and PAW values, I separately modeled on the one hand all Berlin sites plus those Bremen sites containing brick rubble, and on the other hand, the newly filled up sandy sites in Bremen. I assumed that recently created sites in Bremen have different starting conditions than those containing brick rubble. The results showed that the significance as well as the goodness-of-fit of the 'brick rubble models' is strikingly higher than that of the 'no brick model' of the Bremen sites. In addition, the separation of the sites according to their history increased model quality compared to the general model for all sites.

The decline of soil pH over time is consistent not only with several studies dealing with other ecosystems (De Deyn *et al.* 2004, Richter *et al.* 1994; but see Gough *et al.* 2000) but also with investigations concerning unused sandy environments (Sykora *et al.* 2004). The apparent acidification may be due to protons disposed by plant roots absorbing nutrients or because of an accumulation of biomass and an increasing organic layer of soils during the temporal development of the vegetation layer, which was already demonstrated for dune slack ecosystems by Sykora *et al.* (2004) (see also Berendse *et al.* 1998). The increase of soil moisture found on sites containing brick rubble is assumed to be mainly due to an increasing soil humus content. Other reasons can be an increasing above-ground biomass and organic layer and perhaps also an elevated soil density of disturbed sites caused by moving vehicles, trampling, or a general soil settlement of newly filled up areas (Effland & Pouyat 1997, Littlemore & Barker 2001, DeBusk *et al.* 2005). The non-response of nutrient parameters, however, is contrary to the findings of other authors (e.g. Knops & Tilman 2000). Several studies found a significant decline in soil P contents over time (Bautista-Cruz & del Castillo 2005, Aerts & Chapin 2000, De Deyn *et al.* 2004; but see Wang 2002). Possible explanations for the stable soil nutrient contents in urban brownfields may be an ongoing fertilization due to the deposition of railroad dust, to animal excretions (e.g. dogs and rabbits) or to the existence of weathering brick rubble in the soil acting as a source of nutrients.

Looking at the temporal development of the vegetation structure, the results of our study show a general increase of vegetation height and density during the temporal development of urban brownfields, a fact that supports results of other vegetation structure studies (e.g. Otto *et al.* 2006). However, the range of vegetation structure is very wide for all kinds of site ages. Besides stochastic processes (Müller & Rosenthal 1998, Tilman 1990), the varying canopy height and density along the whole range of site ages may again be determined by the individual site conditions influencing the course of succession and therefore species turnover. Obviously, as mentioned before in the case of soil development, site history (Pickett *et al.* 2001) as well as landscape context of sites (Prach *et al.* 2001, Niemelä 1999) should be included into the stratification matrix while generating chronosequences for vegetation structure studies.

The initial hyothesis that the temporal development of the vegetation structure of urban brownfield sites is contingent on environmental conditions but moreover on site age is confirmed by the results of the present study. Using multiple linear regression, site age and thus time for settlement and growth of species turned out to be the main driving factor of urban brownfield vegetation structure and especially of vegetation density. These findings are in agreement with Cook *et al.* (2005), who stated that time since initiation seems to be a primary determinant of variation in plant community composition. In an early study on ruderal succession of urban brownfields, Bornkamm (1986) found that along with time, soil is also a major factor for vegetation structure of urban brownfields. Nutrients have a key role in succession (Wang 2002), particularly in sandy environments (Hrsak 2004). Consistent with this, the results of the present study show that besides time since initiation, nutrient conditions, i.e. soil phosphorus content and water permeability of soil as a measure for nutrient leaching, are also relevant parameters for brownfield vegetation structure. However, contrary to findings of Gough *et al.* (2000) who studied the Alaskan arctic tundra, the expected influence of pH on vegetation structure could not be detected. A reason for this may be that under the nutrient poor conditions of the arctic environment, pH plays a major role due to its influence on rock weathering and nutrient availability. By contrast, in urban brownfields which are often nutrient rich, the role of pH is rather subordinate for nutrient supply and vegetation growth.

Implications of the derived results for nature conservation will be discussed in the last part of the present chapter.

A glance at methods

Deriving PFGs by cluster analysis has become an acknowledged technique in recent scientific studies (Kleyer 2002, Pillar & Sosinski 2003). Instead of including all available plant traits in the process of clustering, I selected a set of uncorrelated candidate traits *a priori*. In my view, the number of included traits is negligible as long as the trait set chosen incorporates all parts of the plant life cycle (McIntyre & Lavorel 2001). With regard to straightforwardness, it is nevertheless desirable to include as few (uncorrelated) traits as possible (McIntyre *et al.* 1999), although a satisfactory classification of PFGs based on one single trait is unlikely (Diaz *et al.* 1999). In my view, composed traits like LAR or RE are a feasible way to combine different aspects of plant traits into one value. However, attention should be paid to their interpretability and to the fact that in some cases surrogation of traits can lead to a loss of information unique to particular traits (Lavorel & Garnier 2002). The question which traits should be included is strongly case and habitat dependent (Wang & Ni 2005). However, again, incorporation of all parts of the plant life cycle is strongly recommended. But even with this preselection of plant traits, the amount of possible trait combinations and especially of PFGs gained by clustering is often very high. Thus, there must be other techniques beyond clustering and preselection of traits to select the aspired PFGs (Semenova & van der Maarel 2000). Instead of selection by mere parsimony (Westoby & Leishman 1997), the present study focused on selection by means of R^2_N-values of clusters formed by a combination of responsive traits. This approach allowed for detecting the trait combination forming PFGs whose models drew nearest to actual conditions and thus turned out to be a feasible way to bridge the gap between parsimony, interpretability and reality-fit.

The modeling of urban brownfield species and PFGs by logistic regression turned out to be a somewhat questionable method since urban brownfields are basically characterized by stochastic processes and at a state of disequilibrium, which does not conform to the principle of equilibrium of static regression models (Gibson *et al.* 2004). Thus, the more influence is gained by dispersal in time and space on the processes of brownfield habitats, the more difficult becomes their prediction by static regression models. This point was reflected by the transferability of the PFG models across cities; the more spatial aspects were neglected by the models, the lower their spatial transferability. The high relevance of dispersal aspects showed that there is a need in urban ecology for a spatio-temporal approach, especially when it comes to predictions (Weiher & Keddy 1999, Diaz *et al.* 1999). A not plot- but space-related study design could help to find out more about dispersal topics as well as about metapopulation and spatial connectivity within urban landscapes (see also Pysek *et al.* 2004). Such an approach would also have been helpful for a more detailed assessment of the spatial dispersion of *Senecio inaequidens* as an invasive species in urban habitats of Berlin (Box 2).

The relevance of spatial aspects for studies of urban habitats is still emphasized by the results concerning the temporal development of environmental conditions and vegetation structure. Models including site age, nutrients and water conditions do not explain more than half of the variance of the observed vegetation height and density. Obviously, there must be other factors influencing vegetation structure of urban brownfields that were not included into the present model. In this regard, the implementation of the landscape context of sites (Niemelä 1999, Prach *et al.* 2001) and metapopulation aspects (Niemelä 1999, Wood & Pullin 2002) can be relevant. In addition, the chronosequences (Pickett 1989, Knops & Tilman 2000) used in our study, based on site age, site size and moisture, did not satisfyingly match the wide variety of possible pathways and thus only show trends of site succession. Obviously, for investigations in an urban context, the site and soil history is an important factor that should be included into the stratification matrix used to generate chronosequences. In this regard, brick rubble content may be just one of a few parameters capable of expressing site history.

Box 1 dealed with the question if the soil moisture parameter PAFC derived from the ‘Bodenkundliche Kartieranleitung’ (Arbeitsgruppe-Boden 1996) is a valid estimate of the real soil moisture and thus can be used in studies outside the national application area of the manual. In my view, PAFC should better be evaluated directly into the laboratory doing desorption experiments by means of soil samples (e.g. method according to German DIN 19683, part 6) instead of measurements of soil water tension (pF), which themselves provide indirect measures of soil moisture. Gathering undisturbed soil samples and processing them will be as laborious as the measurements by pF-meters derived in the present study but implies the advantage of providing direct measures of the parameter concerned.

