

Biodiversity of urban brownfields

**Modelling species occurrence and persistence
in dynamic habitats**

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Summary

Urban brownfields offer habitats for a wide range of species. They can provide ecological as well as social values within cities. The continuous changes in brownfield location (due to redevelopment and abandonment) and in their habitat conditions (due to succession) generate a spatio-temporal mosaic cycle of transient habitats. Aim of this study was to evaluate the potential of brownfields for urban biodiversity conservation and to provide guidelines for urban planning. Particularly, the concept of temporary conservation should be tested. This concept aims to enable both conservation and economic use within the same area by management of such a mosaic cycle of development and different successional stages.

In the first part of this thesis, I used a statistical approach that quantifies the species-environment relationship. The analyses were based on empirical data of 133 sampling plots at brownfield sites in industrial and business areas within the city of Bremen. At these plots, species presence/absence data of vascular plants and phytophagous insects (leafhoppers and grasshoppers) was recorded. Additionally, the environmental conditions at these plots (soil properties, successional site age, vegetation structure, and landscape context variables) were mapped.

First, I built species distribution models (SDMs) by logistic regression and a model averaging procedure. Of 231 vascular plant species recorded at the study plots, 64 had a prevalence of $\geq 10\%$, which is the minimum for statistical model building. Only 37 out of these were responsive and thus modelled by SDMs. Likewise, out of 146 leafhopper and 11 grasshopper species, 41 and 8, respectively, met the prevalence criterium. Of these, 36 leafhopper and 7 grasshopper species, respectively, could be modelled by SDMs. Model performance, which was assessed by a bootstrapping procedure, was of satisfactory quality.

From the SDMs I identified the main driving factors of species occurrence. The plant community was mainly driven by plot based parameters, i.e. soil properties and site age, and less by the landscape context. On the other hand, insect species occurrence showed a strong dependence on the vegetation at the plot and on the landscape context variables. The direct influence of soil properties and site age was much weaker. However, these factors affected insect species indirectly by the present successional stage of the sites' vegetation. This influence of the vegetation on insect occurrences was accounted for by incorporating plant species predictions into the insect SDMs. Nearly all modelled species responded to successional site age on plot or landscape scale. This parameter can be controlled by urban planning by the pace of landscape turnover.

Next, different spatio-temporal land use scenarios were analysed. Using a landscape model I developed, the SDMs were scaled up to the landscape scale. Within this modelling tool the pace of landscape turnover, i.e. the rate at which built-up sites are converted to brownfields by abandonment and brownfields are built-up, respectively, determines the age distribution of brownfield sites. The conservation value of a certain scenario was expressed as species richness and as a rarity index aggregated from single species model predictions. Simulations revealed that a spatio-temporally dynamic landscape yield much higher evaluation criteria in comparison to a static one. In detail, for the modelled species pool an intermediate to slow landscape turnover (average brownfield age of 15 years) resulted in the highest species richness for both species groups and was a good compromise regarding species rarity indices.

In an exemplary planning study the feasibility of the concept of temporary conservation was tested in praxis. To this end, I applied the landscape model to a projected area for business and recreational use in the city of Oldenburg. I compared two different static and dynamic scenarios, which had been developed in cooperation with the municipality, urban planners, and architects. It was shown that the most dynamic scenario, which comprised most changes in land use distribution over the modelling time span of 20 years, resulted in the highest species richness and rarity values (except for plant rarity).

In the second part of this thesis, I applied a dynamic metapopulation approach. For this purpose, I first mapped patch occupancies of two grasshopper species in an industrial area in Bremen over three consecutive years. I intended to analyse extinction and colonisation processes in a dynamic landscape based on this data using an incidence function model. However, no metapopulation structure could be found. Species incidence and colonisation was independent of patch isolation. Merely a positive effect of patch size on occupancy was identified.

Finally, I developed a metapopulation simulation model. By this means, the effect of stochastic landscape turnover (random brownfield generation by abandonment and destruction by redevelopment) and deterministic succession on virtual species was investigated. Species were defined by different niche positions and niche breadths on the successional gradient. Results showed that metapopulation persistence depended on landscape turnover. Species position on the successional gradient determined the range of viable turnover rates. Likewise, species richness was positively related to a certain landscape turnover rate. Furthermore, landscapes of slower succession maintained species survival over a wider range of turnover rates but at lower rates than under faster succession.

In conclusion, the most important finding was that species inhabiting urban brownfields depend on different, temporary successional stages. These species rely on continuous habitat destruction and habitat regeneration to re-initiate succession. This way, a variety of habitats for different species is maintained on the landscape scale. Thus, temporary conservation by the integration of brownfields into urban planning can preserve

and even enlarge urban biodiversity. Even if it might be difficult to control the landscape turnover rate exactly, planners can contribute to urban conservation by allowing brown-fields to undergo succession for a few years. Some additional older and well connected sites can furthermore provide habitat for late successional or dispersal limited species.

Zusammenfassung

Städtische Brachflächen bieten Lebensraum für viele Tier- und Pflanzenarten. Sie sind sowohl von ökologischem als auch von sozialem Wert. Die andauernde räumliche (durch Wiederbebauung und Brachfall) und zeitliche Veränderung der Brachflächen (durch Sukzession) erzeugt einen raum-zeitlichen Mosaikzyklus temporärer Habitats. Ziel dieser Arbeit war es, das Potential urbaner Brachflächen für den Schutz der Artenvielfalt im städtischen Raum zu untersuchen, sowie Orientierungshilfen für die Stadtplanung zu erarbeiten. Insbesondere sollte dabei das Konzept des zeitlich begrenzten Naturschutzes getestet werden. Dieses Konzept versucht, durch das Management des oben erwähnten Mosaikzyklus aus Bebauung und verschiedenen Sukzessionsstadien Naturschutz und Nutzung innerhalb eines Gebietes zu ermöglichen.

Im ersten Teil dieser Arbeit wird mit Hilfe von statistischen Methoden die Beziehung zwischen dem Vorkommen von Arten und ihrer Umwelt quantifiziert. Die Untersuchungen beruhen auf empirischen Daten, die an 133 Untersuchungspunkten auf städtischen Brachflächen in Industrie- und Gewerbegebieten in Bremen erhoben wurden. An diesen Untersuchungspunkten wurde das Vorkommen bzw. Nichtvorkommen von Gefäßpflanzen und phytophager Insekten (Zikaden und Heuschrecken) kartiert. Des Weiteren wurden die Umweltbedingungen (Bodenparameter, Flächenalter, Vegetationsstruktur und Landschaftskontext) aufgenommen.

Auf Grundlage dieser Daten wurden zunächst Habitatmodelle unter Verwendung von logistischer Regression und eines 'Model Averaging' Verfahrens aufgestellt. Von 231 an den Untersuchungspunkten kartierten Pflanzenarten wiesen 64 die Mindestprävalenz für statistische Modellbildung von 10 % auf. Lediglich 37 von diesen Arten zeigten einen signifikanten Zusammenhang zu den Umweltparametern, konnten also durch Habitatmodelle dargestellt werden. Ähnlich erfüllten von 146 erfassten Zikaden- und 11 Heuschreckenarten nur 41 bzw. 8 das Prävalenzkriterium. Von diesen konnten 36 Zikaden- und 7 Heuschreckenarten durch Habitatmodelle beschrieben werden. Die Güte der Habitatmodelle wurde mit einem Bootstrapp-Verfahren abgeschätzt und war von zufriedenstellender Qualität.

Mit Hilfe der Habitatmodelle wurden die Umweltfaktoren identifiziert, welche den größten Einfluss auf das Artvorkommen hatten. Die Pflanzengemeinschaft wurde hauptsächlich von lokalen Parametern, also dem Boden und dem Sukzessionsalter der Fläche beeinflusst und weniger durch den Landschaftskontext. Das Insektenvorkommen zeigte dahingegen eine starke Abhängigkeit sowohl von der Vegetation am Untersuchungspunkt als auch vom Landschaftskontext. Der direkte Einfluss von Bodenparametern und dem

Flächenalter war hier also deutlich schwächer. Trotzdem wirkten diese Faktoren durch das Sukzessionsstadium der Vegetation am Untersuchungspunkt indirekt auf die Insektenarten. Dieser Einfluss der Vegetation auf das Insektenvorkommen wurde durch die Einbindung der Pflanzenvorhersagen in die Insekten-Habitatmodelle berücksichtigt. Nahezu alle modellierten Arten reagierten auf das Sukzessionsalter der Flächen auf lokaler oder auf Landschaftsebene. Dieser Parameter lässt sich über die Geschwindigkeit der Flächenumnutzung von der Stadtplanung kontrollieren.

Als nächstes wurden unterschiedliche raum-zeitliche Landnutzungsszenarien untersucht. Mit Hilfe eines Landschaftsmodells, welches ich entwickelte, wurden dazu die Habitatmodelle auf die Landschaftsebene hochskaliert. Innerhalb dieses Modellierungstools bestimmte die Geschwindigkeit der Umnutzung, also die Rate mit der bebaute Flächen brach fallen bzw. Brachen wiederbebaut werden, die Altersverteilung der Brachflächen. Die naturschutzfachliche Wertigkeit eines Szenarios wurde dabei durch den Artenreichtum und einen Seltenheitsindex des Untersuchungsgebiets ausgedrückt, die jeweils aus den Modellvorhersagen der Einzelartmodelle zusammengesetzt wurden. Die Simulationen zeigten, dass eine raum-zeitlich dynamische Landschaft im Vergleich zu einer statischen sehr viel positiver zu bewerten ist. Im Einzelnen führte eine mittlere bis geringe Umnutzungsrate (mit einem durchschnittlichen Flächenalter von 15 Jahren) zur größten Vielfalt beider Artgruppen und stellte sich als ein guter Kompromiss zwischen den beiden Gruppen in Bezug auf den Seltenheitsindex heraus.

In einer Modellplanungsstudie wurde die Umsetzbarkeit des Konzepts des Naturschutzes auf Zeit in der Praxis getestet. Dazu wendete ich das Landschaftsmodell auf ein Gebiet mit geplanter Gewerbe- und Freizeitnutzung in Oldenburg an. Es wurden jeweils zwei verschiedene statische und dynamische Szenarien miteinander verglichen, die in Zusammenarbeit mit der Stadtverwaltung, Stadtplanern und Architekten entworfen worden waren. Es zeigte sich, dass das dynamischste Szenario, welches die häufigsten Umnutzungen im Verlauf des 20-jährigen Simulationszeitraums aufwies, zu den höchsten Wertigkeiten in Bezug auf Artvielfalt und Seltenheit führte (mit Ausnahme der Seltenheitsindex für Pflanzen).

Der zweite Teil dieser Arbeit beruht auf einem dynamischen Metapopulationsansatz. Zunächst kartierte ich das Vorkommen zweier Heuschreckenarten auf abgegrenzten Flächen in einem Gewerbegebiet in Bremen in drei aufeinander folgenden Jahren. Es sollten mit Hilfe eines 'Incidence Funktion Models' lokale Aussterbe- und Wiederbesiedlungsvorgänge in einer dynamischen Landschaft untersucht werden. Allerdings konnte keine Metapopulationsstruktur nachgewiesen werden. Das Artvorkommen und die Besiedlung einzelner Flächen war unabhängig von deren Isolation. Es konnte lediglich ein positiver Effekt der Flächengröße auf das Vorkommen festgestellt werden.

Schließlich entwickelte ich ein Modell zur Simulation von Metapopulationen. Damit wurde die Auswirkung stochastischer Landnutzungsänderung (zufälliger Brachfall und Wiederbebauung) und deterministischer Sukzession auf virtuelle Arten untersucht. In diesem Modell wurden die Arten durch unterschiedliche Nischenpositionen und -breiten

auf dem Sukzessionsgradienten beschrieben. Die Ergebnisse zeigten, dass das Überleben der Metapopulationen von der Umnutzungsrate abhängt. Die Nischenposition einer Art bestimmte dabei das Turnoverintervall, über welches die Art überlebensfähig war. Ebenso war die Artenvielfalt einer Landschaft positiv mit bestimmten Umnutzungsraten verbunden. Außerdem zeigte sich, dass die Überlebensfähigkeit von Metapopulationen bei langsamerer Sukzession über eine weitere Bandbreite an Umnutzungsgeschwindigkeiten, aber bei insgesamt geringeren Raten, gesichert war.

Zusammenfassend ist das wichtigste Ergebnis dieser Arbeit, dass diejenigen Arten, die Lebensraum auf städtischen Brachflächen finden, von unterschiedlichen, zeitlich begrenzten Sukzessionsstadien abhängen. Diese Arten sind darauf angewiesen, dass durch kontinuierliche Zerstörung und Neuerschaffung ihrer Habitate die Sukzession immer wieder von Neuem beginnt. Auf diese Weise wird auf der Landschaftsebene eine Vielzahl unterschiedlicher Lebensräume für verschiedene Arten aufrechterhalten. Folglich kann der Naturschutz auf Zeit durch die Einbeziehung von Brachflächen in die städtische Planung die Artenvielfalt in Städten erhalten und sogar vergrößern. Auch wenn es schwierig sein mag, die Umnutzungsrate exakt zu kontrollieren, können Planer allein dadurch zum städtischen Naturschutz beitragen, dass sie einige Brachflächen über ein paar Jahre der Sukzession überlassen. Zusätzlich können einige ältere und gut verbundenen Flächen Lebensraum für Arten späterer Sukzessionsstadien oder mit eingeschränktem Ausbreitungsvermögen bieten.

Chapter 1

General introduction

1.1 Background

Cities act as drivers of often negative ecosystem change but also bear valuable habitats. How can the urban system be shaped in a way that reduce the ecosystem service burdens it creates? The proportion of the human world population living in cities increased from about 15 % in 1900 to 50 % in 2005, with even more than 70 % of the European population dwelling in urban areas (McGranahan et al., 2005; UN Population Division, 2008). Although urban settlements occupy only about 2.7 % of the world's land area (McGranahan et al., 2005), urbanisation is regarded, on the one hand, as one of the major threats of biodiversity due to habitat destruction as well a biotic homogenisation (McKinney, 2002; Forsy & Allen, 2005).

On the other hand, cities comprise a rich biodiversity, offering habitat for a diverse flora and fauna (Kühn et al., 2004; Godefroid & Koedam, 2007). They hold not only common, generalist species but also rare and endangered ones (Pickett et al., 2001; Kühn & Klotz, 2006). Additionally, urban green spaces provide ecosystem services like microclimate regulation, air filtering, water regulation as well as recreational, educational, and cultural values, thus being substantial for human well-being (Bolund & Hunhammar, 1999).

Therefore, it is important to conserve and enhance urban green spaces as locations of urban biodiversity. Management of urban brownfields can contribute significantly to this task. Although this special type of urban green space has been rather ignored by urban conservation planning (Godefroid, 2001; Muratet et al., 2007), urban brownfields are increasingly noticed by ecologists (Gibson, 1998; Maurer et al., 2000; Angold et al., 2006).

In this thesis, I want to explore the possibilities urban brownfields offer for urban conservation. To this end, I investigate the main drivers of single species occurrence and community composition on urban brownfields with particular emphasis on the spatio-temporal dynamics of such habitats. From this, I give some recommendations for integrating the concept of temporary conservation into urban planning and biodiversity management.