Final conclusions and implications for conservation and management

As shown in the present study, the niche-based and the dispersal-based approach reinforce each other in case of urban brownfields (Ozinga *et al.* 2005), i.e. the environmental conditions on site but to an even greater extent the spatial conditions of the present site mosaic are crucial factors for the maintenance of the biodiversity of urban brownfields. Hence, conservation and management of urban brownfield sites particularly has to pay regard to the factors ‘spatial layout of the urban brownfield site mosaic within a landscape’ and ‘environmental conditions on site/site history’.

One of the questions to be answered in this context is that of *how* a management should act on site conditions in order to sustain a high regional biodiversity. By measuring species - enviroment relationships quantitatively, habitat models provide a tool to predict the effect of certain management strategies in order to create specific management plans (e.g. Lindenmayer *et al.* 1993, Stephenson *et al.* 2006), or to assess biotopes concerning their habitat suitability for certain species (e.g. Gibson *et al.* 2004). However, to use the predictions made by these models effectively in conservation planning, it is essential to validate the predictive accuracy of the models and thus their general applicability in space and time (Bonn & Schröder 2001, Pearce *et al.* 2001, Bulluck *et al.* 2006). The results of the present study showed that in case of urban brownfields, managers and conservationists should carefully consider habitat types, survey techniques, climate and seasonal variation and especially environmental ranges and site history of the distinct regions (Fleishman *et al.* 2003, Vaughan & Ormerod 2005) when predicting the possible effects of certain management strategies.

Another aspect is that of *when*, i.e. in which stage of brownfield development management should act. The present study confirmed the findings of many studies (e.g. Wang 2002), that the highest biodiversity of ecosystems, in this case of urban brownfields, can be found at mid-stages of the successional sere. But how can these stages be identified in order to be in time for management? Our models showed that site age is not the only factor affecting vegetation height and density of urban brownfields and thus biodiversity. As could be shown in the case of the presence or absence of brick rubble in soils, site specific influences such as soil conditions at the initiation of vegetation development greatly influence the vegetation structure of brownfields. In addition to soil conditions, soil seed bank, landscape context, and other influences obviously induce enough heterogeneity to prevent any unified theory (Blatt *et al.* 2005). Thus, in order to conserve the high biodiversity of urban brownfields, site management cannot only be based on site age. Site age can provide hints for management practices, but before these commence, the development of vegetation structure should be ascertained. In cases of persistent ‘extreme values’ in vegetation structure conditions (e.g. very open sites at higher ages), site management should pay attention to the fact that these sites may bear extreme site conditions that are benign for the existence of rare species. These sites increase habitat variability within a region promising a higher regional biodiversity and should thus not be treated (e.g. by fertilizing) to artificially increase vegetation structure in order to achieve a higher site specific biodiversity.

The biodiversity of urban brownfields cannot be sustained without the inclusion of disturbance events and thus demand for a ‘protection by including utilization’. This utilization can have many faces such as stochastic events of child play or pedestrian traffic, directed utilization by temporal building or *de facto* management acts such as the mechanical removal of upper soil layers. It is however strongly case-dependent which utilization fits the demands of conservation and planning within a city or region.

Summary

Summary

Urban brownfields provide ecological as well as social values within the urban landscape. Due to their spatio-temporal dynamics and their transient character, they comprise a high biodiversity of plant and animal species, yet, urban brownfields often carry a large part of the biodiversity of a city. However, the high biodiversity of urban brownfields is highly contingent on their spatio-temporal dynamics and thus on temporary disturbances. This claims for a conservation management under the premise of 'protection by including utilization', in contrast to the premise of excluding utilization that traditionally characterizes acts of nature conservation. Further scientific research on succession and dynamics of urban brownfields is crucial to form a basis for predictions and thus for decisions on sustainable development of urban brownfields, especially for a reinforced embedding of brownfield qualities in an urban planning context.

The aim of my thesis was to detect relevant strategies for species survival in urban brownfields and to find general rules for the development of this changing environment. Empirical studies were conducted on urban brownfield sites in the cities of Bremen and Berlin, Germany. This two-city approach was carried out to get a broad data basis of sites lying in cities with different environmental conditions and in addition to be able to test the transferability of models from one region to another and thus to assess their general applicability within the context of urban brownfield conservation.

The empirical investigations were conducted on plots randomly distributed on the urban brownfield sites comprising chronosequences that covered different site age, site size and moisture status. Presence/absence data of all vascular plant species were recorded. On every plot within a maximum depth of 80 cm, soil surveys were done and soil samples of every layer were taken for further laboratory analyses. Measurements of several plant traits were carried out on plant species chosen by prevalence.

The first hypothesis of my thesis was that plant traits show a functional response to the changing conditions of urban brownfields, which can be expressed by means of a set of functional traits representing functional groups (PFGs). I assumed further, that those traits which are associated with the spatio-temporal dynamics of the environment are most crucial for species survival in urban brownfields. By clustering and modeling PFGs according to species' traits and environmental conditions, I identified relevant strategies for species survival. The results of the present thesis revealed that dispersal in space and in time as well as vegetative persistence on sites are most crucial factors for plant survival in urban brownfields. Measured by means of the R^2_N-values of the clusters, the models of those PFGs that represent a combination of leaf area ratio (LAR), terminal velocity (TV), and seed longevity index (SLI) drew nearest to actual conditions. The traits showed a response to the environmental conditions; (i) LAR decreased with increasing resource supply by water and nutrients, (ii) SLI was related to site age and the degree of current disturbance and a high SLI seemed to be favorable for plants to survive in a disturbed and patchy environment, (iii) TV values were associated to site age. The results show, that traits associated with the patchy, spatio-dynamic nature and the resource conditions of the sites are most crucial for species survival in urban brownfields. Apparently, in urban brownfields, the niche-based approach, which assumes local processes to be the overriding factor determining local species composition, and the dispersal-based approach reinforce and complement each other. The high relevance of dispersal aspects is still emphasized by two further results: (i) generally low R^2_N values of PFGs models (species predicted but not present because of dispersal limitation) and (ii) the fact that deviance of model predictions are highest at lowest abilities to disperse in space (high TV). The use of static models for predicting urban habitats is challenged by these results. The higher the influence of dispersal, the higher the need for a spatio-temporal approach in urban ecology.

For the application of these findings into nature conservation practice in order to sustain the high biodiversity of urban brownfields, the generality of the derived principles must be assessed by a validation of the models in space and time, i.e. by assessing their transferability. I hypothesized that habitat models of urban brownfield PFGs show similarities across regions and that they are transferrable in space under certain conditions. This hypothesis was tested by applying city-specific habitat models of a common set of PFGs for the cities of Stuttgart, Berlin, and Bremen to the respective other cities, measuring the transferability by means of the squared Pearson correlation coefficient r^2. The results demonstrated (i) that despite many landscape specific responses models of urban brownfield PFGs showed considerable similarity and (ii) that model transferability was highly contingent on the environmental comparability of the regarded cities. Dissimilarity of relevant model parameters lowered the transferability of models. In addition, for urban habitats, the inclusion of site history parameters turned out to be essential to cover the city-specific effects especially on species dispersal, which shaped up as a major trait inducing the transferability of PFG models.

In the third part of the thesis, an assessment of general rules in the temporal development of urban brownfields was conducted. This was done to give additional useful hints for a management of sites in order to know not just *how* sites should be arranged into the regional mosaic but also to know *in which stage* of succession sites should be disturbed to sustain a high regional biodiversity. I initially assumed that soil parameters of urban brownfields change during the development of sites over time. The temporal development of the vegetation structure is contingent on these changes but moreover on site age expressing time for settlement and growth. This was investigated by linking soil parameters and vegetation structure parameters to site age using single and multiple linear regression. My results show that soil parameters of the sites are in general not clearly linked to site age. Dividing the sites by their soil history, I found pH responding negatively and plant available water responding positively to site age on sites that were in human use before abandonment, while on sites newly created by heaping up sandy material very variable conditions inhibited clear trends of temporal development. Nutrient conditions in general showed no temporal trend. Vegetation height and density increased significantly over time, being mostly contingent on site age, soil phosphorus content and water permeability of the soil. In addition, vegetation density depends on plant available water. The present thesis revealed that vegetation structure and thus biodiversity of sites is not only contingent on site age, a fact which has to be taken into account for a management to sustain the biodiversity of urban brownfields.