1.2 Urban habitats

The abiotic conditions of urban areas differ remarkably from their surroundings (Gilbert, 1989): The heat island effect generally results in increased temperatures by 0.5–1.5 °C with maximum difference of up to 10 °C. Both precipitation and sky cover are 5–10 % higher, while global radiation and average wind speed are reduced by 15–20 % and 10–20 %, respectively. Furthermore, air pollution by aerosols, sulphur dioxide, and other pollutants is increased within cities. Urban hydrology is modified towards decreased evapotranspiration and groundwater recharge as well as increased surface runoff (Pickett et al., 2001). Most urban soils are altered by human activities. Nutrient content can be poor to highly enriched. Likewise, habitats range from wet to dry, but dry ones are more common (Rebele, 1994). Soils can be very densely compacted by heavy machinery, or contain brick rubble which alters water permeability as well as nutrient status.

Obviously, another factor shaping urban habitats are anthropogenic disturbances due to building activities, gardening or recreation (Rebele, 1994). These disturbances can be of small or larger scale, resulting for instance in the creation of small open spots or in the complete destruction of a habitat patch.

The variety of actual and historical land uses and social contexts create a great heterogeneity of habitats in urban areas (Pickett et al., 2001; Zerbe et al., 2003). The wide range of environmental conditions and the presence of continuous disturbance events on different scales result in the coexistence of different successional stages. Hence, urban areas exhibit a multitude of different but challenging and often, compared to natural ecosystems, fundamentally altered habitats. They bear true urban communities, which cannot be found elsewhere (Alberti et al., 2003).

1.3 Urban brownfields

Brownfield habitats

Urban brownfields (also referred to as derelict, postindustrial, or wasteland sites) comprise previously developed land, abandoned railway tracks, industrial dumps, and landfills. Some of these sites might be contaminated or otherwise critical due to their former use (e.g. by chemical industry, dry cleaners or fuel stations) and have to be cleaned up before serving as public accessible green space (De Sousa, 2003; Wedding & Crawford-Brown, 2007). In the context of this thesis, the emphasis is laid on abandoned, but non-hazardous brownfields. These artificial habitats are among the most valuable ones in urban areas as they exhibit a very diverse flora and fauna (Maurer et al., 2000; Zerbe et al., 2003; Angold et al., 2006), providing habitat for rare and regionally endangered species (Eversham et al., 1996; Eyre et al., 2001, 2003). The blue winged grasshopper (*Oedipoda caerulea*) for instance is endangered due to large-scale loss of its original habitats (Detzel, 1998). In the city of Bremen, which was under study, this species was common as it finds new habitats in urban brownfields. Like urban habitats in general,

urban brownfields owe their high biodiversity to the heterogeneity in habitat conditions resulting from differences in soil substrates, levels of disturbance, micro-climatic conditions, and site histories.

Brownfields emerge when buildings or industrial facilities are abandoned. However, after the man-made creation they remain rather undisturbed, which makes them the 'wildest' among the urban ecosystems (Harrison & Davies, 2002). The course of succession urban brownfields undergo is highly dependent on soil conditions, anthropogenic interferences like sowings, and regional differences. A general pattern of succession can be described as follows (Gilbert, 1989) (examples in figure 1.1): Open soils are first colonised by ruderal annuals, which are replaced after 3–6 years by short-lived annual and biennial herbs. Later on, perennials and especially grasses establish and become dominant. The climax stage is characterised by scrubs and woody species. Not only the plant composition changes with time but also the occurring animal species, as they often rely on certain vegetation structures, host plants or micro-climatic conditions. For instance, the occurrence of herbivore insects is directly correlated to site age and depends even stronger on vegetation structure (Sanderson, 1992; Angold et al., 2006).

Hence, in contrast to other, more static urban green spaces like parks or gardens, brownfields form dynamic habitats in space - as their locations shift due to redevelopment and abandonment - and in time - due to continuous changes through the course of succession (Gibson, 1998; Wood & Pullin, 2002). Abandonment, succession, and destruction of brownfields by redevelopment form a spatio-temporal mosaic of built-up areas and habitat patches of different conditions. Within this mosaic, some sites run through the whole succession series but the majority exists for a rather short period of time. From the species point of view, only certain successional stages of brownfield habitats might be suitable for instance due to colonisation by superior competitors, the stage of soil development, or the dependence on certain vegetation parameters as outlined above. Thus, these valuable habitats are mostly ephemeral, while the role of their dynamics for species occurrence remains unknown.

Turnover of urban brownfields

What do the dynamics of urban brownfields look like in detail? How large is the actual proportion of brownfield sites in cities and how old do they grow? In this context, a study of aerial photographs of industrial areas was conducted in six German cities (Berlin, Bottrop, Bremen, Darmstadt, Munich, and Stuttgart) over the time span from around 1950 to 2004 by Emptner (2006). In that study, more than 900 study plots in total were analysed. These plots had been randomly distributed along a building density gradient (very dense, mixed, low density) in the latest aerial photographs. Here, I reprocess the data and summarise some of the findings.

The fraction of study plots that were identified as brownfield over the years differed notably between the six cities and exhibited fluctuations over the study period (figure 1.2). The average fraction lay between 20 and 30 % with no temporal trend.



Figure 1.1: Examples of brownfield sites of different successional stages. From left to right, from top to bottom: abandoned railroads, open vegetation, dense grassy and herbaceous vegetation, pre-forest vegetation.

The most important result was that on average nearly 60 % of all study plots saw at least one brownfield period (defined as being derelict land or untended company premises) during the 55 years investigated (figure 1.3, left). While some cities exhibited a higher dynamic, indicated by an increased fraction of plots that lay waste for two or more times (e.g. Bremen), others were rather static (e.g. Stuttgart).

The length of the brownfield periods between the years 1950 and 2004 aggregated for the six cities was clearly skewed to site ages under 10 years (figure 1.3, right). On the one hand, this age distribution might be biased to smaller values due to the fact that the current brownfield period is cut off at the last time step of investigation. Likewise, the duration of the first period in the time series is possibly underestimated. On the other hand, very short periods might have remained undetected as half of the time intervals between two aerial photographs were longer than 5 years (with the longest delay of even 17 years).

To summarise, this analysis confirmed that a considerable proportion of sites within industrial areas has been abandoned over the last 55 years. Brownfield sites were destroyed at some point of time and recreated at another location. Furthermore, the brownfield durations are distributed in a way that arise from random and independent turnover events. Such a distribution I will also assume in the following chapters.

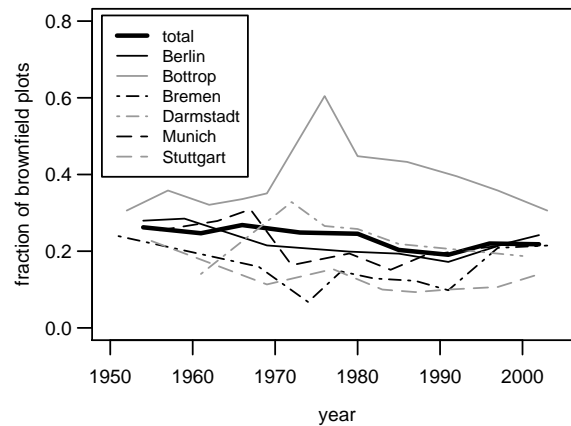


Figure 1.2: Fraction of study plots that were identified as brownfields over time. The thick line indicates the average of the six cities.

Brownfields in urban conservation management

The importance of conserving urban biodiversity by means of planning and management is increasingly recognised (Kühn et al., 2004; Pauleit et al., 2005; Pickett & Cadenasso, 2008). In urban areas even the protection of rather common species can be of high local value (Gibson, 1998; Miller & Hobbs, 2002).

Facing the threat of urban sprawl, the redevelopment of brownfields from derelict, vacant land within cities seems an appropriate counteraction. However, it would destroy valuable informal open green space (Pauleit et al., 2005). On the other hand, many cities are confronted with the problem of shrinkage due to population and often also economic decline, resulting in an increase of unused lots. In this case, the potential of these brownfield sites for social, residential, and ecological improvement of urban areas often remains unrealised (Haase, 2008).

The integration of *temporary* conservation of brownfield sites contributes to both situations: It does not irreversibly exclude the sites from development, while the formal recognition of their ecological value and recreational potential would counter their negative image (Harrison & Davies, 2002; Herbst & Herbst, 2006). The traditional concept of stationary, isolated protected areas, which could hardly stop biodiversity decline outside of cities (von Haaren & Reich, 2006), is not appropriate within urban areas. Furthermore, it is insufficient to maintain a variety of ephemeral successional stages which are the key feature determining the value of urban brownfields. Hence, maintaining urban brownfields in a spatio-temporal mosaic of dynamic habitats, comparable with the concept of dynamic nature reserves (Bengtsson et al., 2003), suits the situation much better.

However, there are only a few and rather ad hoc suggestions of how long brownfields sites should undergo natural succession before redevelopment (Angold et al., 2006; Mu-

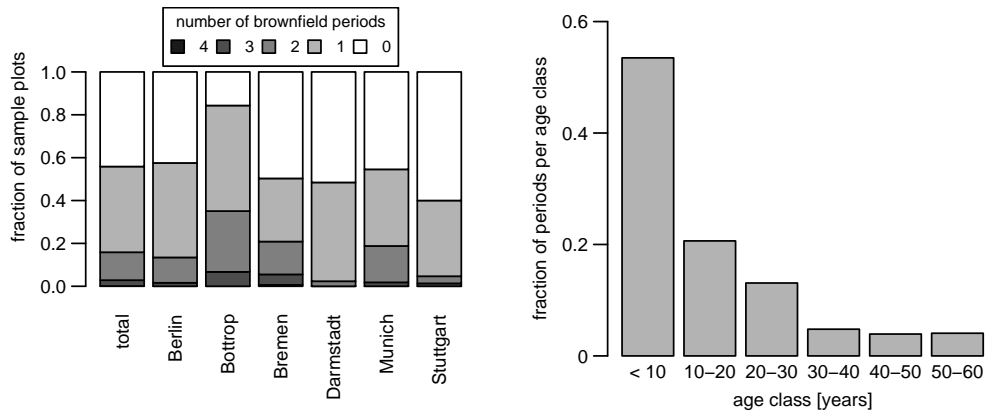


Figure 1.3: Number (left) and duration (right) of brownfield periods. The left graph shows the number of brownfield periods for the single cities and the aggregated value. The right one shows the distribution of brownfield period lengths aggregated over the six cities and the whole time frame investigated.

ratet et al., 2007). Thus, precise recommendations are needed how the temporal and spatial component of urban brownfields should look like to include biodiversity aspects into the urban planning process (Wintle et al., 2005). The TEMPO-project contributes to this need from different perspectives.

1.4 The TEMPO project

This thesis is imbedded into the interdisciplinary project 'TEMPO - temporary biodiversity and building' which focuses on the concept of temporary conservation within urban areas. It aims at investigating the feasibility of a sustainable use of industrial and business areas by conceiving open and built-up sites as two complementary states of a spatio-temporal cycle, enabling both conservation and development.

Subprojects investigated strategies which enable plant and insect species survival in dynamic environments like urban brownfields (Schadek, 2006; Strauss & Biedermann, 2008) and described the development of such habitats through the course of succession with respect to vegetation structure and soil characteristics (Schadek et al., 2008). Furthermore, insight into the driving forces that shape insect communities of urban brownfields was gained (Strauss & Biedermann, 2006). The generality of the applied statistical modelling strategies to predict the occurrence of plant functional groups and insect species was also assessed (Schadek, 2006; Strauss & Biedermann, 2007).

Another emphasis lay on the feasibility of the TEMPO-concept with respect to architectural design of temporary buildings (Draeger, 2008). Likewise, urban planning,

socio-economic aspects and legal issues were assessed (Scheele et al., 2005).

My contribution to the project was (i) to built species distribution models applicable on the landscape scale, (ii) to develop a landscape model which uses these models to investigate scenarios of different brownfield turnover rates and spatial configuration for deriving recommendations for urban planning, (iii) apply the concept to a real planning area, and (iv) to analyse the role of succession on species survival in a dynamic landscape in more detail using a metapopulation approach.

1.5 Outline

In this thesis, first (chapter 2) I give a short introduction into the two modelling approaches namely species distribution models and metapopulation models. Second (chapter 3), an overview over the study area and data collection is given. Also, I outline some additional methods I used to manipulate the input data for statistical model building.

Chapter 4 investigates the species-environment relationship in urban brownfields. It describes the model building procedure for statistical species distribution models and names the the main driving factors of species occurrence. It also introduces the landscape model I developed to analyse scenarios of different brownfield turnover rates and proportions. Furthermore, this chapter gives some first recommendations for maintaining urban biodiversity by means of temporary conservation. This concept of temporary conservation I explore in more detail in chapter 5, where I use the landscape model to compare static vs. dynamic urban land use and identify possible management options. The application of the TEMPO-concept to a real landscape is given in chapter 6, which compares exemplary urban planning scenarios of different dynamics.

The next two chapters move from statistical regression models to dynamic approaches. In chapter 7, I describe the fieldwork I accomplished to collect data on grasshoppers to built incidence function models. I summarise the data, conclude that it is insufficient to be applied in a metapopulation approach and suggest some reasons for that incidence. In chapter 8 I investigate species fate in dynamic landscapes from a different point of view using a metapopulation simulation model. Here, I explore species persistence in a landscape which is characterised by both disturbance and succession with special emphasis on species position on the successional gradient.

The last chapter (chapter 9) synthesises the results on main driving factors of species occurrence and viability in dynamic, successional landscapes. It also gives some more insight into the characteristics of the species pool modelled by SDMs in this study. Finally, I draw conclusions about management options to maintain species diversity in dynamic landscapes with special respect to urban brownfield habitats.

Chapter 2

Modelling approaches

2.1 General remarks

In this thesis, I used ecological modelling to analyse the effects of spatio-temporal landscape configurations on species occurrence or persistence. To this end, I first employed a pattern oriented, statistical approach (species distribution models) based on extensive field data. By this means, I explored the main drivers that shape species occurrence in urban brownfield habitats and species reaction to certain management options. Second, I applied a dynamic metapopulation model for virtual species to investigate species survival in spatio-temporal dynamic landscapes. In both cases, habitat quality was an essential component of the model. In the first case, it described the species-environment relationship and thus determined predicted presence or absence. In the latter case, habitat quality, which was defined by successional age, controlled population extinction and colonisation probabilities.

I applied both modelling approaches to draw general conclusions about species reactions to landscape dynamics and derive management recommendations. Thus, the exact layout of the landscapes (which lots exactly were built-up and which ones were open) was no matter of interest here with exception of the exemplary planning study in chapter 6. For this reason, I employed repeated simulations within randomly generated land use configurations. Hence, even when using species distribution models, which result in species occurrence probabilities at certain spatial locations, I aggregated the results over the whole study area and over all replicate simulation runs. The same applies for the metapopulation approach: The landscape was newly randomly generated within certain constraints for each simulation run and the results aggregated for all replicates.

Detailed descriptions of the model building and formulation are given in the respective chapters (chapters 4, 5, and 8). Here, I only give a general introduction into the two modelling approaches.

2.2 Species distribution models

General concept

Species distribution models (SDMs) relate species occurrence or abundance to environmental predictor variables by means of regression techniques (Guisan & Zimmermann, 2000). Thus, they apply a pattern-based approach seeking a statistical species-habitat relationship.

SDMs can be used for two purposes, the first one being as explanatory models (Guisan et al., 2002). In this case, even though statistical regression does not reveal causal relationships, they can indicate the main driving factors of species distribution. Thus, SDMs are used to develop theory about the underlying processes and to identify species main susceptibilities. Second, SDMs are used to predict species occurrence probabilities under future conditions (e.g. altered climatic conditions (Broennimann & Guisan, 2008)) or at unsampled locations in conservation and environmental management (applications e.g. in Gibson et al., 2004; Wintle et al., 2005; Schröder et al., 2008). In the present study, I use SDMs for both identification of the main driving factors of species occurrence and predictions within different scenarios.