This thesis highlighted that the environmental conditions on site but to an even greater extent the spatial conditions of the site mosaic are crucial factors for the preservation of biodiversity of urban brownfields. Hence, conservation and management of urban brownfield sites particularly has to pay attention to the spatial layout of the urban brownfield site mosaic within a landscape and to the environmental conditions on site/site history while finding answers to the question, how and when urban brownfield sites should be managed.

Zusammenfassung

Zusammenfassung

Brachflächen sind für die urbane Landschaft sowohl von hohem ökologischen als auch von sozialem Wert. Aufgrund ihrer typischen raum-zeitlichen Dynamik und ihres transitorischen Charakters beinhalten sie eine Vielzahl an unterschiedlichen Lebensräumen und damit eine hohe Vielfalt an Tier- und Pflanzenarten. Städtische Brachflächen tragen damit in höchstem Maße zur Biodiversität von Städten bei. Das typische Artenspektrum ist jedoch sehr abhängig von der Flächendynamik und von einer zeitweisen Störung der Flächen. Im Gegensatz zum eher traditionellen Naturschutzansatz von „Schutz durch Nutzungsausschluss“ muss ein Management dieser Habitate somit eher unter der Prämisse „Schutz trotz Nutzung“ ablaufen. Für die Erhaltung des typischen Artenspektrums städtischer Brachen, insbesondere im Hinblick auf ein verstärktes Einbeziehen von Brachflächen in den urbanen Planungskontext, sind wissenschaftliche Grundlagen bezüglich ihrer Entwicklung und Dynamik von hoher Bedeutung.

Das Ziel dieser Arbeit war es, wesentliche Überlebensstrategien von Pflanzen auf städtischen Brachflächen sowie generelle Zusammenhänge bezüglich der Habitatentwicklung zu ermitteln. Dazu wurden auf zahlreichen Industrie- und Gewerbebrachen in den Städten Bremen und Berlin Untersuchungen durchgeführt. Der Untersuchungsansatz umfasste zwei Städte, um zum einen die Auswertungen auf eine breitere Datenbasis zu stellen, und zum anderen, um die regionale Übertragbarkeit der Modelle im Hinblick auf eine Anwendbarkeit im Flächenmanagement zu ermitteln.

Die empirischen Untersuchungen wurden mittels zufällig verteilter Probepunkte entlang einer Chronosequenz durchgeführt. Dafür erfolgte im Vorfeld eine Stratifizierung der Untersuchungsflächen bezüglich Flächenalter, -größe und Feuchtezustand. Auf jedem Plot wurde die Präsenz bzw. Absenz der Gefäßpflanzen erfasst. Bodenaufnahmen sowie die horizontweise Entnahme von Bodenproben erfolgten auf jedem Plot bis zu einer Maximaltiefe von 80 cm. Des Weiteren wurden an ausgewählten Pflanzenarten Messungen von Pflanzenmerkmalen (Traits) durchgeführt.

Die erste Hypothese meiner Arbeit war, dass die Merkmale von Pflanzen einen Zusammenhang mit den veränderlichen Umweltbedingungen von Brachflächen haben. Dieser Zusammenhang kann mit Hilfe eines Sets funktioneller Merkmale (den sog. funktionellen Pflanzengruppen, PFGs) ausgedrückt werden. Weiterhin wurde angenommen, dass genau solche Merkmale für das Überleben von Pflanzen wichtig sind, die in einem Zusammenhang mit der raum-zeitlichen Dynamik von städtischen Brachflächen stehen. Durch eine Clusterung und Modellierung von PFGs konnten wesentliche Überlebensstrategien von Brachepflanzen ermittelt werden. Anhand der Ergebnisse stellte sich heraus, dass die Ausbreitung in Zeit und Raum wie auch die vegetative Überdauerung von Pflanzen auf der Fläche wesentlich zum Überleben der Pflanzen beitragen. Gemessen wurde dies anhand der Nagelkerke (R^2_N) - Werte der modellierten Cluster. Es zeigte sich, dass diejenigen PFGs die bestehende Situation am besten beschrieben, die aus einer Kombination der Merkmale Blattflächenverhältnis (LAR), Fallgeschwindigkeit der Samen (TV) und Samenüberdauerungsindex (SLI) gebildet wurden. Dabei zeigten die Merkmale folgende Zusammenhänge mit den Umweltbedingungen:

(i) LAR nahm mit zunehmender Verfügbarkeit von Nährstoffen und Wasser ab, (ii) SLI hing zusammen mit den Faktoren Flächenalter und Grad der aktuellen Störung, wobei ein hoher SLI günstig für das Überleben von Pflanzen in gestörten und lückenhaften Habitatmosaiken erschien, (iii) TV zeigte eine Reaktion auf das Flächenalter. Die Ergebnisse bestätigen die Eingangshypothese, dass solche Merkmale von Pflanzen ihr Überleben auf Brachflächen sichern, die eine Anpassung an die raum-zeitliche Dynamik des Lebensraums und den veränderlichen Ressourcenhaushalt bieten. Offensichtlich ergänzen und verstärken sich im Falle städtischer Brachflächen ausbreitungsbasierte und nischenbasierte Effekte gegenseitig. Die hohe Bedeutung von Ausbreitungsmechanismen wurde zusätzlich durch zwei weitere Ergebnisse bekräftigt: (i) das Auftreten von generell niedrigen R^2_N-Werten der PFG-Modelle (durch eine Vorhersage von Arten dort, wo tatsächlich kein Vorkommen vorlag) und (ii) die Tatsache dass die Abweichungen bei den Modellvoraussagen umso höher waren, je geringer die Ausbreitungsfähigkeit der entsprechenden Arten im Raum war. Die Nutzbarkeit statischer Modelle für die Vorhersage von urbanen Habitatveränderungen wird durch diese Ergebnisse in Frage gestellt. Je größer der Einfluss von Ausbreitungsmechanismen, desto größer ist offensichtlich der Bedarf für einen raum-zeitlichen Ansatz im Kontext der Stadtökologie.

Um eine Anwendbarkeit im Zusammenhang mit einem nachhaltigem Flächenmanagement herzustellen, muss die Allgemeingültigkeit der sich ergebenden Zusammenhänge ermittelt werden. Dies geschieht am besten durch eine Validierung der Modelle in räumlicher und zeitlicher Hinsicht, z.B. durch Ermittlung ihrer Übertragbarkeit. Meine Hypothese in diesem Zusammenhang war, dass die Habitatmodelle von PFGs, angewendet auf die einzelnen Regionen, Ähnlichkeiten zeigen und dass sie unter bestimmten Voraussetzungen erfolgreich auf die Bedingungen anderer Städte übertragen werden können, d.h. räumlich übertragbar sind. Hierzu wurden stadtspezifische Habitatmodelle eines gemeinsamen Satzes von PFGs für die Städte Stuttgart, Berlin und Bremen auf die jeweils anderen Städte übertragen. Die Übertragbarkeit wurde dabei mit Hilfe des quadrierten Pearson Korrelationskoeffizienten r^2 gemessen. Die Ergebnisse zeigten, (i) dass die Modelle trotz vieler landschaftsspezifischer Reaktionen durchaus Ähnlichkeiten aufwiesen und (ii) dass die Modellübertragbarkeit sehr stark davon abhängig war, wie vergleichbar die Umweltbedingungen zwischen den Städten waren. Eine Unähnlichkeit der relevanten Modellparameter zwischen den Städten setzte die Übertragbarkeit der Modelle herab. Noch dazu stellte es sich als wesentlich heraus, Parameter der Flächenentstehung und –geschichte in die Modellierung der PFGs einzubeziehen, um die stadtspezifischen Effekte auf die Ausbreitung der Arten zu erfassen.