Limitations of SDMs and solutions

Empirical data of species occurrence and environmental conditions reflect usually only a snapshot in time. Static models based on such data intrinsically assume equilibrium between observed species response and the predictor variables (Guisan & Zimmermann, 2000). Additionally, statistical modelling approaches of species-habitat relationships lack the consideration of biotic interactions explicitly. However, the observed species distributions in the empirical data sets used to construct SDMs are already constraint to the realised niche by competition processes (Silvertown, 2004).

Using statistical SDMs under landscapes dynamics - whether caused by climatic changes, natural disturbances like flood or fire, or due to destruction of habitat by redevelopment of urban brownfield lots and abandonment at other locations like in this study - implicitly assumes an instantaneous incidence of a new equilibrium. However, due to limitations in dispersal ability species might not reach a location with fitting environmental conditions, resulting in on overestimation of species occurrence. Second, differences in dispersal abilities might yield altered community compositions leading to changes in biotic interactions and in turn in shifts of the realised niche. These shifts cannot be tracked by SDMs constructed on data of former environmental conditions.

An alternative approach to static, equilibrium restricted models are dynamic simulations, which can explicitly consider e.g. population dynamic processes, dispersal, and competition. However, such complex models rely on amounts of data that are hardly available for larger sets of species. Compared to that, data for parameterising SDMs of numerous species is rather of low-effort.

In this study, I included successional site age into the set of predictor variables, thus, on the one hand relaxing the equilibrium assumption and on the other hand partly accounting for species dispersal abilities (see also chapter 9.4). Furthermore, the predictors describing the landscape context (vegetation structure and successional site age around the sampling plots; see chapter 3) reflect both patch size and the current functional connectivity of the landscape (Radford & Bennett, 2004). Their effect on species occurrence gives a proxy for species dispersal ability, as a highly mobile species will be less influenced by low proportions of a certain landscape context parameter than a dispersal limited one.

2.3 Metapopulation models

General concept and variations

The first metapopulation models were originally developed for species inhabiting islands of similar size and isolation (Levins, 1969). A more relaxed definition, which also explicitly considers habitat patch size and location, conceives spatially separated local populations which are linked by limited exchange via dispersal as a metapopulation (Hanski & Thomas, 1994). Metapopulation dynamics are driven by the extinctions of local subpopulations resulting from population dynamic processes due to interactions, resource constraints, and disturbance and by (re-)colonisation events resulting from migration. Long-term persistence of the metapopulation is allowed for by an equilibrium between extinction and colonisation.

There are two different applications of metapopulation models. The first type investigates real populations using field data for parameterisation. Hence, these studies aim at gaining insight into the processes driving such populations and at analysing their reactions for instance to habitat destruction or changes in habitat configuration (e.g. Hokit et al., 2001; Wahlberg et al., 2002; Biedermann, 2004). On the other hand, there is a vast amount of theoretical metapopulation studies which try to find general rules of metapopulation survival (Keymer et al., 2000; Johst et al., 2002; Wimberly, 2006; Vuilleumier et al., 2007). Moreover, both model types contribute to building ecological theory. The complexity of model formulations ranges from simple occupancy models as used in this study (Johnson, 2000; Wilcox et al., 2006), over the description of population dynamics (Boughton & Malvadkar, 2002), and stage based matrix models (Bossuyt & Honnay, 2006), to individual based ones (Topping et al., 2003).

Here (chapter 8), I used a theoretical metapopulation model, to simulate patch occupancy (occupied or unoccupied) in a dynamic landscape subject to disturbance and succession. I chose to model species incidence rather than population dynamics to keep the approach comparable to the SDMs used in the other chapters, which predict species presence or absence as well. I also collected data (chapter 7) for parameterisation of an empirical incidence function model.

Limitations of patch occupancy models and performance

Like SDMs, metapopulation models have several limitations. The fundamental one is the underlying assumption of spatially separated subpopulations. Many empirical studies proved the existence of metapopulations e.g. in grasshoppers (Appelt & Poethke, 1997; Carlsson & Kindvall, 2001), froghoppers (Biedermann, 2000), spiders (Bonte et al., 2003; Maes & Bonte, 2006), small mammals (Franken & Hik, 2004), and epiphytes (Snäll et al., 2003; Löbel et al., 2006). However, not all species living in patchy habitats necessarily form metapopulations (Driscoll, 2008; see also chapter 7). For instance, species with good dispersal abilities might be much more limited by the amount of suitable habitat than by isolation (Wood & Pullin, 2002).

Occupancy models ignore local population dynamics as they assume that local extinctions and colonisations are slow compared to demographic processes (Hanski, 1999; Keeling, 2002). Thus, a patch's population size is assumed to reach a value near carrying capacity instantaneous after colonisation. Moreover, varieties among individuals are not taken into account. Nevertheless, despite these broad simplifications, occupancy models perform comparably well to more detailed metapopulation models: Kindvall (2000) compared an incidence function model, a logistic regression model and a demographic model for a bush cricket. Turnover and occupancy were properly predicted by all three models. Likewise, Hokit et al. (2001) tested an incidence function model and a stage-based matrix metapopulation model against field occupancy data of the Florida scrub lizard. He found comparably satisfactory prediction accuracies. The spatially implicit Levin's model, which is even a more simplified version of the real world than stochastic patch occupancy models, proved to be accurate and robust when comparing it to an individual based model (Keeling, 2002).

Hence, although the underlying assumptions and simplifications should be kept in mind, metapopulation models based on patch occupancies are a valuable and widespread tool in conservation management as well as in theoretical ecology. Their predictive power can be remarkably enhanced by adding some complexity by integration of habitat quality measures (Dennis & Eales, 1997; Fleishman et al., 2002; Franken & Hik, 2004; Schooley & Branch, 2007).

Chapter 3

Studied species groups, study area, sampling design, and data preparation

All field work for the species distribution models (chapters 4, 5, and 6) was accomplished by Ute Schadek (plants, soil parameters) and Barbara Strauss (insects, vegetation structure and types). Here I give a short summary about the study area and the sampling design, on which more details can be found at Schadek (2006) and Strauss (2007), and describe the data preparation I carried out.

3.1 Studied species groups

This study focuses on vascular plants, leafhoppers, grasshoppers, and bush crickets. Most species depend directly or indirectly on the presence of vegetation for e.g. food, shelter, or micro-habitat provision. Furthermore, vegetation provides ecosystem services like air filtering, micro-climatic and rainwater regulation, noise reduction as well as social and cultural values, which are particularly important in urban areas (Bolund & Hunhammar, 1999).

Leafhoppers (see Biedermann et al. (2005) and references therein) suck plant assimilates or xylem sap contents. In doing so, they have considerable impact on plants and thus also on the competitive balance between plant species and on their community composition. They are prey of birds, spiders, ants, and other predator groups. Due to their short generation times, they react quickly to habitat changes.

Grasshoppers and bush crickets (see Hein et al. (2007) and references therein) are indicators of structural diversity as they depend on different vegetation structure types during their life cycle. Therefore, their habitat requirements might include those of a variety of other species. Hereafter, grasshoppers and bush crickets are referred to as 'grasshoppers'.

3.2 Study sites

The study area was located in the city of Bremen in north-west Germany. This city covers about 325 km² and has a population of approx. 550,000.

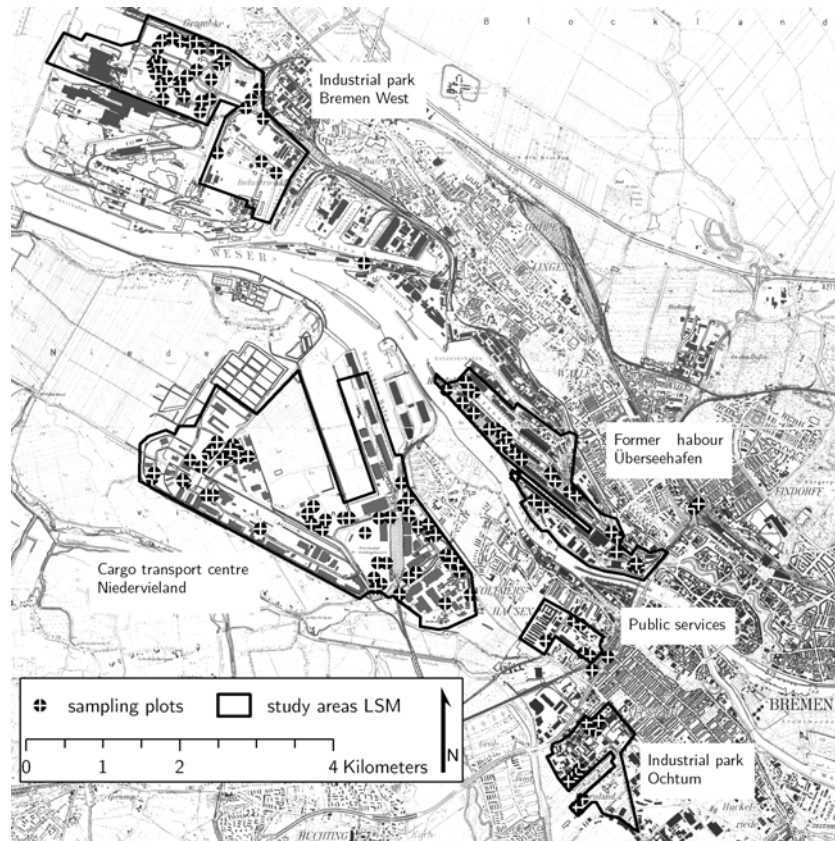


Figure 3.1: Sampling plots for species distribution models in Bremen. The landscape model (LSM) was applied to all marked study areas in chapter 4 and only to the cargo transport centre Niedervieland in chapter 5; the grasshopper sampling patches of chapter 7 are also located within Niedervieland.

Sampling plots to build SDMs were restricted to brownfield sites, consisting of previously developed land, abandoned railroads, and vacant areas within industrial and business centres (figure 3.1). The vegetation of these sites comprised of different successional stages ranging from open, bare soil to pre-forest vegetation (figure 1.1). I used data on 133 sampling plots for building SDMs. These plots had been chosen in a random stratified way (Guisan & Zimmermann, 2000) along three gradients: site age, site size and soil moisture.

3.3 Dependent variables

At the plots presence/absence of all vascular plant species within a quadrat of 4 m × 4 m was recorded in April for the early flowering species and in June for the summer species in 2003.

Grasshoppers (Orthoptera) and leafhoppers (Hemiptera: Auchenorrhyncha) were each sampled within a quadrat of 15 m × 15 m. To this end, diurnal grasshoppers were recorded by acoustic monitoring (Bellmann, 1993) in late July to early August in 2003. Additionally, the blue winged grasshopper *Oedipoda caerulea* was detected by searching the sampling plots in random walks. Leafhoppers were sampled by sweepnet sampling in four courses from early June to early September 2003. The catches were killed with ethyl acetate and determined to species level (Biedermann & Niedringhaus, 2004).

Only those plant and insect species whose prevalence (proportion of occupied plots) lay between 10 % and 90 % entered the model building procedure.

3.4 Explanatory variables

At the plots, soil nutrients status (P, K, and cation exchange capacity), parameters characterising the soil water regime, pH, and calcium carbonate content were measured. Site age, as time since initiation of succession, was derived from a time series of aerial photographs. A table of all explanatory variables is given in the appendix (table A).

Basing on a map of vegetation types, landscape context variables at different spatial scales were calculated. To this end, I grouped vegetation types into 'pre-forest/forest' and 'grassy or herbaceous vegetation'. The latter group was subdivided into sparse (less than 50 % cover) or dense, and low (less than approx. 30 cm in height) or high vegetation. For these vegetation types, I calculated landscape context variables within a GIS as the proportions of each vegetation group within different radii around every plot (25, 50, 75, and 100 m). They were used for insect distribution models as independent variables.

A temporal landscape context parameter in both plant and insect models was successional site age, which was divided into nine classes (0-4, 0-6, 0-8, 0-11, 6-11, 10-20, 15-25, 25-30, and > 25 years) and calculated in radii of 25, 50, 100, and 200 m, respectively, around each plot.

3.5 Data manipulation for insect SDMs

As grasshoppers and leafhoppers are highly influenced by vegetation structure and host plants at the plot as well as by vegetation types in the landscape context (Strauss & Biedermann, 2006), these parameters should enter the insect species distribution models. However, they require extensive fieldwork and are not at hand if unsampled scenarios are to be analysed. Thus, I used the information provided by plant SDMs to derive some surrogate variables to predict insect occurrences. Ellenberg indicator values for pH, N,

moisture, and light (Ellenberg, 1992) were not directly calculated from the plant relevé data but by multiplying the predicted plant occurrence probability by the according indicator values.

Plot scale: PLS dimension reduction

To account for vegetation structure and host plants at the sampling plots, I used the plant occurrence probabilities calculated by SDMs. I carried out a dimension reduction by means of partial least squares (PLS) (Guisan & Zimmermann, 2000; Boulesteix, 2004), to prevent collinearity and reduce the number of predictor variables (i.e. not to use every single plant occurrence probability as a single explanatory variable). The transformed variables were subsequently treated as the other parameters in the model building of the insect SDMs.

PLS regression is used to handle large data sets of numerous explanatory variables like in the field of near-infrared (NIR) spectroscopy or molecular biological microarray data analysis. A detailed description of the PLS method can be found at Boulesteix (2004). I used the R package `pls.genomics` which includes the SIMPLS algorithm by de Jong (1993). PLS regression is a supervised dimension reduction method. It combines the original predictors (here: the predicted plant occurrence probabilities at the plots, X) by a linear transformation to new components (Z) of lower dimension than X . The PLS method seeks the transformation matrix A to calculate

$$Z = A \cdot X. \quad (3.1)$$

To derive A linear transformations of X are computed which are mutually uncorrelated and have maximum covariance to the dependent variable (the insect occurrences at the plots). I determined the dimension of Z (i.e. the number of PLS components for the following insect SDM building) using a bootstrap algorithm. This algorithm computed the number of components with the lowest mean square root error in 100 bootstrap repetitions. It resulted for all insect species in one or two PLS variables. The transformed PLS variables entered the insect SDMs linearly (without a quadratic term) as they give the linear relationship between plant occurrence probabilities and insect occurrence.

A graphical example for three fictive plant species and one insect species is given in figure 3.2. The occurrence probabilities of the plant species are summarised to one PLS-component, which is subsequently used in a sigmoidal, univariate logistic regression of insect occurrence.

Landscape scale: vegetation type

Assignment of plant species to vegetation types using statistical fidelity

Statistical fidelity measures are a means of identifying indicator species for vegetation units in the field of vegetation classification. They describe the concentration of species

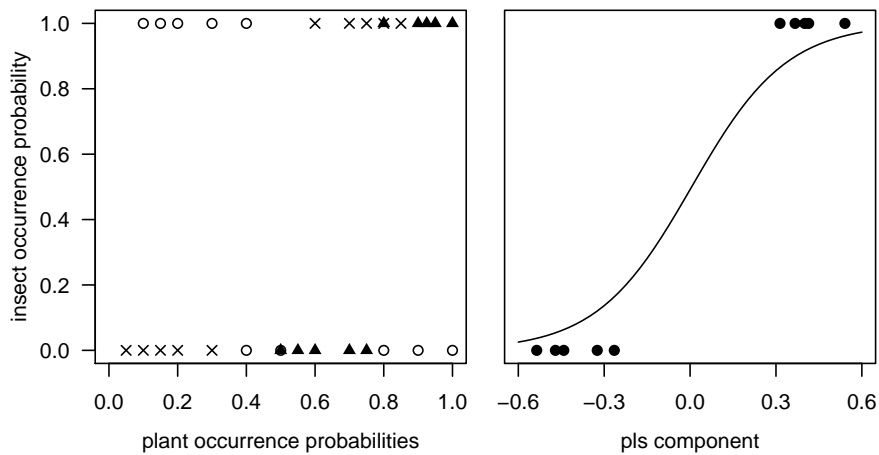


Figure 3.2: Example for dimension reduction using PLS. The left graph shows the occurrence of one insect species in relation to the predicted occurrence probabilities of three plant species (different symbols). The right one shows insect occurrence on relation to the resulting PLS component (dots) and a logistic regression (line).

occurrence in vegetation units (Chytrý et al., 2002).

I applied such a fidelity measure to assign the plant species to the vegetation types used as landscape context descriptors in the insect models. Each plant species a SDMs had been obtained for was tested. I used the program JUICE (Tichy & Holt, 2006) to identify the vegetation types the plants were faithful to (sparse, dense or pre-forest/forest and low, high or pre-forest/forest, respectively). If the absolute value of the fidelity measure (u , hypergeometric, continuity corrected (Chytrý et al., 2002)) was larger than 1.96 (equivalent to $p \leq 0.05$) the plant species was assigned to the vegetation type tested. The resulting assignment was revised for plausibility (Schadek, pers. comm.) and yielded the classification given in table 3.1.

Table 3.1: Assignment of plant species to vegetation types by statistical fidelity. Occurrence probabilities of these plant species (calculated with the according SDM) were summed and used as partition parameters in classification trees.

Species	pre-forest				
	/ forest	sparse	dense	low	high
<i>Arrhenatherum elatius</i>			x		
<i>Artemisia vulgaris</i>			x		
<i>Betula pendula</i>	x				
<i>Bromus sterilis</i>				x	
<i>Cerastium holosteoides</i>			x		
<i>Coryza canadensis</i>		x			
<i>Corynephorus canescens</i>		x		x	
<i>Dactylis glomerata</i>			x		
<i>Festuca rubra</i>			x		x
<i>Holcus lanatus</i>			x		x
<i>Plantago lanceolata</i>	x				
<i>Plantago major</i>			x		
<i>Poa annua</i>				x	
<i>Poa compressa</i>				x	
<i>Poa pratensis</i>		x			
<i>Poa trivialis</i>			x		
<i>Senecio inaequidens</i>				x	
<i>Sisymbrium altissimum</i>		x			
<i>Taraxacum officinale</i>					
<i>Trifolium repens</i>		x		x	
<i>Vicia angustifolia</i>			x		
<i>Vicia hirsuta</i>			x		x
<i>Vulpia myuros</i>		x			

Prediction of vegetation types using classification trees

The occurrence probabilities of all plant species assigned to a vegetation type were summed. I used the R function `rpart` (Venables & Ripley, 1999) to calculate classification trees of the landscape context vegetation types. This linear statistical method partitions the space based on independent explanatory variables to predict the class of a dependent variable. Here, the mapped vegetation type at the sampling plots are the dependent variables. The sums of the predicted plant occurrence probabilities assigned to a vegetation type served as explanatory variables. Within the tree building, I used a ten-fold cross-validation and pruned the trees to the leafs with the lowest cross-validation error. This procedure resulted in two classification trees (figure 3.3): one to distinguish pre-forest/forest vegetation from herbaceous and grassy low or high vegetation; and another one to distinguish pre-forest/forest vegetation from herbaceous and grassy scarce or dense vegetation.

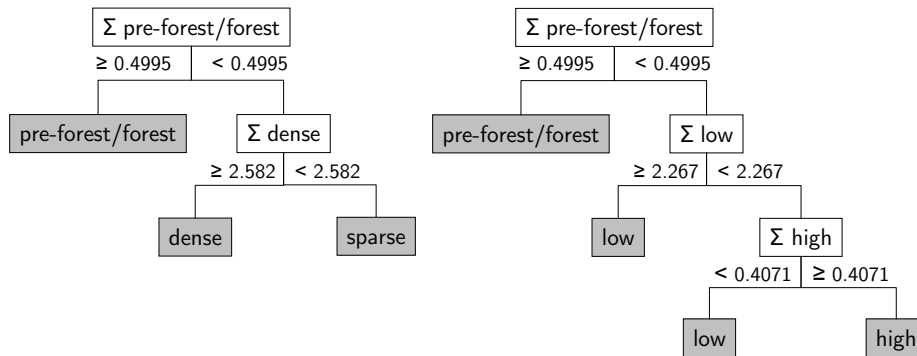


Figure 3.3: Classification trees to distinguish sparse, dense or pre-forest/forest vegetation from each other (left) and low, high or pre-forest/forest vegetation (right). The grey rectangles indicate the leaves of the classification trees, while the white ones indicate the partition parameter.

Chapter 4

Modelling multi-species response to landscape dynamics: Mosaic cycles support urban biodiversity

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Abstract

The importance of the spatial as well as the temporal structure of habitat patches for urban bio-diversity has been recognised, but rarely quantified. In dynamic environments the rate of habitat destruction and recreation (i.e. the landscape turnover rate), the minimum amount of potential habitat, its spatial configuration as well as the environmental conditions determining habitat quality are crucial factors for species occurrence. We analysed species responses to environmental parameters and to the spatio-temporal configuration of urban brownfield habitats in a multi-species approach (37 plant and 43 insect species). Species presence/absence data and soil parameters, site age, vegetation structure and landscape context were recorded by random stratified sampling at 133 study plots in industrial areas in the city of Bremen (Germany). Based on the field data, we predicted species occurrences by species distribution models using a multi-model inference approach. Predicted species communities were driven by successional age both at the scale of a single building lot and at the landscape scale. Minimum average succession time of brownfield habitats required to support all and especially regionally rare species depended on the proportion of available open space; the larger the potential habitat area the faster the acceptable turnover. Most plant, grasshopper, and leafhopper species modelled could be maintained at an intermediate turnover rate (mean age of 10 to 15 years) and a proportion of open sites of at least 40 %. Our modelling approach provides the opportunity of inferring optimal spatio-temporal land-scape configurations for urban conservation management from patch scale species-environment relationships. The results indicate that urban planning should incorporate land use dynamics into the management of urban biodiversity.

Chapter 4: Modelling multi-species response to landscape dynamics

keywords: dynamic landscape, species distribution model, habitat model, urban brown-fields, model averaging, landscape context, conservation planning, succession

4.1 Introduction

In dynamic landscapes, species are facing habitats of changing quality and location. Landscape dynamics can arise from land use, succession, or natural disturbances like wind, fire or flood. Often, habitat destruction for one species allows for habitat creation for another.

An example of dynamic ecosystems are urban brownfields (derelict land). Brownfields represent artificial habitats which are fundamentally influenced by humans (Gibson, 1998) and comprise previously developed land, abandoned railway tracks, landfills, and industrial dumps. They often support a diverse flora and fauna (Angold et al., 2006; Godefroid & Koedam, 2007; Muratet et al., 2007), including rare species (Eyre et al., 2003). In contrast to other urban green spaces like parks or gardens, brownfields form dynamic habitats in space and in time: Landscape turnover causes spatial shifts of habitats due to redevelopment and abandonment while succession causes continuous temporal changes in habitat quality (Gibson, 1998; Wood & Pullin, 2002). These two processes result in a spatio-temporal mosaic of patches of different successional stages, and built-up areas. Hence, brownfields form a special case of mosaic cycles, which have been described for natural and human-influenced ecosystems (Kleyer et al., 2007).

While not accounting for habitat patch dynamics in conservation management might cause overoptimistic estimates of population persistence (Akçakaya et al., 2004), it can also result in an underestimation of habitat connectivity (Wimberly, 2006), depending on species' dispersal abilities. Thus, a critical issue in maintaining urban biodiversity in such a dynamic environment is the landscape turnover rate, which describes the rate of habitat destruction and redevelopment (Roy et al., 2004). Moreover, the minimum amount of potential habitat, its spatial configuration as well as the environmental conditions determining habitat quality are crucial factors (Garden et al., 2006).

On the one hand, the effect of the landscape dynamics on species occurrence and (meta-) population viability has been analysed in several theoretical multi-species studies (e.g. Keymer et al., 2000; Roy et al., 2004). Furthermore, some detailed empirical single species studies consider habitat creation in space and time (Snäll et al., 2005) or explicitly account for population dynamics at patch scale (Akçakaya et al., 2004). However, such process-based models can hardly be parameterised for many species in biodiversity analyses and are thus limited in the number of modelled species and in their generality (Jeltsch et al., 2008). On the other hand, in empirical studies species' responses to the environment are mostly analysed at the patch scale, while habitat turnover takes place at the landscape scale. Spatially explicit statistical modelling offers the opportunity to both working with a manageable amount of data and extrapolating species-environment relationships from patch scale - focus of empirical studies - to landscape scale - focus of planning and management issues (Corsi et al., 2000).

We use species distribution models (SDMs; also called habitat suitability models or habitat models) to analyse the response of plant and insect biodiversity to spatio-temporal changes in habitat quality. SDMs are statistical models which relate species incidence

or abundance to environmental predictors, and have become an important and frequently applied tool in ecology as well as in conservation biology in recent years (Guisan & Thuiller, 2005).

To reflect species' varying habitat requirements and susceptibilities, a multi-species approach is needed (Garden et al., 2006). Following the recommendations of Olden et al. (2006), we predict species composition of plant and insect communities as the sum of individual species occupancies, which are modelled by single species distribution models. Although SDMs are widely used on different species groups, only a few attempts have been made so far to model community composition in this way (Olden, 2003; Pepler-Lisbach & Schröder, 2004).

We developed a modelling shell which integrates the generation of urban land use scenarios, the prediction of numerous species occurrences on the landscape scale using SDMs, and the evaluation of the results from the conservational perspective considering species richness and regional rarity. To represent the complex links between vegetation and phytophagous insects, we chose plants, leafhoppers and grasshoppers (and one bush-cricket (*Metrioptera roeseli*), hereafter referred to as grasshopper) as study species. Altogether, the response of 37 plant species and 43 insect species to abiotic and biotic conditions at the landscape scale were analysed. We defined spatio-temporal dynamics by (1) the landscape turnover (i.e. the rate at which brownfield habitat is destroyed by redevelopment and new habitat is created by abandonment) and (2) temporal changes in habitat quality due to succession.

We apply the modelling approach to industrial and business areas in the city of Bremen (Germany) to assess the following questions:

- How important is the spatio-temporal configuration vs. other environmental variables for species occurrence?
- How relevant is the proportion of brownfields within urban industrial areas (i.e. the proportion of potential habitat) from a nature conservation point of view, and what minimum proportion is required?
- Is there an optimal turnover rate of brownfields and built-up areas to maintain as many species as possible, especially rare ones?

4.2 Methods

Approach

In this study, we analyse each single species' response on the landscape scale to different proportions of brownfield area and different landscape turnover rates. For this purpose, we generate repetitions of artificial urban planning situations for each scenario of brownfield proportion and turnover rate and aggregate the results for each scenario.

Thus, modelling results reflect single species' and biodiversity's response to the spatial-temporal landscape configuration.

Modelling shell

Our modelling shell is based on a grid-based geographic information system, which divides the study area (see below) into 63000 raster cells of size 12.5 m by 12.5 m. The shell consists of three modules. In the scenario creation module the proportion of potential habitat patches (i.e. brownfield proportion) and the age distribution of these patches (resulting from different paces of abandonment and redevelopment, i.e. different turnover rates) are set. The location of potential habitat is assigned randomly. Site age is drawn randomly for every lot from an exponential distribution with mean value $1/\lambda$, representing a certain average turnover rate.

The modelling module calculates plant and insect species occurrence for every raster cell in response to the environmental variables using SDMs (species distribution models). Since SDMs are static models which relate species distribution to the present environment (Guisan & Zimmermann, 2000), their outcome is independent of past states making time series simulation unnecessary. Succession as well as landscape turnover change the spatio-temporal landscape configuration. However, this altered configuration is identical to that of another replicate simulation run if the overall ratio of brownfield to built-up sites and the turnover rate remain constant over time.

Within the evaluation module, modelling results are rated from the nature conservation perspective. First, species richness as the total number of occurring plant and insect species in the study area is calculated. To ignore unviably small populations, a species must occur on at least 0.1 % of the raster cells. Second, an average rarity value over all brownfield cells is calculated. To this end, a regional rarity value ranging from 1 (very common) to 5 (very rare) was assigned to every species (see figure 4.5) on the basis of distribution atlases (plants and grasshoppers (Hochkirch & Klugkist, 1998; FloraWeb, 2007)) or, in case of leafhoppers, expert knowledge (Robert Biedermann). For all species, the number of occupied cells is multiplied by the species' rarity value. The result is summed over all species, divided by the total number of brownfield cells, and normalised by dividing it by the sum of rarity values over all species. Third, the response of every single species to the spatio-temporal configuration is calculated as the proportion of occupied brownfield cells.

Study area and sampling design

The study area is located in the city of Bremen in north-west Germany. Sampling plots were restricted to brownfield sites, consisting of previously developed land, abandoned railroads, and vacant areas within industrial and logistics centres. Soil at the sampling plots comprised mainly of sandy landfills. Plots were chosen in a random stratified way along three gradients: site age, site size and soil moisture. At 133 plots, pres-

ence/absence of all vascular plant species within an area of 16 m², and of leafhoppers and grasshoppers within an area of 225 m² was sampled. Leafhoppers were recorded by sweepnet sampling and grasshoppers by acoustic monitoring and visual inspection (*Oedipoda caerulescens*). At the plots, soil water budget parameters, soil nutrients status (P, K, and cation exchange capacity), pH, and calcium carbonate content were measured (table 4.1). A detailed description of sampling methods is given in Schadek et al. (2008) and Strauss & Biedermann (2006). Site age, as time since initiation of succession, was derived from a time series of aerial photographs. All samples were taken in 2003.

To implicitly account for structural connectivity (the physical arrangement of the landscape) as well as functional connectivity (i.e. individual species behavioural response to the landscape) (Radford & Bennett, 2004), we included landscape context variables at different spatial scales into the set of predictors in the SDMs. Vegetation type around each plot was mapped and grouped into 'shrubs and trees' and 'grassy or herbaceous vegetation' for the insect models. The latter group was subdivided into sparse (less than 50 % cover) or dense, and low (less than approx. 30 cm in height) or high vegetation. A temporal landscape context parameter in both plant and insect models was successional site age, which was divided into nine classes (0–4, 0–6, 0–8, 0–11, 6–11, 10–20, 15–25, 25–30, and > 25 years). All landscape context variables were calculated within a GIS as the proportions of each vegetation group and age class, respectively, within different radii around every plot (25, 50, 75, 100, and 200 m).