Die Erfassung genereller Zusammenhänge der zeitlichen Entwicklung von Stadtbrachen kann u.a. zur Ableitung von Hinweisen für ein nachhaltiges Flächenmanagement dienen. In diesem Zusammenhang war nicht nur wichtig, wie die Flächen im Raum angeordnet sein sollten, sondern auch, in welchem Zustand ihrer Entwicklung ein Flächenmanagement einsetzen sollte. Die Eingangshypothese war, dass sich die Bodenbedingungen von Stadtbrachen im Laufe der Flächenentwicklung verändern. Weiterhin wurde angenommen, dass die Entwicklung der Vegetationsstruktur der Flächen abhängig ist von diesen abiotischen Veränderungen, jedoch ebenfalls vom Flächenalter als Ausdruck für die Zeit für Etablierung und Aufwuchs von Arten abhängt. Um dies zu untersuchen, wurden Boden- und Vegetationsstrukturparameter mit dem Alter der Flächen mittels einfacher und multipler linearer Regression in Beziehung gesetzt. Die Ergebnisse zeigten, dass die Bodenbedingungen von Stadtbrachen sich mit zunehmendem Flächenalter nicht eindeutig ändern. Durch eine Aufteilung der Datensatzes nach der Entstehungsgeschichte der Flächen konnte jedoch festgestellt werden, dass sich der Faktor pH auf ehemals genutzten Flächen negativ und der Faktor pflanzenverfügbares Wasser positiv zum Flächenalter verhält. Auf neu aufgeschütteten Flächen verhinderten offensichtlich die zunächst sehr uneinheitlichen Bedingungen der jungen Flächen das Erkennen von klaren zeitlichen Entwicklungstrends der genannten Faktoren. Die Nährstoffparameter Phosphor und Kalium zeigten keine deutliche zeitliche Entwicklung. Die Vegetationshöhe und –dichte zeigten einen signifikanten Anstieg im Laufe der Zeit und waren dabei hauptsächlich abhängig vom Flächenalter, dem Phosphorgehalt des Bodens und von der Wasserdurchlässigkeit im wassergesättigten Boden (im Fall von Höhe und Dichte) sowie zusätzlich vom pflanzenverfügbaren Wasser (im Fall von Dichte). Die vorliegende Arbeit zeigt demnach, dass die Vegetationsstruktur und damit auch die Artenvielfalt einer Fläche nicht alleine vom Flächenalter abhängt, eine Tatsache die im Rahmen von Managementmaßnahmen in Betracht gezogen werden sollte.

Diese Arbeit stellte heraus, dass für den Erhalt der brachflächentypischen hohen Artenvielfalt sowohl der räumliche Aufbau des Flächenmosaiks als auch die Umweltbedingungen auf den Flächen selbst entscheidend sind. Daraus leitet sich ab, dass der Schutz und das Management von städtischen Brachflächen vor allem den Faktoren „räumliche Anordnung der Flächen zueinander“ sowie „Umweltbedingungen/Entstehungsgeschichte der Flächen“ Rechnung tragen muss, wenn es darum geht, wie und wann Maßnahmen auf Brachflächen wirken sollen.

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Appendix

Appendix

Table A - 1: Correlation coefficients (Spearman rho) of Bremen explanatory variables used in Chapter 3. Abbreviations: age_site = site age, size_site = size of site belonging to a plot, age_quarter = general age of surveyed city quarter, moss cover = ratio of moss dominance per plot, PAW = plant available water, disturb_curr = degree of current disturbance, P = phosphorus, K = potassium, ECEC = effective cation exchange capacity, kf = water permeability in saturated soil, AP = air porosity, PAFC = plant available field capacity, $CaCO_3$ = calcium carbonate.

	kf [cm*d^{-1}]	**AP** [mm]	**PAFC** [mm]	**pH**	**age_site** [y]	**size_site** [ha]	**moss cover** [prop]	**age_quarter**	**PAW** [mm]	**ECEC** [cmol$_c$*kg^{-1}]	**P** [kg*ha^{-1}]	**K** [kg*ha^{-1}]	**$CaCO_3$** [kg*ha^{-1}]	**disturb_curr**
kf [cm*d^{-1}]	1													
AP [mm]	0.83	1												
PAFC [mm]	-0.44	-0.13	1											
pH	-0.09	-0.31	-0.23	1										
age_site [y]	-0.22	-0.18	0.08	-0.39	1									
size_site [ha]	0.32	0.36	-0.13	-0.16	-0.20	1								
moss cover [prop]	-0.02	0.00	-0.03	-0.37	0.29	0.11	1							
age_quarter	-0.38	-0.34	-0.02	0.05	0.39	-0.15	0.02	1						
PAW [mm]	-0.32	-0.03	0.78	-0.21	0.20	-0.15	-0.09	0.03	1					
ECEC [cmol$_c$*kg^{-1}]	-0.68	-0.53	0.28	0.06	0.13	-0.23	-0.08	0.30	0.16	1				
P [kg*ha^{-1}]	-0.35	-0.35	0.21	0.46	-0.11	-0.15	-0.31	0.15	0.19	0.43	1			
K [kg*ha^{-1}]	-0.58	-0.59	0.32	0.36	-0.03	-0.33	-0.26	0.15	0.24	0.43	0.59	1		
$CaCO_3$ [kg*ha^{-1}]	-0.22	-0.41	-0.21	0.66	-0.34	-0.19	-0.19	-0.02	-0.20	0.13	0.43	0.41	1	
disturb_curr	0.08	0.02	-0.03	0.13	-0.34	0.03	0.05	0.04	-0.18	-0.05	-0.09	-0.13	0.05	1

Table A - 2: Correlation coefficients (Spearman rho) of Bremen trait data used in Chapter 3. Abbreviations: LAR = leaf area ratio, RE = reproductive effort, TV = terminal velocity, SLI = seed longevity index, PLS = plant life span.

	LAR	**RE**	**TV**	**SLI**	**PLS**
LAR	1				
RE	0.1510989	1			
TV	-0.04324881	0.31858508	1		
SLI	0.12066562	0.24357725	-0.08518534	1	
PLS	-0.2703601	-0.45246794	-0.18397094	-0.31270065	1

Table A - 3: Plant species chosen for statistical analysis of Chapter 3 and their trait attributes. Species marked with a 1 were chosen despite low prevalence because of commonness in the investigation area, *Tragopogon dubius* (marked with a 2) was chosen because of its Red List status (Garve 1993). Abbreviations and units: LAR = leaf area ratio [mm^2/mg], RE = reproductive effort [no unit], TV = terminal velocity [m/sec], SLI = seed longevity index [<0.3 : transient, 0.3-0.55 : short term persistent, >0.55 : long term persistent], PLS = plant life span [1 : annual, 2: biennial, 3: perennial].