Table 4.1: Predictor variables for the species distribution models, their scale, and aggregation to groups used in figure 4.1

predictor variables	scale	predictor group
coefficient of permeability	plot	soil
air porosity	plot	soil
field capacity	plot	soil
plant available water at field capacity	plot	soil
plant available water over the year	plot	soil
effective cation exchange capacity	plot	soil
pH (in CaCO ₃)	plot	soil
plant available phosphorus (P)	plot	soil
plant available potassium (K)	plot	soil
calcium carbonate (CaCO ₃)	plot	soil
brick rubble	plot	soil
site age	plot	site age
current disturbance	plot	site age
vegetation structure (PLS regression)	plot	vegetation
site age (9 classes)	landscape	landscape context site age
vegetation type (5 classes, regression trees)	landscape	landscape context vegetation type
brownfield ratio	landscape	landscape context brownfield ratio

Species distribution models

Most approaches of building SDMs aim to find one 'best' model (Guisan & Zimmermann, 2000). To overcome the problems arising from variable selection, and the risk of over-fitting the model (Rushton et al., 2004), Burnham & Anderson (2002) suggest a method of multi-model inference. This model averaging approach has successfully been used in ecology (Gibson et al., 2004). The weights obtained in the averaging process can be used to assess the relative importance of the environmental variables (Burnham & Anderson, 2002).

We estimated logistic regression models (GLMs with logistic link) from species presence/absence data using the function 'logistf' for R (Heinze & Ploner, 2004) for all species with a prevalence between 10 % and 90 %. A detailed description of the model building is given in the appendix 4.6. Logistic regression models predict occurrence probabilities. To distinguish between presence and absence of a species, we chose the threshold value which maximises Cohen's kappa (Fielding & Bell, 1997). To evaluate model performance, we used as measures of discrimination the threshold independent AUC as well as threshold-dependent Cohen's kappa, and CCR (overall correct classification rate); R_N^2 was used as a measure of model calibration (Hosmer & Lemeshow, 2000; Manel et al., 2001).

As an internal validation of each SDM we applied a bootstrapping procedure since there was no independent data set available. The bootstrap method estimates the optimism of model performance measures, which arises when these measures are calculated from the same data set as used for model building (Harrell, 2001). We estimated corrected values AUC_{cor} and R_{Ncor}^2 for the averaged model of each species (described in more detail in the appendix 4.6).

Vegetation in the landscape context and vegetation structure as well as host plants at the plot are important predictors for insect occurrence (Strauss & Biedermann, 2006). To transfer insect distribution models from plot to landscape scale, these parameters must be supplied at the landscape scale. We used information on plant species occurrence probabilities provided by the plant distribution models to determine these vegetation parameters. First, we analysed the statistical fidelity of every modelled plant species to the vegetation types (see section sampling design) (Chytrý et al., 2002). The occurrence probabilities of all plant species assigned by the fidelity measure to a vegetation type were summed up. Classification trees (Venables & Ripley, 1999) were built using these aggregated variables to predict the vegetation types on the landscape scale. Second, to account for vegetation structure and host plants for insects, we merged plant occurrence probabilities to one or two new predictors by partial least squares (PLS) regression (Boulesteix, 2004). These new variables were treated as the other parameters in the insect model building.

Community models

Species composition models of the plant and insect communities, respectively, were derived as additive models based upon the presence/absence predictions of the single-species models (Ferrier et al., 2002a). Performance of the community model (i.e. agreement between observed and predicted communities per plot) was quantified by Cohen's kappa, sensitivity (correctly predicted species presences), specificity (correctly predicted absences), and CCR (Fielding & Bell, 1997). We used a randomisation test with 10 000 repetitions to calculate performance (Strauss & Biedermann, 2006). The community model was considered to achieve predictions significantly better than chance at the plot tested, if less than 5 % of the randomised trials performed better than the model prediction.

The relative importance of predictors for the plant and insect communities was assessed by summing, for each group of variables (soil, site age or vegetation at the plot; site age, vegetation type or brownfield ratio in the landscape context; table 4.1), the AIC_c -weights of all models that contained the variable as demonstrated by Strauss & Biedermann (2006).

Modelling scenarios

Using the modelling shell, brownfield proportion was varied between 10 % and 90 % to analyse species response to available habitat area. The impact of the pace of brownfield turnover was assessed by setting mean site age of brownfields to 3, 6, 10, 15, and 20 years, respectively. The maximum age of a site was restricted to 50 years, as this was the maximum value found in the field data set. Soil properties at the study area could not be spatially predicted in this study. But as artificial landfills are the main soil type at the study sites, soil properties do not vary much between sites. Nutrient and soil water parameters were assigned to the brownfield sites according to the estimated most similar sampling plot. We applied the modelling shell in 45 scenarios (every combination of brownfield proportion and age distribution) in 500 replicates per setting to industrial areas in Bremen with a total area of about 9850 ha.

4.3 Results

Single species models

For 88 % of the insect species with prevalence ≤ 10 % distribution models could be constructed, whereas only about 55 % of the plant species, which passed the prevalence threshold, could be modelled (appendix, tables B, C, and D). Model performance according to R_{Ncor}^2 ranged from > 0.2 to > 0.41 , which is good for logistic regression models (table 4.2). Most of the SDMs reached AUC_{cor} values exceeding 0.8, some of them exceeded 0.9, which is regarded as outstanding (Hosmer & Lemeshow, 2000).

A lower prevalence resulted in better model performance in terms of AUC_{cor} and CCR (Spearman's ρ -0.69, -0.71 and -0.51, -0.65 for plants and insects, respectively), but not in terms of $R^2_{N_{cor}}$ (Spearman's $\rho < |0.5|$). However, neither a relationship was found between the local rarity value of a species (used in the evaluation of the scenarios) and its prevalence nor with its model performance (Spearman's $\rho < |0.5|$).

Table 4.2: Overview of habitat model performance. AUC_{cor} and $R^2_{N_{cor}}$: corrected by bootstrap validation; kappa: Cohen's kappa; CCR: correct classification rate; q 25, q 75: 25 % and 75 % percentile.

		plants	leafhoppers	grasshoppers
number of modelled species (prevalence > 10 %)		38 (60)	36 (41)	7 (8)
$R^2_{N_{cor}}$	median	0.28	0.37	0.35
	q 25	0.23	0.27	0.26
	q 75	0.38	0.41	0.40
AUC_{cor}	median	0.82	0.84	0.86
	q 25	0.78	0.81	0.82
	q 75	0.87	0.87	0.88
kappa	median	0.51	0.58	0.56
	q 25	0.45	0.50	0.54
	q 75	0.57	0.64	0.60
CCR	median	0.85	0.87	0.85
	q 25	0.76	0.80	0.83
	q 75	0.89	0.92	0.90

Community models

Performance of the community models was of satisfactory quality (table 4.3). Concerning sensitivity, CCR, and Cohen's kappa, species composition predictions were better than chance predictions for the majority of plots. Due to the rather low prevalence of several species, chance predictions for specificity (i.e. correct absences) were high, resulting in low proportions of plots for which the community models exceeded these high values (only 26 % and 47 % for plants and insects, respectively).

The most important predictors for the plant community model were soil parameters, which accounted for about 50 % of the predictor weights (figure 4.1, grey boxes). At least one predictor of each plant SDM was a soil parameter. Site age at the plot and in the landscape context both accounted for about 20 % of the predictor weights and were involved in approx. 80 % and 70 % of the models, respectively.

As opposed to that, the leafhopper and grasshopper community was mainly driven by vegetation at the plot, vegetation type and site age in the landscape context, which made up about 25 % of the predictor weights and were involved in about 90 % of the species

models, each. (figure 4.1, white boxes). Site age at the plot and soil parameters played only a minor role (about 11 and 15 %, respectively), but were involved in about 60 % and 80 % of the habitat models.

Table 4.3: Overview of community model performance. sens: sensitivity; spec: specificity; CCR: correct classification rate; kappa: Cohen’s kappa; q 25, q 75: 25 % and 75 % percentile; % sig: percentage of plots with significantly better than chance species composition predictions.

	plant community				insect community			
	sens	spec	CCR	kappa	sens	spec	CCR	kappa
median	0.70	0.89	0.84	0.54	0.79	0.90	0.86	0.66
q 25	0.57	0.83	0.79	0.40	0.70	0.82	0.81	0.53
q 75	0.86	0.93	0.89	0.67	0.85	0.94	0.91	0.72
% sig	63	26	65	72	71	47	89	89

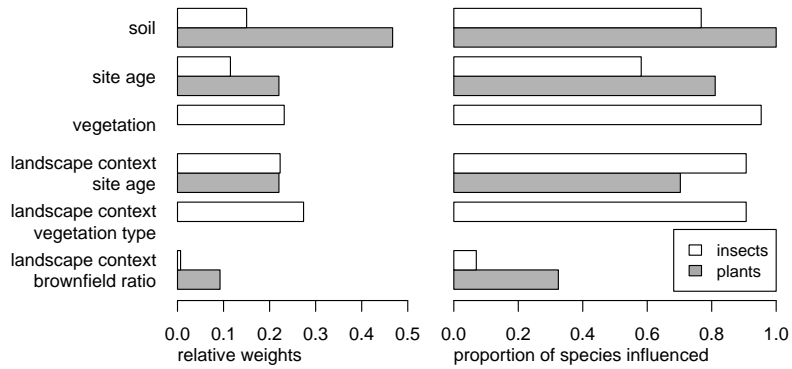


Figure 4.1: Relative weights of environmental factor group in the community model (left) and ratio of species influenced by at least one factor of the group (right). Plants are indicated by grey, insects by white boxes.

Landscape modelling scenarios

For each brownfield turnover rate (mean site age of 3, 6, 10, 15, and 20 years, respectively), the variance in the results over the 500 replicates per setting decreased with increasing brownfield proportion (figures 4.2, 4.3, and 4.4). The higher the proportion of brownfield area, the smaller was the mean age of brownfield sites (i.e. the faster the turnover) above which co-occurrence of all plant species was predicted in nearly every replicate simulation run (figure 4.2). Insects reacted similarly, but additionally, at slow turnover (mean age of 20 years), occurrence of all species together was predicted only for very large proportions of brownfield area.

The average plant rarity value over all brownfield cells increased slightly with increasing brownfield proportion but remained constant for insects (figure 4.3). With increasing turnover average plant rarity value increased, whereas the insect rarity value decreased. A linear decrease with decreasing average site age could be found for plants, while the insect rarity value reached its maximum at a mean habitat age of 15 years.

Diverse reactions to the spatio-temporal structure were found on the single-species level (figure 4.4). *Senecio inaequidens*, for instance, benefited from increasing brownfield proportion and its occurrence decreased with increasing mean site age. As opposed to this, increasing brownfield proportion had a negative effect and turnover had no effect on *Cerastium holosteoides*. *Cicadella viridis* showed no reaction to brownfield area, but a maximum occurrence at medium mean site ages. For some species (e.g. *Aphrodes makarovi*), increasing brownfield proportion intensified the effect of turnover rate on the occurrence (causing steeper slopes), while higher site age itself had a positive impact.

Species can be grouped into those reacting positively, or reacting negatively to fast site turnover, or being indifferent to mean site age (figure 4.5). Some benefited strongly from fast turnover, their predicted incidences were highest at a low mean site age (e.g. *S. inaequidens*). On the other hand, there was a group of species with maximum occurrence when site turnover was low, resulting in many older sites (*A. makarovi*). A third group favoured intermediate turnover rates (e.g. *C. viridis* or *Poa trivialis* and *Rumex acetosella*). Several species were not or only marginally influenced by mean site age with constant occurrences over all scenarios (like *Poa pratensis*).

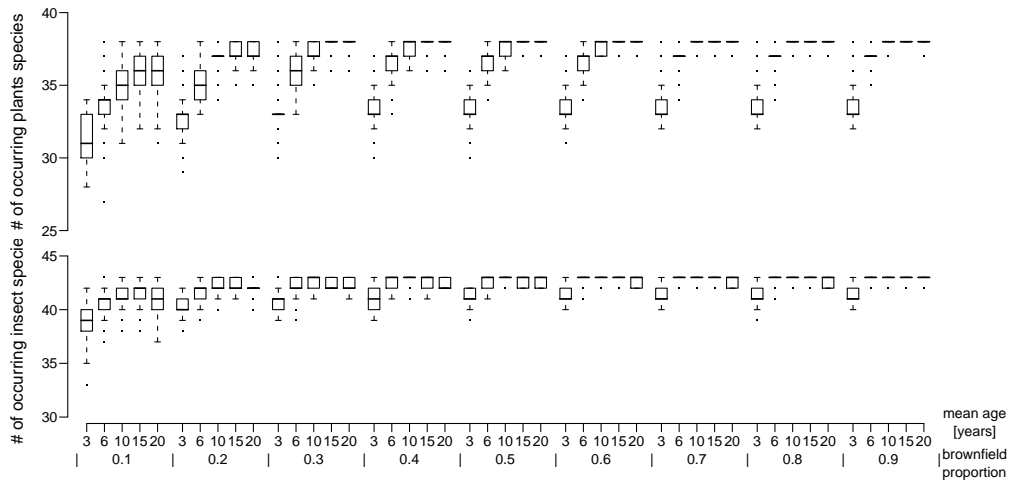


Figure 4.2: Biodiversity of the plant and insect community as the total number of occurring species in the study area. The upper x-axis gives the mean brownfield age, the lower the brownfield proportion in relation to the whole study area.

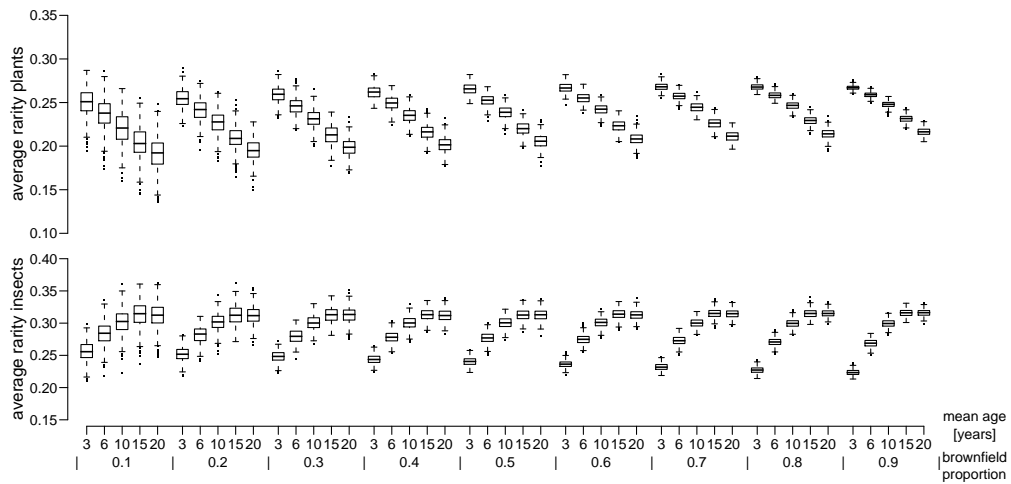


Figure 4.3: Rarity of the plant and insect community, averaged over all brownfield cells. x-axis as in figure 4.2.

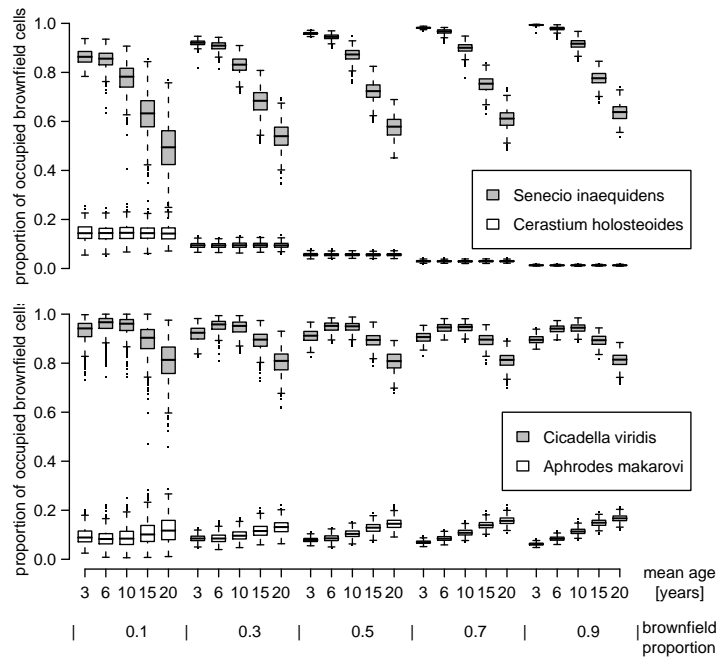


Figure 4.4: Single species reaction to various brownfield turnover rates for two example plant species.

4.4 Discussion

Cumulated species distribution models to assess urban biodiversity

Species distribution models are widely used in conservation biology for a variety of species and taxa (Ferrier et al., 2002b; Grand et al., 2004; Wintle et al., 2005). All those applications use predictive modelling to analyse realised niches or to identify the spatial location of habitat of single species. An important contribution from this study is that within the limitations of static statistical modelling these models can be used to predict biodiversity for specific spatio- temporal configurations of habitat. Hence, the focus lay on the mean response of species and communities on the landscape scale, as opposed to predicting the exact spatial distribution of a single species or a single patch's contribution to biodiversity.

Species with very low prevalence, which may be endangered ones of special conservation interest, had to be excluded from the analysis as data was insufficient for model building. Prediction of diversity indices in response to environmental factors, regardless of species identity might seem attractive to overcome this problem. However, such an approach neglects the fact that species numbers can stay quite constant over the course

of succession or be equal at different spatial locations, while the species composition varies considerably (Strauss & Biedermann, 2006). Additionally, in statistical models of species numbers, important predictors for single species occurrence like isolation might be excluded from the model resulting in misleading conclusions for conservation (Bastin & Thomas, 1999). This can be tracked down by the assessment of community composition with a species-specific modelling technique.

Our modelling approach assessed the response of a large set of plant and insect species. The SDMs used were based on an intensive field survey and constructed using advanced multimodel inference techniques and a validation procedure. The model building approach yielded SDMs which were well transferable in space and time (Strauss & Biedermann, 2007).

Relative importance of abiotic conditions and spatio-temporal habitat configuration

More than half of the predictor weights of both plant and insect communities were related to spatio-temporal parameters (site age and landscape context variables). This indicates the importance of spatial arrangement and landscape dynamic for species occurrence as it has been shown in metapopulation studies (Biedermann, 2004; Wilcox et al., 2006) or vegetation succession experiments (Cook et al., 2005).

The plant community was highly influenced by successional site age, both at the plot and in the landscape context. In accordance, Prach & Rehoukuvá (2006) showed in a review of studies on vegetation succession that time since abandonment has nearly always a significant influence on vegetation pattern. However, soil properties played a bigger role than landscape context variables in determining plant species occurrences (cf. Godefroid & Koedam, 2007). Thus, spatio-temporal processes (i.e. destruction at one place and regeneration at another) driving plant biodiversity are complemented by the abiotic conditions defining habitat quality.

The influence of landscape context variables was much stronger on leafhoppers and grasshoppers than on the plant community. Their reaction differed from that of carabid beetles on brownfields, for which only little response of a few species to these parameters has been found (Small et al., 2006). The insect community was also driven by the vegetation at the site (and thus indirectly by soil parameters and site age). Carabid assemblages on urban brownfields are strongly influenced by the stage of vegetation succession as well (Small et al., 2003). Strauss & Biedermann (2006) found comparable weights of the main driving factors for grasshoppers and leafhoppers when including detailed measures of horizontal and vertical vegetation structure and host plant cover in the SDMs, although vegetation structure measures made up a greater proportion of the driver weights. Hence, PLS-dimension reduction seems to be a valid simplification in this context but contains probably less information than detailed measures.

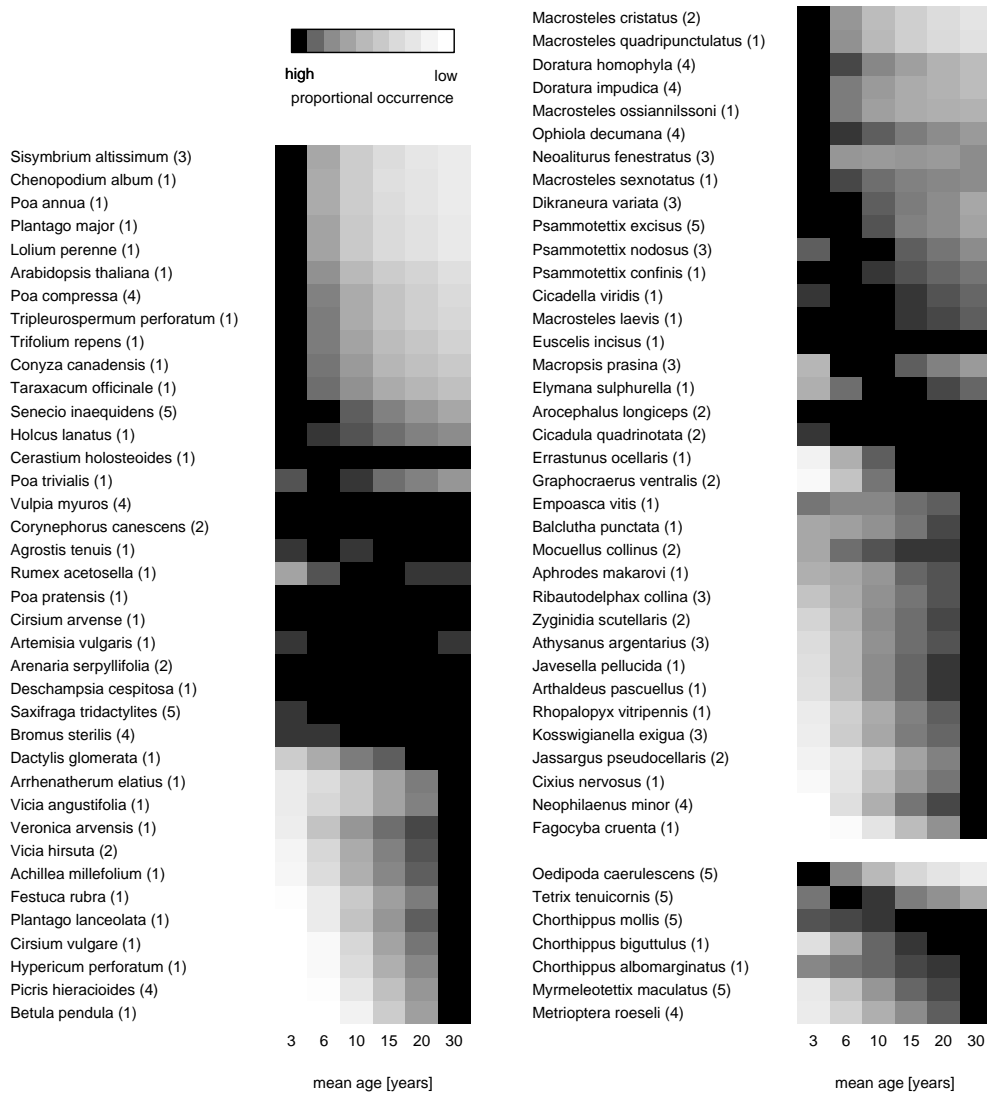


Figure 4.5: Occurrence of plant (left) and insect (right) species over mean site age. In brackets: regional rarity value. Brownfield proportion is fixed to 0.4. The graphic shows the median proportion of occupied brownfield cells per mean site age, standardized by division by the maximum value per species.

Effects of turnover rates and habitat area on species richness and rarity

On the single-species level, the response to brownfield turnover rate was very distinct and variable. This is due to the major role site age plays in determining species' response as revealed by the SDMs. Some species benefited from many young sites (i.e. a fast turnover, figure 4.5), while others depended on older sites in the surrounding or at the plot. In terms of rarity no clear trend could be found on the single-species level. There were regionally rare plant species which benefited strongly from fast turnover (e.g. *Poa compressa*), but others did not show any preference (such as *Vulpia myuros*) or a positive reaction to many older sites (e.g. *Picris hieracioides*). For grasshoppers results were similar. Only regionally rare leafhoppers seemed to depend on a low mean site age, with *Neophilaenus minor* (rarity value 4) being the only rare species which, though preferring young and open habitats, benefits from many older sites in the landscape context. This contrasts the averaged findings for insect rarity which increased with decreasing turnover. It is caused by low predicted occurrences of regionally rare species depending on fast turnover resulting in many young, open sites (e.g. *Doratura impudica* and *Oedipoda caerulea*) as opposed to high predicted incidences of rare species benefiting from slow turnover (e.g. *Metrioptera roseli*). This difference between community and single-species results and the species dependent reaction to dynamics demonstrates that biodiversity indices alone (such as species richness) reflect effects on species communities inadequately (Olden et al., 2006) and that management decisions may depend strongly on which species is given priority (Bastin & Thomas, 1999) if only single species are considered.

In terms of biodiversity and rarity value of the study area, modelling revealed that a multitude of different successional stages is necessary to maintain the conservational value. At proportions of brownfield area under 50 %, sites should undergo succession for about 10 - 15 years on average to maintain the regional species pool, as Muratet et al. (2007) suggested on the basis of simple estimates. At higher brownfield proportions, landscape turnover can be faster because there is a higher chance that some brownfield lots reach old successional stages. Species rarity value is relatively unaffected by the proportion of potential habitat area. Nevertheless, the decreasing variance of modelling results with increasing brownfield proportion suggests a lower susceptibility of the communities to habitat turnover. The opposing trend in the rarity value (decreasing for insects but increasing for plants with faster turnover) suggests an intermediate optimal turnover.

According to the results of our case study we recommend an intermediate rate of redevelopment and abandonment (mean age of 10 to 15 years) and a brownfield proportion of at least 40 % to maintain most modelled plant, grasshopper, and leafhopper species. The actually mapped proportion of open space in our study area was 31 % with an average successional site age of about 8 years. Thus, in the absence of any conservation management within the area the conditions found are already quite close to our recommendations. Furthermore, a detailed study of business areas of six German cities

(including Bremen) based on the analyses of aerial photographs over the time series from 1950 to 2004 (Emptner, 2006) revealed that 34 % of all analysed sites experienced one, 22 % two, and 7 % even three open periods over the whole time span. Thus, site turnover including a period of open space and free succession can indeed be found in industrial areas.

4.5 Conclusions

In landscapes of temporary habitats with succession-dependent quality, species persistence is controlled by the dynamics of the landscape and by species dispersal ability (Wimberly, 2006). Conservation management in such spatio-temporal mosaics of habitat patches has to find the appropriate habitat turnover rate and the minimum sufficient amount of habitat, additionally to factors like habitat connectivity and patch size.

We showed that landscape dynamics, resulting in a shifting mosaic of habitats of different successional stages, could support urban biodiversity. This means to allow for a 'temporary conservation' which, in contrast to common practice in traditional nature conservation, generates mosaic cycles and excludes only some areas from development at a time while accepting the destruction of habitat at one place for creation of new habitat at another. This concept dissolves the conflict between redevelopment of abandoned sites and conservation interests (Gibson, 1998), and accounts for the importance of successional young habitats for species diversity (Small et al., 2003).

The modelling approach used here can be adapted to other dynamic landscapes in which habitat patches shift in location, and habitat quality is dependent on patch age. It provides a tool to evaluate species response on the landscape scale to the spatio-temporal arrangement and demonstrates the value of landscape modelling for practical planning issues.

Acknowledgements

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4.6 Appendix

A Estimation of species distribution models

To built species distribution models we first performed a univariate screening of the relationship between environmental conditions and species occurrence. Only significant predictors ($p \leq 0.05$) with $R_N^2 \geq 0.05$ (Nagelkerke's Pseudo- R^2) were considered for further analysis. At this step, we also determined the shape of the relationship (either sigmoidal or bell-shaped unimodal). Second, multiple models for each species with every combination of two, three, and four not strongly correlated (Spearman's $\rho \leq 0.7$) parameters were built. For each model, we performed an LR-test to check if the model was better than any model with one variable less ($p \leq 0.05$), examined whether parameter coefficients were significant ($p \leq 0.2$) and R_N^2 was ≥ 0.2 . If we had obtained several multivariate models for a species, model averaging following the method by Burnham & Anderson (2002) was carried out. To this end, the AIC_c (Akaike information criterion corrected for small sample size) was calculated as a measure of model fit constraint by model complexity. A smaller AIC_c indicates a better model. If the difference (Δ_i) of a model's AIC_c to the AIC_c of the best model of the species was not greater than 10, a model weight (w_i) was calculated:

$$w_i = \frac{\exp(-0.5 \cdot \Delta_i)}{\sum \exp(-0.5 \cdot \Delta_i)}$$

An averaged model for each species was obtained by multiplying the model coefficients with the corresponding w_i and summing the weighted coefficients of each variable over all multiple models per species. An arithmetic example of the procedure can be found at Strauss & Biedermann (2006).

B Validation of species distribution models

To correct for overoptimistic performance measures we applied the following procedure in 500 repetitions for each model which was used to construct the averaged model of a species. First, the model coefficients were recalculated using a bootstrap sample. Second, AUC and R_N^2 of this bootstrap model were estimated for the sample and for the original data set. We assessed bias of the model performance measures from the mean difference over all repetitions between values obtained from sample and original data set, respectively. To estimate corrected values AUC_{cor} and R_{Ncor}^2 for the averaged model of each species, the weighted average of the bias over all multiple models was calculated using the AIC_c -weights, and subtracted from the original AUC and R_N^2 .

Chapter 5

Temporary conservation of urban biodiversity

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submitted to *Landscape and Urban Planning*.

Abstract

Cities hold a rich biodiversity offering habitat for many and especially several rare species. Urban green spaces provide ecosystem services, thus are substantial for human well-being. However, open, wild habitats like urban brownfields (derelict land) are threatened e.g. by economic development or counteractions against urban sprawl. The question arises of how much area has to be set aside to maintain urban biodiversity and whether there is a way to do so other than excluding it completely from economic development.

We use a simulation model based on species distribution models for plants, grasshoppers, and leafhoppers to compare the effects of static vs. spatially dynamic conservation approaches. To this end, scenarios of different proportions of open sites, different paces of habitat turnover and different lot sizes are analysed.

Our simulations showed that a dynamic land use supports urban biodiversity. Hence, we recommend to integrate the concept of 'temporary conservation' into urban planning of industrial and business areas. This concept requires habitat to be destroyed by redeveloping brownfield sites but simultaneously creating new open spaces due to abandonment at other locations. This way, a variety of habitat conditions in a spatio-temporal mosaic of different successional stages is maintained. Moreover, the economic value of business areas can be enhanced due to higher ecological values but also due to the possibility to react fast on new economic trends by the (temporary) provision of available open sites.

keywords: dynamic landscape, species richness, temporary buildings, brownfields, wasteland, species distribution model.

5.1 Introduction

Cities hold a rich biodiversity (Rebele, 1994; Pickett et al., 2001; Godefroid & Koedam, 2007), which is distributed over various types of green space like maintained parks and gardens as well as informal habitats such as ruderal and derelict sites (Venn & Niemelä, 2004). These green spaces form a complex spatio-temporal mosaic of habitat, characterised by altered climatic conditions, altered water and nutrient fluxes as well as potentially contaminated soil, air, and water (Wilby & Perry, 2006). They bear unique urban communities, often constituted of a variety of native and non-native species (Alberti et al., 2003).