species	prevalence in 133 plots	LAR	RE	TV	SLI	PLS
Achillea millefolium	20	3.3	0.0633	1.4	0.1	3
Agrostis stolonifera	13	7.2	0.0232	1.2	0.4	3
Agrostis tenuis	20	4.9	0.0081	1.2	0.7	3
Arabidopsis thaliana	12	12.5	0.3469	1.2	0.8	1
Arenaria serpyllifolia	43	6.2	0.3534	1.8	0.7	2
Arrhenatherum elatius	15	2.6	0.1901	2.7	0.2	3
Artemisia vulgaris	29	6.4	0.2789	1.6	0.8	3
Betula pendula S	15			0.4	0.9	3
Betula pendula T^1	5			0.4	0.9	3
Bromus sterilis	22	3.8	0.4146	2.9	0.0	1
Bromus tectorum^1	6	9.1	0.4831	2.5	0.6	1
Calamagrostis epigejos	32	2.6	0.0121	0.7	0.4	3
Carex arenaria	19	6.9	0.0567	2.9	1.0	3
Carex hirta	31	7.5	0.0463	3.5	0.1	3
Cerastium holosteoides	27	6.5	0.0933	1.8	0.6	3
Cerastium semidecandrum	22	6.7	0.0862	1.3	0.5	1
Chenopodium album	14	3.5	0.0477	3.0	0.9	1
Cirsium arvense	18	2.8	0.0159	0.3	0.3	3
Cirsium vulgare	36	3.7	0.1154	0.6	0.3	2
Conyza canadensis	49	6.8	0.0305	0.2	0.8	1
Corynephorus canescens	19	2.5	0.1835	1.3	1.0	3
Dactylis glomerata	18	6.7	0.0709	2.6	0.2	3
Daucus carota	13	3.3	0.2926	2.6	0.7	2
Deschampsia cespitosa	25	1.9	0.1156	1.5	0.3	3
Elymus repens	28	3.1	0.0281	3.0	0.2	3
Erophila verna	16	21.4	0.3944	1.5	0.6	1
Festuca ovina	20	1.5	0.0873	2.7	0.2	3
Festuca rubra	54	2.0	0.1542	2.8	1.0	3
Holcus lanatus	75	0.5	0.0359	0.9	0.6	3
Hypericum perforatum	34	4.3	0.0673	1.8	0.9	3
Hypochoeris radicata	40	8.2	0.4252	0.4	0.3	3
Lolium perenne	18	3.1	0.1266	3.2	0.2	3
Lotus corniculatus	15	5.8	0.2014	3.6	0.3	3
Matricaria maritima	23	3.6	0.3638	2.3	1.0	2
Medicago lupulina	47	6.7	0.481	3.1	0.6	2
Melilotus officinalis	15	2.1	0.6218	3.8	0.6	2
Oenothera biennis	23	2.9	0.2515	2.7	0.9	2
Phalaris arundinacea	20	1.7	0.0262	2.7	0.2	3
Picris hieracioides	11	8.3	0.1333	0.5	0.8	3
Plantago lanceolata	23	9.7	0.0786	3.4	0.3	3
Plantago major	18	12.0	0.5164	2.7	0.8	3
Poa annua	28	11.3	0.0364	1.9	0.9	1
Poa compressa	24	5.8	0.0389	1.3	0.0	3
Poa palustris	11	5.0	0.0135	1.5	0.3	3
Poa pratensis	23	4.4	0.0388	2.1	0.4	3
Poa trivialis	48	4.2	0.08	1.3	0.8	3
Polygonum persicaria	10	7.3	0.0974	3.5	0.9	1
Rumex acetosella	45	4.2	0.3754	2.9	0.7	3
Saxifraga tridactylites	13	7.7	0.2106	1.2	0.5	1
Senecio inaequidens	76	5.6	0.1084	0.5	0.5	3
Senecio viscosus	10	7.7	0.0962	0.6	1.0	1
Sisymbrium altissimum^1	5	2.4	0.2103	2.3	1.0	1
Solidago gigantea	32	4.6	0.0506	0.6	0.0	3
Tanacetum vulgare	41	4.9	0.0546	2.3	0.1	3
Taraxacum officinale	55	10.4	0.0976	0.6	0.3	3
Tragopogon dubius^2	6	4.9	0.2581	0.6	1.0	2
Trifolium arvense	26	4.8	0.16	1.4	0.6	1
Trifolium campestre^1	8	10.8	0.1632	3.1	0.3	1
Trifolium pratense	22	6.3	0.0228	2.4	0.3	3
Trifolium repens	34	7.8	0.1812	3.7	0.4	3
Tussilago farfara	11	8.5	0.1209	0.2	0.1	3
Veronica arvensis	16	21.5	0.1767	1.8	0.5	1
Vicia angustifolia	26	9.6	0.5713	4.8	1.0	1
Vicia hirsuta	28	11.0	0.2311	4.7	0.5	1
Vicia tetrasperma^1	8	5.3	0.5618	5.1	0.4	1
Vulpia myuros	18	1.5	0.6708	3.1	0.3	1

Table A - 4: Plant functional groups (PFG) from the combination of LAR, TV, and SLI - regression coefficients for site characteristics. Abbreviations:age_site = site age, size_site = size of site belonging to a plot, age_quarter = general age of surveyed city quarter, moss cover = ratio of moss dominance per plot, PAW = plant available water, disturb_curr = degree of current disturbance, atmosphere = soil atmosphere (value generated from principal component analysis), nutrients = nutrient conditions (value generated from principal component analysis)).

	PFG								
Parameter	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	
pH	-	2.298	-	-	0.868	-	-	-	pH
	0.112	-0.279	-0.048	-	-	0.032	0.099	-	pH^2
age_site	-	-	-	0.060	-	-	-0.479	-	age_site
	-	-	-	.	0.001	-0.002	-		age_site^2
size_site	-	-0.379	-0.555	-	-	.	0.122	-	area_site
	-	0.013	0.015	0.002	-	.	.	0.007	area_site^2
moss cover	6.369	.	-	1.861	-	7.417	-	-	moss cover
	-9.634	-3.175	-	-	-	-7.205	-	-	moss cover^2
PAW	-0.110	-	-	-	-	-	-	.	PAW
	0.002	-	-	-	-	-	-	0.003	PAW^2
disturb_curr	-	-	-	82.707	-	-	-	-	disturb_curr
	-	-	-		-	-	-	-	disturb_curr^2
age_quarter	-0.680	-0.297	-	-	-	-	0.970	-	age_quarter
	-	-	-	-	-	0.072	-	-	age_quarter^2
nutrients	-	0.325	-0.357	-	-	-	-	-	nutrients
	-	-	-	-	-	-	0.083	-	nutrients^2
atmosphere	-0.249	-0.267	-1.012	-	-0.362	-	-	-	atmosphere
	-	-	-0.306	-	-0.319	-	-	-	atmosphere^2
Intercept	-4.028	-3.993	0.444	-3.479	-6.819	-2.834	-8.074	-8.148	

Table A - 5: Correlation coefficients (Spearman rho) of the pooled Stuttgart/Berlin/Bremen explanatory variables used in Chapter 4. Abbreviations: disturb_curr = degree of current disturbance, age_site = site age, ECEC = effective cation exchange capacity, P = soil content of phosphorus, K = soil content of potassium, PAW = plant available water.

	study location	**disturb_curr**	**age_site** [y]	**ECEC** [cmol$_c$*kg^{-1}]	**P** [kg*ha^{-1}]	**K** [kg*ha^{-1}]	**pH**	**PAW** [mm]
study location	1							
disturb_curr	-0.25	1.00						
age_site [y]	-0.25	0.19	1.00					
ECEC [cmol$_c$*kg^{-1}]	-0.63	0.22	0.08	1.00				
P [kg*ha^{-1}]	0.10	-0.16	-0.13	-0.23	1.00			
K [kg*ha^{-1}]	-0.37	-0.01	-0.14	0.30	0.22	1.00		
pH	-0.44	0.09	-0.10	0.12	0.26	0.43	1.00	
PAW [mm]	-0.18	0.16	0.10	0.63	-0.11	0.06	-0.18	1.00

Table A - 6: Correlation coefficients (Spearman rho) of Stuttgart/Berlin/Bremen trait data used in Chapter 4. Abbreviations:PLS = plant life span, SLA = specific leaf area, seed number/TV^2 = seed number divided by squared terminal velocity, SLI = seed longevity index.

	PLS	**SLA**	**canopy height**	**seed weight**	**seed number/TV^2**	**SLI**	**clonality**
PLS	1						
SLA	-0.12	1					
canopy height	0.25	-0.06	1				
seed weight	-0.09	0.09	0.30	1			
seed number/TV^2	0.20	-0.16	0.43	-0.33	1		
SLI	-0.30	-0.23	-0.21	-0.25	0.06	1	
clonality	0.69	0.00	0.06	-0.17	-0.05	-0.23	1

Table A - 7: Plant species chosen for statistical analysis of Chapter 4 and their trait attributes. Abbreviations and units: PLS = plant life span [1 : annual, 2: biennial, 3: perennial], seed number/TV²= seed number divided by squared terminal velocity [no unit], SLI = seed longevity index [<0.3 : transient, 0.3-0.55 : short term persistent, >0.55 : long term persistent], clonality = existence and length of clonal growth organs [0.0 : not clonal, 0.5 : <10 cm, 1.0 : >10 cm]).

species	prevalence in 303 plots	PLS	seed number/TV²	SLI	clonality
Achillea millefolium	66	3	446.96	0.11	1.0
Agropyron repens	92	3	277.49	0.42	0.5
Agrostis capillaris	25	3	39.57	0.32	1.0
Arenaria serpyllifolia	101	2	215.53	0.71	0.0
Arrhenatherum elatius	46	3	23.32	0.17	0.5
Artemisia vulgaris	116	3	4856.12	0.76	0.5
Bromus sterilis	91	1	4.83	0.00	0.0
Calystegia sepium	20	3	19.92	0.21	1.0
Cerastium semidecandrum	70	1	25.93	0.57	0.5
Chenopodium album	50	1	56.35	0.71	0.0
Conyza canadensis	111	1	114.65	0.66	0.5
Corynephorus canescens	23	3	42.42	1.00	0.5
Dactylis glomerata	58	3	449.02	0.52	0.5
Daucus carota	102	2	98.81	0.44	0.5
Festuca rubra	84	3	11.10	0.60	0.5
Hypericum perforatum	78	3	473.35	0.90	0.5
Lactuca serriola	56	2	507533.33	0.12	0.0
Linaria vulgaris	32	3	635.92	0.43	0.5
Lolium perenne	51	3	2.95	0.20	0.5
Matricaria maritima	60	2	1629.98	1.00	0.0
Medicago lupulina	136	2	39.36	0.64	0.5
Melilotus officinalis	23	2	19.49	0.57	0.0
Oenothera biennis	61	2	637.42	0.88	0.0
Picris hieracioides	32	3	4743.70	0.75	0.5
Plantago lanceolata	51	3	4.40	0.35	0.5
Plantago major	60	3	325.56	0.79	0.5
Poa angustifolia	33	3	84.23	0.17	0.5
Poa annua	58	1	7.87	0.90	0.5
Poa compressa	111	3	53.42	0.00	0.5
Poa pratensis	55	3	26.85	0.39	1.0
Poa trivialis	86	3	69.66	0.75	1.0
Polygonum aviculare	27	1	3.02	0.80	0.0
Rumex acetosa	15	3	111.65	0.14	0.5
Rumex acetosella	54	3	52.27	0.69	0.5
Rumex obtusifolius	11	3	1605.97	0.36	0.0
Saxifraga tridactylites	22	1	326.50	0.50	0.0
Sonchus oleraceus	10	1	30340.57	0.50	0.0
Taraxacum officinale agg.	158	3	1049.99	0.30	0.5
Trifolium repens	60	3	9.56	0.40	0.5
Veronica arvensis	55	1	13.28	0.55	0.0
Vicia angustifolia	65	1	2.74	1.00	0.0
Vicia hirsuta	47	1	5.42	0.45	0.0

Table A - 8: Plant functional groups (PFG) derived from Stuttgart/Berlin/Bremen data by the combination of PLS, seed number/TV^2, SLI and clonality - regression coefficients for site characteristics. Abbreviations: ln disturb_curr = degree of current disturbance (ln-transformed), age_site = site age, PAW = plant available water. nutrients = nutrient conditions (value generated from principal component analysis of P, K and ECEC). For units see Table A - 5.

PFG	**city**	**Intercept**	**study location**	**study location^2**	**ln disturb_curr**	**ln disturb_curr^2**	**age_site**	**age_site^2**	**pH**	**pH^2**	**PAW**	**PAW^2**	**nutrients**	**nutrients^2**
1	ST	-1.9070	0	0	0	0	0	0	0	0	0	0	0	0
	BE	-4.7934	0	0	0	0	-0.0521	0	0	0.0475	0	0	0	0
	HB	-2.3751	0	0	0	0	-0.3823	0.0098	0	0	0	0.0007	0	0
2	ST	0.0000	0	0	0	0	0	0	0	0	0	0	0	0
	BE	-1.8548	0	0	0	0	0	0	0	0	0	-0.0016	0	0
	HB	-4.5327	0	0	0	0	0.1541	-0.0030	0.2875	0	0	0.0001	0	0.3796
3	ST	-5.6454	0	0	0	0	0	0	0	0	0	0	0	0
	BE	0.0000	0	0	0	0	0	0	0	0	0	0	0	0
	HB	-16.5858	0	0	0	0	0.6849	-0.0136	1.0315	0	0	0.0006	0	0
4	ST	-4.0218	0	0	0	0	0	0	0	0	0	0	0	0
	BE	-8.4882	0	0	0	0	0.9244	-0.0274	0	0	0	0	0	0
	HB	9.2600	0	0	0	0	0	0	-2.8359	0	0	0	0	0
5	ST	-0.5565	0	0	0	183050.0000	0	0	0	0	-0.0550	0	0	0
	BE	-0.0820	0	0	0	0	-0.0885	0	0	0	0.1585	-0.0066	0	0
	HB	-23.6551	0	0	0	0	0	0	0	0.4186	-0.0736	0	0	0
6	ST	-5.4004	0	0	0	668316.0000	0	0	0	0	0	0	0	0.1559
	BE	-3.9218	0	0	11186.9000	-3687353.0000	0.2272	-0.0036	0	0	0	0	0	0
	HB	-11.9467	0	0	0	0	0.6202	-0.0120	0	0	0.0696	0	0	0
7	ST	-4.0171	0	0	0	0	0	0	0	0	0	0	-3.7097	0.7876
	BE	0.3616	0	0	0	0	0	-0.0100	0	0	0	-0.0014	0	0
	HB	-5.6008	0	0	0	0	0	0	0	0.1191	-0.2590	0.0035	0	0
8	ST	0.0000	0	0	0	0	0	0	0	0	0	0	0	0
	BE	16.0168	0	0	0	0	-0.8793	0	0	0	0	-0.0138	0	0
	HB	0.0000	0	0	0	0	0	0	0	0	0	0	0	0
9	ST	0.0000	0	0	0	0	0	0	0	0	0	0	0	0
	BE	22.3592	0	0	0	0	-0.9891	0	0	-0.2742	0	0	0	0
	HB	0.0000	0	0	0	0	0	0	0	0	0	0	0	0

Table A - 9: List of plant species found in Bremen plots. The species selected for trait measurements and for inclusion into further analysis are marked with an ‘x’. Abbreviations: T = tree layer, S = shrub layer, A = species anthropogenically sown, EN = endangered, CR = critically endangered. Red list status according to Garve (1993).