Among the most valuable urban habitats are urban brownfield sites, composed of derelict land, abandoned railway tracks, landfills, and previously developed land, because they often support a rich flora and fauna including rare species (Eyre et al., 2003 and references therein; Maurer et al., 2000; Godefroid, 2001; Small et al., 2003). These sites offer heterogenous, often ephemeral, but during their lifetime rather undisturbed habitats of different successional stages, but are, however, often ignored by urban conservation planning (Godefroid, 2001; Muratet et al., 2007), receiving much less attention by urban ecologists than parks and gardens (e.g. Smith et al., 2006b,a). Moreover, a current paradigm of urban planning is that brownfield sites should be prioritised over greenfield sites (i.e. sites outside the cities) for development of new housing and industry (Department of Communities and Local Government, 2000; Pauleit et al., 2005). While this paradigm is certainly useful to restrict urban sprawl, it is in conflict with the goal to preserve urban biodiversity.

This study introduces the concept of temporary biodiversity and building and assesses its validity. The concept allows for both an urban renaissance and the conservation of biodiversity on brownfield sites. It conceives the urban habitat as a spatio-temporal mosaic of built-up sites and abandoned brownfields, with colonisation of brownfields by plants and animals and redevelopment of brownfields for housing or industry later on. Though little is known about current turnover rates from built-up sites to brownfield sites and again to built-up ones, there is evidence that the duration of use of industrial buildings has declined in recent years and will continue so in the future due to short-term, fast-moving markets and new economic trends (Hassler & Kohler, 2004).

For plants and animals, brownfield emergence and loss result in habitat conditions that shift in space. Additionally, undisturbed brownfields are characterised by vegetation succession causing changes in vegetation structure (Schadek et al., 2008), which in turn drives for instance insect community assembly (Small et al., 2003). Thus, habitat quality is not only a function of abiotic conditions, but is also rendered by successional change during the lifetime of an individual brownfield site. Species can only persist in this mosaic cycle (Kleyer et al., 2007) if they are able to track the spatial and temporal shifts in habitat quality.

Here, we analyse the consequences of these shifts in spatio-temporal habitat availability and quality in the framework of temporary biodiversity and building. We evaluate

two alternative hypotheses: (1) constant habitat conditions provide higher biodiversity (no turnover), or (2) habitat turnover due to periodical rebuilding and demolition provides higher biodiversity. In the latter case, the question arises as to which turnover rate supports the highest biodiversity.

To test these hypotheses, we use a simulation model based on species distribution models (SDMs), which have become an important tool in ecology as well as in conservation biology in recent years (Guisan & Thuiller, 2005). In this multi species approach (Garden et al., 2006), we relate species occurrences (plants, leafhoppers, and grasshoppers) to abiotic soil conditions, landscape context variables, and successional site age based on field data. We extrapolate the SDMs from plot scale to landscape scale and combine single species response to community response. Landscape scenarios of different habitat configuration in space and time (Rudner et al., 2007; Schröder et al., 2008) are assessed to derive recommendations for maintaining biodiversity of urban industrial and business areas. From this modelling study we provide general guidelines for practical urban conservation planning (Opdam et al., 2002) by evaluating the concept of 'temporary conservation' and discussing its implementation into urban planning.

5.2 Methods

Species distribution models

Species distribution models (SDMs) are regression models which relate species' incidence or abundance to environmental predictors (Guisan & Zimmermann, 2000). A widely used modelling approach is based on generalised linear models (GLMs) with a logistic link function (Rushton et al., 2004). The occurrence probability (Y) of a species is given by

$$Y = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n)}} \quad (5.1)$$

with the predictor variables X_i , the intercept β_0 , and the coefficients β_i . A bell-shaped relationship between Y and X can be described by introduction of a quadratic term (figure 5.1).

We built SDMs for 38 plant species and 43 insect species (leafhoppers, grasshoppers and one bush-cricket (*Metrioptera roeseli*), hereafter referred to as grasshopper) based on species incidence data collected at 133 sampling plots on brownfield sites (derelict sites, previously developed land, and abandoned railroads) in Bremen, north-west Germany, in 2003 (appendix, tables B, C, and D). Predictor variables included soil properties, successional site age, landscape context variables, and, for the insect models, vegetation parameters (appendix, table A). Time since initiation of succession (site age), was derived from a time series of aerial photographs. As most ecological processes are related to larger spatial scales instead of only to patch characteristics (Holland et al., 2004), landscape context variables were mapped around each sampling plot. These variables described the proportion of vegetation types and site age classes, respectively, within

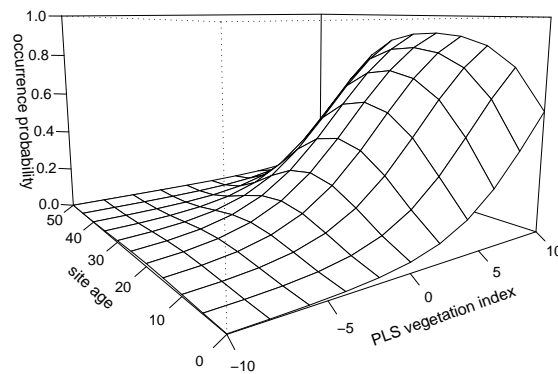


Figure 5.1: Example plot of a multivariate glm-regression model for *Chorthippus mollis* with sigmoidal relationship of occurrence probability to vegetation and unimodal relationship to site age.

different radii around every sampling plot (25, 50, 75, 100, and 200 m). The model building based on multi-model inference (Burnham & Anderson, 2002) and included an internal validation step. For a detailed description of sampling design see Schadek et al. (2008) and Strauss & Biedermann (2006), for information on the SDM building procedure and evaluation see the appendix 5.6 and Kattwinkel et al. (2009).

Modelling shell

We developed a modelling shell to upscale the SDMs from plot scale to landscape scale and thus to analyse scenarios of different proportions of build-up sites, turnover rates, and lot sizes.

The effect of each scenario on single species and biodiversity was investigated by modelling species occurrence under artificial urban planning situations generated according to each scenario. Thus, for each scenario the following procedure was executed in 1000 repetitions: The program sequence started by reading in the allocation of lot boundaries and scenario settings (figure 5.2). Land use (built-up or brownfield) was assigned randomly to the lots according to the scenario settings. Next, soil and age properties were defined. Nutrient and water balance parameters in industrial areas were unpredictable at newly established sites or after abandonment, but the soils in our study area comprised of sandy, artificially filled up material. Thus, soil parameters were randomly assigned to the brownfield sites in a set of values as found at the sampling plots. For every open lot, time since abandonment ('site age') was drawn randomly from an exponential distribution. This distribution describes the turnover of brownfield to built-up sites and vice versa as a constant rate of change, holding the overall ratio between the two land use types constant. Its mean value ($1/\lambda$) gives the average site age (see appendix 5.6).

Subsequently, plant species occurrence probabilities were estimated within an integrated grid-based GIS by applying the SDMs to every single grid cell. Due to the interaction between vegetation and insect occurrence, vegetation structure at the plot and vegetation type in the landscape context (i.e. the surrounding of the plot) are important predictors for insect occurrence (Strauss & Biedermann, 2006). Hence, plant occurrence probabilities were merged to a new explanatory variable for insect species occurrence by partial least squares (PLS) regression (Boulesteix, 2004) as a proxy for vegetation structure and host plants. Vegetation type in the landscape context (e.g. low vegetation or woody vegetation) was assessed by classification trees also using the plant occurrence probabilities for every raster cell (Venables & Ripley, 1999). Now, the insect SDMs were applied. From the predicted species occurrence probability maps, species incidences were computed using a threshold value based on Cohen's kappa (Fielding & Bell, 1997). For every replicated simulation run, the number of overall predicted species and the number of occupied cells per species were recorded.

Simulation results were evaluated from the nature conservation perspective by means of (i) species richness as the overall number of occurring plant and insect species, and (ii) the average species rarity of the study area. For the latter, regional rarity ranging from 1 (very common) to 5 (very rare) was assigned to every species as follows: We rated a species as very rare, if it was recorded in species distribution atlases at less than 20 % of the marsh and geest area of northwest Germany for plants (Haeupler & Schönfelder, 1988) or of Bremen for grasshopper species (Hochkirch & Klugkist, 1998); a species was classified as rare (4) at an occupied area of less than 40 % and so on (table 5.2). For leafhoppers, the classification was based on expert knowledge (Robert Biedermann). Additionally, the standard variation of the two evaluation parameters over the replicate runs is calculated.

As SDMs represent static models relating species occurrence to the present environment (Guisan & Zimmermann, 2000), their outcome is independent of past states. In this context, it is unnecessary to simulate time series of land use distributions. If the ratio of open to built-up sites and the turnover rate remain constant over time, the changed spatio-temporal configuration caused by succession and patch dynamics is identical with another replicate simulation run. For this reason, we analyse snapshots of the landscape arising from different scenarios.

Study area and scenarios settings

Simulations were carried out on a raster grid with a spatial resolution of 12.5 m by 12.5 m. The study area for the simulations comprised a cargo transport centre in the city of Bremen, which covered about 550 ha, situated within an agriculturally used matrix (figure 5.3). The centre was established in 1985 by successively filling up wetlands with sandy material, but parts of the area were already developed in 1974. Due to the sandy landfills, soil properties were rather homogenous. About 45 % of the sites were not built-up in 2006 and consisted of open spaces of different successional stages ranging from

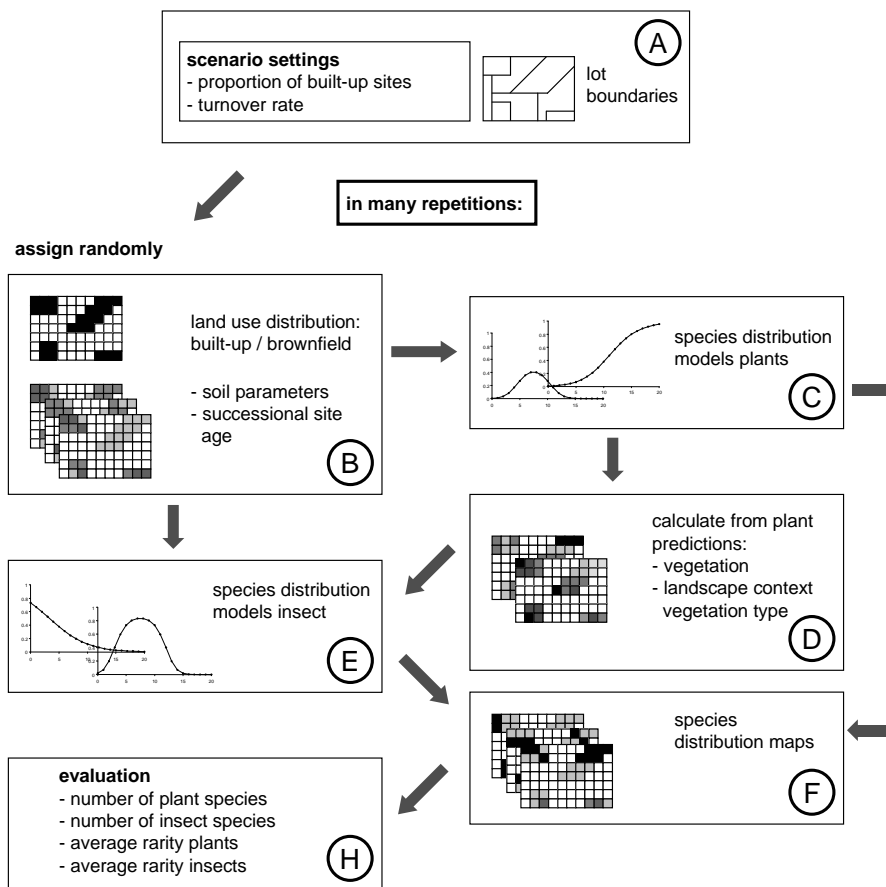


Figure 5.2: Flow chart of the modelling shell. First (A), the allocation of lot boundaries and scenario settings are read in. In the next step (B), land use, successional age, and soil properties are assigned to the sites and this information is converted into raster maps. Then (C), plant occurrence probabilities are calculated by application of the SDMs to every raster cell. From these, vegetation parameters are estimated (D), and subsequently (E) the insect models are applied. The maps of species occurrence probabilities (F) are aggregated to evaluation parameters in the last step (G).

bare soil to pre-forest vegetation.

We assessed the effect of a static land use (open sites stay open, built-up sites remain constantly used) versus dynamic land use (a certain proportion of land is converted from built-up to open and vice versa every year). For the static setting, we assigned the same site age of 0, 3, 6, 10, 15, 20, 30, 40, and 50 years, respectively, to all open sites. As opposed to that, in the dynamic setting landscape turnover was represented by assigning exponentially distributed site age with the same mean values as in the static setting to the

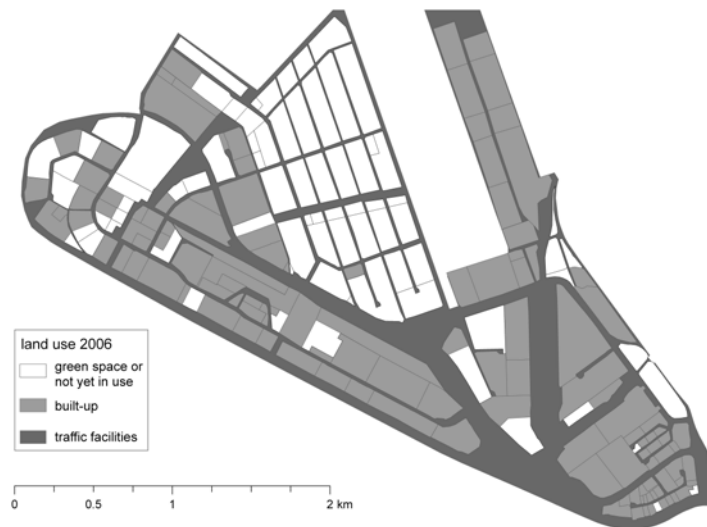


Figure 5.3: Layout and current land use in 2006 of the study area .

brownfield lots.

Species response to available habitat area was tested by varying the proportion of built-up land between 40 % and 90 %. We chose 40 % (and not 0 % like possibly in a nature reserve) as the minimum proportion of built-up area as our study system were urban industrial and business areas which necessarily comprise buildings. Furthermore, habitat turnover, which is assumed to be a driving force of species occurrence, is caused by the abandonment of buildings and redevelopment of open lots. To study the influence of the turnover pace, mean successional age of brownfields was set to 3, 6, 10, 15, and 20 years, respectively, with maximum age restricted to 50 years as the oldest open site found in the field. A lower mean age represents a faster turnover.

To analyse the effect of lot size on species occurrence, we designed lot boundaries in four different settings (Table 5.1). The first one comprised the original layout of lots ('original') as found in the field. Another one was characterised by very large sites ('large'), typically found in logistic centres. The third setting comprised many small lots ('small'). The latter was designed as several large sites with associated small sites to serve as possible expansions ('backup').

Table 5.1: Lot sizes used in the scenarios. 'Original' is the layout found in the field.

lot size [ha]	original (187)	small (508)	large (57)	backup (225)
mean	2.58	0.95	8.97	2.14
min	0.11	0.11	4.68	0.13
max	12.10	1.98	13.39	10.22

5.3 Results

Comparison of dynamic vs. static land use

Static land use had a negative effect on both plants and insects (figure 5.4). With ongoing succession without disturbance (static land use), the number of predicted species to occur within the study area decreased for plants for site ages exceeding 3 years. For insects, species richness stayed rather constant at about 33 predicted species up to a site age of 20 years and then decreased rapidly. At a site age of 50 years for all open lots, only about half of all modelled species of both taxa were predicted within the study area in the static setting. Opposed to that, open land with shifting locations (dynamic setting) resulted in higher species richness regardless of the pace of turnover.