traits measured and included into analysis	**species**	**red list status**	**preval. in 133 plots**
	Acer campestre		2
	Acer platanoides		1
	Acer pseudoplatanus		1
x	*Achillea millefolium*		20
	Aegopodium podagraria		1
	Agrostis gigantea		1
x	*Agrostis stolonifera*		13
x	*Agrostis tenuis*		20
	Alchemilla cf. vulgaris	EN	1
	Allium ascalonicum		1
	Alopecurus geniculatus		7
	Alopecurus pratensis		2
	Anthoxanthum odoratum		4
	Anthriscus sylvestris		1
x	*Arabidopsis thaliana*		12
	Arabis hirsuta	CR	1
	Arctium lappa		1
x	*Arenaria serpyllifolia*		43
x	*Arrhenaterum elatius*		15
x	*Artemisia vulgaris*		29
	Deschampsia flexuosa		1
	Bellis perennis		1
	Berteroa incana		2
	Betula pendula		
x	*Betula pendula* T		5
x	*Betula pendula* S		15
	Betula pubescens		3
	Betula pubescens x pendula		2
	Betula pubescens x pendula S		2
	Bromus hordeaceus		6
	Bromus inermis		1
x	*Bromus sterilis*		22
x	*Bromus tectorum*		6
	Calamagrostis arundinacea		1
x	*Calamagrostis epigejos*		32
	Calystegia sepium		1
	Capsella bursa-pastoris		6
x	*Carduus crispus*		4
	Carex arenaria		19
	Carex cf. demissa		2
	Carex cf. flava agg.		5
	Carex gracilis		2
x	*Carex hirta*		31
	Carex leporina		3
	Carex spicata		1
	Cerastium arvense		1
	Cerastium glomeratum		8
x	*Cerastium holosteoides*		27
x	*Cerastium semidecandrum*		22
x	*Chenopodium album*		14
	Chenopodium glaucum		2
	Chenopodium polyspermum		1
	Chenopodium spec.		1
x	*Cirsium arvense*		18
	Cirsium palustre		6
x	*Cirsium vulgare*		36
	Clematis vitalba		1
	Convolvulus arvensis		8
x	*Conyza canadensis*		49
	Cornus sanguinea		6
x	*Corynephorus canescens*		19
	Crataegus cf. monogyna S		1
	Crataegus spec.		9
	Crataegus spec. S		2
	Crepis biennis	EN	2
x	*Dactylis glomerata*		18
x	*Daucus carota*		13
x	*Deschampsia cespitosa*		25
	Echium vulgare	EN	3
x	*Elymus repens*		28
	Epilobium adnatum		5
	Epilobium angustifolium		9
	Epilobium ciliatum		5
	Epilobium hirsutum		3
	Epilobium palustre		2
	Epilobium parviflorum		1
	Epilobium spec.		5
	Equisetum arvense		17
	Equisetum palustre		1
	Erigeron acris		3
	Erodium cicutarium		2
x	*Erophila verna*		16
	Euphorbia cyparissias		4
	Festuca arundinacea		1
x	*Festuca ovina agg.*		20
x	*Festuca rubra*		54
	Filago minima	EN	5
	Fragaria vesca		1
	Fraxinus excelsior		1
	Galeopsis cf. tetrahit		3
	Galium aparine		2
	Galium mollugo		1
	Geranium cf. rotundifolium		1
	Geranium molle		1
	Geranium robertianum		9
	Geranium rotundifolium		1
	Geum urbanum		3
	Glechoma hederacea		9
	Heracleum sphondylium		1
	Herniaria glabra		2
	Hieracium bauhinii		1
	Hieracium laevigatum		1
	Hieracium pilosella		5
	Holcus cf. lanatus		2
x	*Holcus lanatus*		75
	Holcus mollis		2
x	*Hypericum perforatum*		34
x	*Hypochoeris radicata*		40
	Jasione montana		3
	Juncus articulatus		3
	Juncus compressus		5
	Juncus conglomeratus		8
	Juncus effusus		10
	Juncus tenuis		7
	Lactuca serriola		2
	Lamium album		1
	Lamium purpureum		1
	Lathyrus pratensis		2

Table A - 9 continued.

traits measured and included into analysis	species	red list status	preval. in 133 plots
	Lepidium campestre	EN	1
	Lepidium cf. densiflorum		1
x	*Lolium perenne*		18
	Lolium perenne A		5
x	*Lotus corniculatus*		15
	Luzula luzuloides		1
	Lythrum salicaria		2
	Mahonia aquifolium		1
	Malva neglecta		1
	Matricaria discoidea		6
x	*Matricaria maritima*		23
	Medicago cf. arabica		1
x	*Medicago lupulina*		47
	Medicago x varia		3
	Melilotus alba		1
x	*Melilotus officinalis*		15
	Myosotis cf. arvensis		1
	Myosotis ramosissima	EN	2
	Myosotis stricta		1
x	*Oenothera biennis*		23
	Padus serotina		4
	Padus serotina S		2
	Papaver dubium		1
	Papaver somniferum		1
x	*Phalaris arundinacea*		20
	Phleum pratense		2
	Phragmites australis		3
x	*Picris hieracioides*		11
	Pinus nigra		1
x	*Plantago lanceolata*		23
x	*Plantago major*		18
	Poa angustifolia		3
x	*Poa annua*		28
x	*Poa compressa*		24
	Poa compressa A		2
	Poa nemoralis		1
x	*Poa palustris*		11
x	*Poa pratensis*		23
x	*Poa trivialis*		48
	Polygonum amphibium		1
	Polygonum aviculare		7
	Polygonum lapathifolium		1
x	*Polygonum persicaria*		10
	Populus alba		1
	Populus alba S		1
	Populus tremula		3
	Populus tremula T		2
	Populus tremula S		3
	Potentilla anserina		4
	Potentilla cf. inclinata		1
	Potentilla cf. intermedia		2
	Potentilla cf. recta		1
	Potentilla norvegica		1
	Potentilla recta		1
	Potentilla reptans		5
	Prunus padus S		1
	Quercus robur		
	Quercus robur T		1
	Quercus robur S		5
	Ranunculus acris		4
	Ranunculus arvensis		1
	Ranunculus repens		2
	Ranunculus sceleratus		2
	Reseda lutea		1
	Reseda luteola		1
	Ribes rubrum		1
	Robinia pseudoacacia		1
	Robinia pseudoacacia S		1
	Rorippa palustris		4
	Rosa cf. gallica		1
	Rosa spec.		
	Rosa spec. S		7
	Rubus fruticosus agg.		
	Rubus fruticosus agg. S		4
	Rubus idaeus		5
	Rubus idaeus S		3
	Rumex acetosa		
x	*Rumex acetosella*		45
	Rumex cf. crispus		1
	Rumex crispus		3
	Rumex obtusifolius		1
	Sagina procumbens		3
	Salix caprea		1
	Salix caprea S		1
	Salix caprea x cinerea		1
	Salix caprea x cinerea S		2
	Salix cf. acutifolia		1
	Salix cf. acutifolia S		1
	Salix cf. caprea		2
	Salix cf. cinerea S		4
	Salix cf. viminalis		12
	Salix cf. viminalis S		10
	Salix cinerea		6
	Salix cinerea S		6
	Salix viminalis S		3
	Salix viminalis x caprea S		1
	Sanguisorba minor	CR	1
	Saponaria officinalis		1
	Sarothamnus scoparius S		1
x	*Saxifraga tridactylites*		13
	Sedum acre		2
x	*Senecio inaequidens*		76
x	*Senecio viscosus*		10
	Senecio vulgaris		7
	Silene pratensis		2
x	*Sisymbrium altissimum*		5
	Sisymbrium officinale		1
	Solanum dulcamara		1
	Solidago canadensis		2
x	*Solidago gigantea*		32
	Solidago spec.		1
	Solidago virgaurea		1
	Spergula morisonii		9
	Stachys germanica	CR	2
	Stachys spec.		2
	Stellaria graminea		1
	Stellaria media		2
	Symphytum officinale		5
x	*Tanacetum vulgare*		41
x	*Taraxacum officinale*		55

Table A - 9 continued.

traits measured and included into analysis	species	red list status	preval. in 133 plots
	Thlaspi arvense		1
x	*Tragopogon dubius*	EN	6
x	*Trifolium arvense*		26
x	*Trifolium campestre*		8
x	*Trifolium pratense*		22
x	*Trifolium repens*		34
	Triticum spec. A		7
x	*Tussilago farfara*		11
	Urtica dioica		7
	Verbascum densiflorum		2
	Verbascum thapsus		6
x	*Veronica arvensis*		16
	Veronica serpyllifolia		6
	Veronica verna	CR	1
x	*Vicia angustifolia*		26
	Vicia cf. cracca		2
	Vicia cf. dasycarpa		1
	Vicia cf. tenuifolia		1
	Vicia cf. tenuissima		1
	Vicia cracca		2
x	*Vicia hirsuta*		28
x	*Vicia tetrasperma*		8
x	*Vulpia myuros*		18

Table A - 10: List of plant species found in Berlin plots. The species selected for trait measurements and for inclusion into further analysis are marked with an ‘x’. Abbreviations: T = tree layer, S = shrub layer, EN = endangered, CR = critically endangered. Red list status according to SDUD (2001).

traits measured and included into analysis	**species**	**red list status**	**preval. in 133 plots**
	Acer negundo T		1
	Acer negundo		19
	Acer negundo S		5
	Acer platanoides		5
	Acer pseudoplatanus		2
	Acer pseudoplatanus S		1
x	*Achillea millefolium*		36
	Aegopodium podagraria		1
	Agrostis stolonifera		1
	Agrostis tenuis		6
	Agrostis vinealis		1
	Alliaria petiolata		1
	Alopecurus geniculatus		3
	Alopecurus pratensis		1
	Anthemis spec.		2
	Anthriscus caucalis		1
	Anthriscus sylvestris		3
	Anthyllis vulneraria	CR	1
x	*Arabidopsis thaliana*		12
x	*Arctium lappa*		9
x	*Arenaria serpyllifolia*		42
x	*Arrhenaterum elatius*		13
	Artemisia campestris		2
	Artemisia cf. pontica		1
	Artemisia siversiana		1
x	*Artemisia vulgaris*		70
	Atriplex cf. littoralis		1
	Atriplex micrantha		4
x	*Berteroa incana*		31
	Betula pendula T		1
	Betula pendula		11
	Betula pendula S		4
	Bromus hordeaceus		6
	Bromus inermis		1
x	*Bromus sterilis*		41
x	*Calamagrostis epigejos*		49
x	*Capsella bursa-pastoris*		19
	Cardaminopsis arenosa		3
	Carduus crispus		1
	Carex arenaria		2
x	*Carex hirta*		13
	Carex muricata agg.		1
	Cerastium arvense		1
x	*Cerastium glomeratum*		7
x	*Cerastium holosteoides*		18
	Cerastium pumillum agg.		1
x	*Cerastium semidecandrum*		42
x	*Chenopodium album*		22
	Cirsium arvense		2
	Cirsium eriophorum		1
x	*Cirsium vulgare*		22
	Clematis vitalba		4
x	*Convolvulus arvensis*		12
x	*Conyza canadensis*		42
	Cornus sanguinea		3
	Cornus sanguinea S		1
	Corynephorus canescens		4
	Crataegus spec.		2
x	*Dactylis glomerata*		21
x	*Daucus carota*		51
	Descurainia sophia		2
	Diplotaxis muralis		1
	Diplotaxis tenuifolia		5
	Echium vulgare		6
x	*Elymus repens*		41
	Epilobium cf. roseum		1
	Epilobium cf. tetragonum		1
	Equisetum arvense		4
	Erigeron cf. annuus		4
x	*Erodium cicutarium*		11
x	*Erophila verna*		13
	Erysimum cheiranthoides		3
	Euphorbia cyparissias		4
	Fallopia convolvulus		1
x	*Festuca rubra agg.*		13
x	*Festuca ovina agg.*		16
	Fraxinus cf. ornus		1
	Fraxinus excelsior		1
	Fraxinus excelsior S		1
	Fumaria cf. officinalis		1
	Galium aparine		6
	Geranium cf. molle		8
	Geranium cf. rotundifolium		1
	Geranium pusillum		6
	Geranium robertianum		1
	Glechoma hederacea		4
	Helichrysum arenarium		1
	Heracleum mantegazzianum		1
	Herniaria glabra		5
	Holcus lanatus		2
	Hordeum cf. murinum		5
x	*Hypericum perforatum*		30
	Jasione montana		1
x	*Lactuca serriola*		32
	Lamium album		1
	Lamium purpureum		3
	Lepidium cf. densiflorum		1
	Leucanthemum vulgare		3
x	*Linaria vulgaris*		20
x	*Lolium perenne*		18
	Lotus corniculatus		2
	Mahonia aquifolium		1
	Matricaria discoidea		6
x	*Matricaria maritima*		25

continued

Table A - 10 continued.

traits measured and included into analysis	species	red list status	preval. in 133 plots
	Medicago falcata		1
x	*Medicago lupulina*		56
x	*Medicago x varia*		12
	Melilotus cf. officinalis		4
	Myosotis discolor	CR	1
	Myosotis ramosissima		8
	Myosotis stricta		4
x	*Oenothera biennis*		39
	Oxalis corniculata		2
	Papaver argemone	EN	1
	Papaver dubium		5
	Papaver rhoeas	EN	2
	Petrorhagia prolifera		2
	Phalaris arundinacea		2
	Phleum pratense		2
x	*Plantago lanceolata*		27
x	*Plantago major*		15
x	*Plantago media*		10
x	*Poa annua*		22
	Poa bulbosa		1
x	*Poa compressa*		54
	Poa nemoralis		1
x	*Poa pratensis*		27
x	*Poa pratensis ssp. angustifolia*		13
x	*Poa trivialis*		24
x	*Polygonum aviculare*		10
	Polygonum persicaria		4
	Populus alba		1
	Populus tremula		2
	Populus tremula S		3
	Potentilla argentea		7
	Potentilla cf. supina		1
	Potentilla reptans		1
	Quercus rubra S		1
	Ranunculus acris		1
	Reseda lutea		1
	Robinia pseudoacacia		4
	Robinia pseudoacacia S		2
	Rorippa palustris		1
	Rosa cf. canina		1
	Rosa cf. canina S		3
	Rubus fruticosus		6
	Rumex acetosella		8
x	*Rumex thyrsiflorus*		27
	Salix spec.		4
	Salix spec. S		3
	Sambucus nigra		1
	Saponaria officinalis		5
	Sarothamnus scoparius		1

continued

	Saxifraga tridactylites	EN	5
	Sedum acre		5
x	*Sedum album*		7
	Senecio inaequidens		3
x	*Senecio vernalis*		26
	Senecio viscosus		5
	Senecio vulgaris		1
x	*Silene alba*		15
x	*Sisymbrium altissimum*		14
x	*Sisymbrium loeselii*		30
	Solidago canadensis		5
x	*Solidago gigantea*		49
x	*Stellaria media*		7
x	*Tanacetum vulgare*		40
x	*Taraxacum officinale agg.*		63
	Thlaspi arvense		5
	Tragopogon dubius		1
x	*Trifolium arvense*		16
x	*Trifolium campestre*		17
x	*Trifolium pratense*		23
x	*Trifolium repens*		18
	Trisetum flavenscens		1
x	*Tussilago farfara*		14
	Urtica dioica		5
	Verbascum thapsus		6
x	*Veronica arvensis*		33
	Veronica chamaedrys		1
	Veronica hederifolia (ssp. hederifolia)	EN	3
	Veronica serpyllifolia		5
x	*Vicia angustifolia*		37
	Vicia cf. lathyroides		1
x	*Vicia hirsuta*		19
	Vicia sativa		6
	Vicia tetrasperma		1
x	*Vicia villosa*		12
	Viola arvensis		2

Dank

Dank

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‚... Und jedem Anfang wohnt ein Zauber inne, der uns beschützt und der uns hilft zu leben...' (H. Hesse)

Curriculum vitae

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April 2001 – September 2002	NWP Planungsgesellschaft mbH, Oldenburg; Aufgabenschwerpunkt: GIS in der Landschaftsplanung

Publications & Reports

Rudner, M., Schadek, U. & Damken, C. (2004): Habitatmodelle und ihre mögliche Integration in die Planungspraxis – ein Diskussionsbeitrag. – In: *Habitatmodelle – Methodik, Anwendung, Nutzen* (eds. Dormann, C.F., Blaschke, T., Lausch, A., Schröder, B. & D. Söndgerath). Tagungsband zum Workshop vom 08.-10. Oktober 2003 am UFZ Leipzig. UFZ-Berichte 9/2004. Leipzig: 167-171.

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Erklärung

gemäß § 10 Abs. 2 der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg vom 11.12.2003

Hiermit erkläre ich ehrenwörtlich, die vorliegende Arbeit in allen Teilen selbständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Diese Dissertation hat weder in gleicher noch in ähnlicher Form in einem anderen Prüfungsverfahren vorgelegen. Des Weiteren erkläre ich, dass ich früher weder akademische Grade erworben habe, noch zu erwerben versucht habe.

Oldenburg, 31.07.2006

(Ute Schadek)