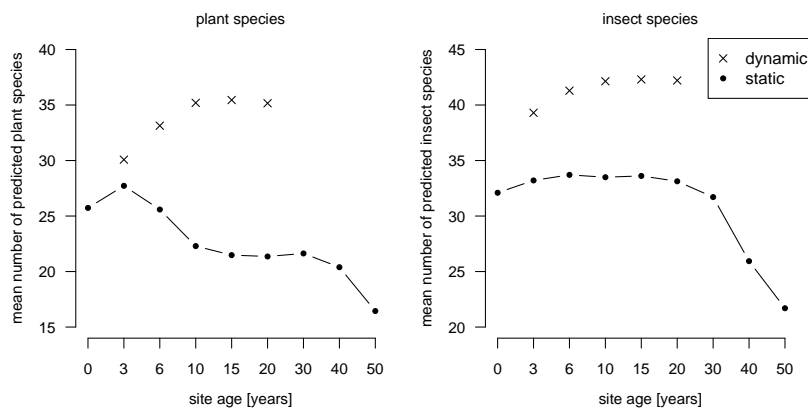


Figure 5.4: Plant (right) and insect (left) species richness for dynamic land use (turnover) and static land use (same age for all sites). Lot boundary setting as found in the field ('original') and proportion of open sites is 0.4. Site age (x-axis) gives the age of all open lots for the static setting, but the average site age for the dynamic setting.

Influence of turnover and proportion of open space

Species richness of the study area was influenced by both the pace of site turnover and the proportion of open space (figure 5.5). The more green space was available, the higher was the number of predicted species. Plant species richness showed a peak at a mean site age of 15 years, while insect richness peaked at 10 to 15 years. Variation over the 1000 simulation runs (expressed as the standard deviation; figure 5.5, bottom) increased with increasing density of built-up sites. For plants at built-up area between 40 and 80 %, the lowest variation was found at a mean site age of 15 years. For insects, this minimum was found to be 15 - 20 years. In comparison to plant species, an altogether higher proportion of insect species was predicted with a lower variation in the results of the replicate runs for all scenarios. Likewise, the overall rarity value of the study area was influenced by turnover rate and proportion of potential habitat (figure 5.6). The more sites were left open, the higher was the rarity value for both taxa. However, rare plant species benefited from a fast turnover (low mean site age), while insects profited by a slow one.

Influence of lot size

If lot size in the study area was large, less species were predicted to occur over all scenario settings than for the other three lot size layouts ('original', 'small', and 'backup') (figure 5.7, left). Furthermore, variation over the 1000 simulation runs per setting was highest for the layout with the largest lot sizes (figure 5.7, right). Again, the other three size layouts resembled each other. The same pattern was found for the rarity value for both, plants and insects: large lot sizes resulted in lower values and higher variation. However, the differences were rather small (e.g. for a built-up proportion of 60 % and a mean site age of 10 years, about 41 insect species were predicted for large lot sizes and approx. 42.5 species for small lot sizes) but increased with decreasing proportion of open sites.

5.4 Discussion

Factors influencing urban biodiversity

With respect to the two alternative hypotheses, i.e. no turnover vs. turnover, we conclude that a turnover of brownfield sites to built-up sites and vice-versa provides higher biodiversity than no turnover. Our simulations showed that the conservation value of the study area declined rapidly over the course of succession, if a certain proportion of land was set aside for urban conservation but without any management in a static spatial configuration (the same sites stay open over the whole period of time). As opposed to that, a dynamic land use, which temporarily excluded some areas from development, could maintain and even enhance the ecological value of an industrial area. The destruction of habitat by redevelopment of brownfield sites combined with simultaneous creation of

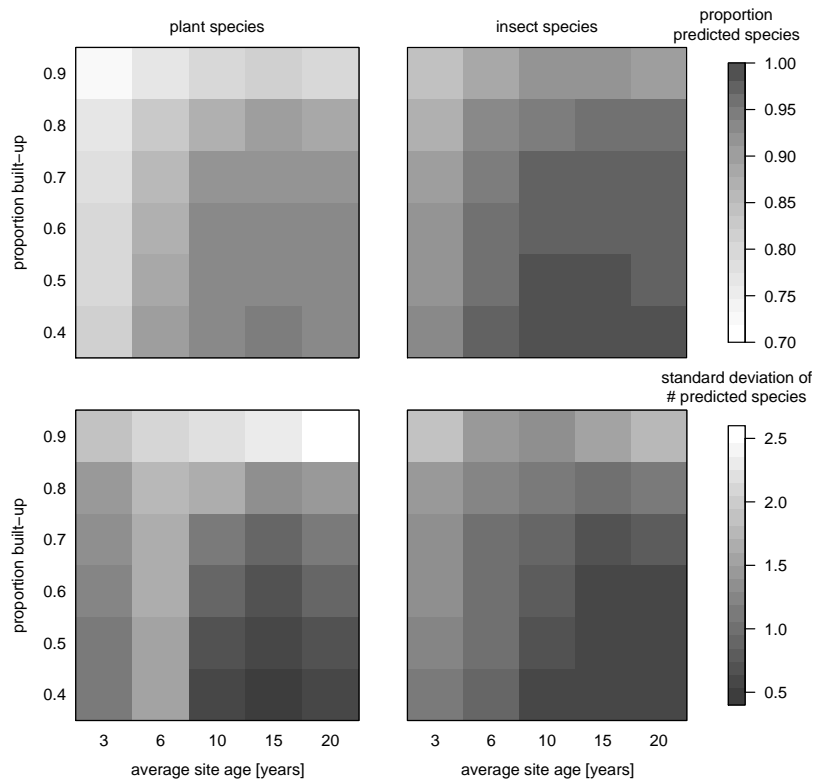


Figure 5.5: Species richness (top) and its standard deviation (bottom) of plants (left) and insects (right) as a function of mean site age and proportion of built-up area. The top graph shows the mean number of predicted species in relation to the number of modelled ones (37 plant species and 43 insect species, respectively), the bottom one shows the standard deviation of the number of predicted species over the 500 simulation runs per scenario setting.

new open spaces due to abandonment at other locations maintains a variety of different habitat conditions by the creation of a spatio-temporal mosaic of different successional stages. Accordingly, planning for a dynamic urban land use can maintain urban ecosystem services (Flores et al., 1998).

Proportion of open space and rate of turnover from open to built-up sites (two factors that can be accessed by urban conservation planning) both strongly affect the plant and insect community and consequently the nature conservation value of urban green spaces. Thus, different spatio-temporal patterns of landscape dynamics result in different ecological pattern and values as proposed by Alberti et al. (2003). The two factors turnover rate and proportion of open space complement each other; a higher proportion of built-up sites can be balanced by a slower turnover. The predicted species richness at a

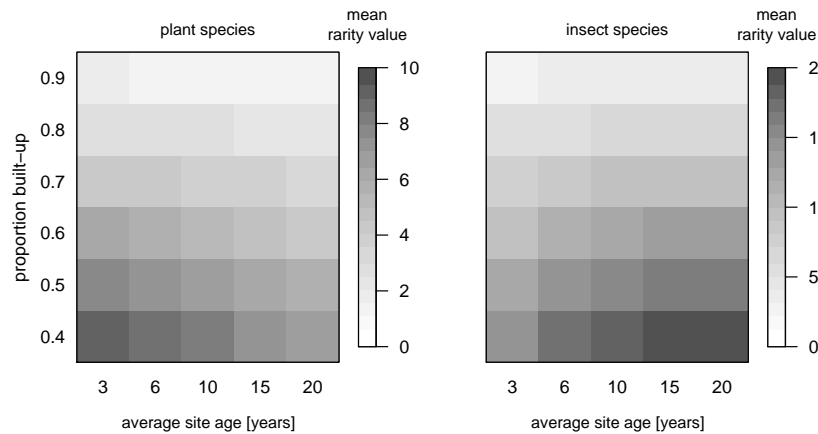


Figure 5.6: Rarity value of the study area for plant species (left) and insect species (right) as a function of mean site age and proportion of built-up area.

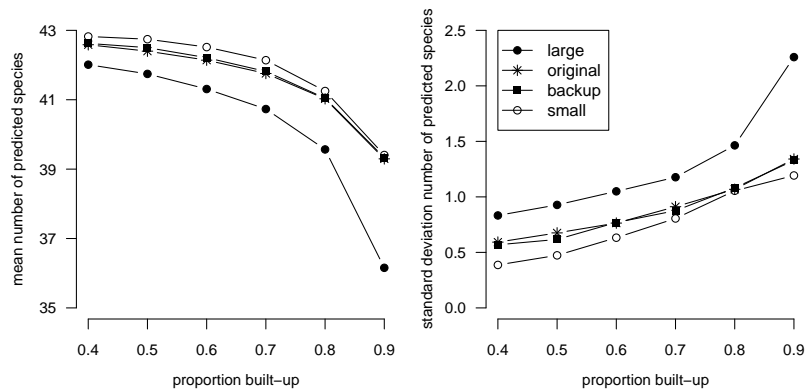


Figure 5.7: Insect species richness (mean number of overall occurring species; left) and its variation (standard deviation; right) at different lot sizes as a function of the proportion of built-up area. 'Original' refers to the lot layout as found in the study area; 'large' to fewer, but larger sites; 'small' to many small lots; and 'backup' to several large lots with associated small expansion sites. Mean site age set to 10 years.

proportion of built-up sites of 70 % and a mean site age of 10 years for instance, is higher than at higher proportions of open area but faster turnover for both taxa (figure 5.5). As species richness is driven both by local factors (e.g. soil properties, successional age of a patch) and by landscape factors (landscape context variables), urban conservation has to be implemented on landscape scale, but not on patch scale. This fact has been recognised (Flores et al., 1998; Mörtberg et al., 2007) but is nevertheless often neglected.

The higher conservation value resulting from larger proportions of open space was not only caused by the larger amount of habitat provided, but this trade-off between built-up area and biodiversity arises also in the lower variation of the replicate simulations. This means, the chance to meet the requirements of many and especially many rare species was increased with the proportion of open space (figure 5.5). On the other hand, a certain proportion of built-up area is necessary to maintain site dynamics by abandonment and redevelopment. The variation in the simulation results could be additionally reduced by decreasing the pace of turnover (i.e. allowing open spaces to grow older in average).

The comparison of different spatial layouts (lot sizes) indicated the advantage of settings leading to more heterogeneity within the study area (Deutschewitz et al., 2003). Thus, settings with many smaller sites ('small', 'backup', and 'original') were rated better than the one with fewer, larger sites ('large'), as they offered more different habitats at the same proportion of open space. As we set soil properties to be constant within one lot in the model, we do not account for the larger heterogeneity within patches of larger area (Ouin et al., 2006), though. Additionally, we did not consider population dynamic processes, which could result in lower extinction risks of populations inhabiting larger patches (Hanski & Thomas, 1994). Nevertheless, by including variables describing the landscape context at different spatial scales into the predictors for species occurrence (Dauber et al., 2005), the SDMs implicitly account for connectivity and patch area. Moreover, the interaction of vegetation and insects (Garden et al., 2006) is accounted for by predicting vegetation type and structure from the plant SDMs as predictor variables in the insect SDMs.

Recommendations for urban conservation

Additionally to extrapolating SDMs through space and time, our modelling study also gives hints on how to integrate biodiversity research into the urban planning applications (Opdam et al., 2002; Wintle et al., 2005). Synthesising the results for the species pool considered here, we recommend a proportion of open space of 50–60 % with an average site age of 15 years as a good compromise between plants and insects. At first glance, such a proportion of open space might seem high for industrial areas, where the German law allows a lot cover index of 0.8 (i.e. leaving only 20 % of open space; BauNVO). However, conceiving industrial areas rather as business parks of lower density, allows not only to increase their ecological value but also to add leisure and recreational functions. Furthermore, an analysis of land use distributions of industrial and business areas of six German cities (including Bremen) based on aerial photographs revealed that on average already 40 % of the area consisted of open, pervious land like brownfields, storage ground, unpaved traffic area (Emptner, 2006). The mean age of these open areas was 15 years averaged over the six cities and 10 years for Bremen, in both cases showing an exponential distribution.

Even though a minimum prevalence was necessary for statistical modelling, several of the grasshoppers and leafhoppers modelled are rare and endangered (table 5.2). As

opposed to that, most plant species considered here are rather common (table 5.2). However, even green spaces bearing common species can be valuable for urban biodiversity (Gibson, 1998) and provide important ecosystem services like micro-climate regulation, air filtering, water regulation as well as recreational, educational, and cultural values, thus being substantial for human well-being (Bolund & Hunhammar, 1999). Additionally, providing habitat for common species can also entail positive effects on rare ones.

Integrating temporary conservation into urban planning

The German law requires ecological compensation during planning and construction processes. Similar regulations can be found for other European countries even though mostly less strict or extensive (Peter et al., 2002). Embedding the concept of temporary conservation into urban planning can create such compensation area within industrial areas under construction without the need for adequate compensation areas at other locations. Hence, the land consumption of such green industrial parks would be larger, but its ecological value will be much higher than without the in situ compensation and can even be enhanced compared to the former land use (e.g. agricultural). Urban development contracts between city administration and property holders can be a means of regulating temporary open spaces. The city of Leipzig, for instance, offers legal advice to arrange agreements between temporary users of abandoned sites and the owners, which regulate the duration and kind of use while preserving the development rights of the owner and even exclude the lot from real estate tax (Stadt Leipzig, 2005). As this city has been facing severe problems associated with shrinking cities (population decline, many abandoned houses and properties), the city council invites citizens to conceive of temporary uses like playgrounds, gardens or for other leisure activities highlighting the positive implications of shrinkage (Haase, 2008). This innovative approach, developed to moderate the consequences of economic decline rather than to integrate conservation management into urban planning, could be adopted and expanded to the concept of temporary conservation.

Combining economic use and biodiversity management within the same area, opens a new perspective on environmental policy and can overcome the difficulties that arise when it is regarded as being a separate issue (Pedersen et al., 2004). Green, wild spaces with open public access support human well-being while simultaneously increasing the economic value of urban areas (Hobden et al., 2004; McGranahan et al., 2005). Everyday contact with natural urban landscapes can enhance the concern of city dwellers for natural ecosystems and the general public support for conservation issues (Savard et al., 2000), while the desire for a contact with nature can be found among urban residents throughout the world (Matsuoka & Kaplan, 2008). Furthermore, short-term temporal use of green spaces (e.g. for exhibitions or gastronomy) can help to integrate ecological preservation into everyday life while the intended destruction of some habitat (combined with the creation of new open space at other locations) can reduce the reservations of stakeholders into conservation issues. If the public perception of brownfield sites is im-

proved by linking them to ecological value instead of relating them to wasteland and social problems (Herbst & Herbst, 2006), even in times of temporarily low economic development they can have a positive effect on the overall appraisal of business areas.

Widespread changes can be observed in commercial construction today shifting the focus to short-term, largely due to the economy and its influence on architecture. Nevertheless, a study of Dissmann & Hopp (2002) showed that 80 % of industrial construction facilities still grow older than 20 years. If, for example, the brownfield proportion was 50 %, as recommended here, with a mean age of open sites of 15 years, this would result in a mean turnover of built-up sites to brownfields per year of 6.7 % and a corresponding average durability of buildings of also 15 years. In this study we assumed that every brownfield site has the same probability to become built-up per year independently of its age, which resulted in an exponential distribution of site ages. Such a distribution is rather unlikely for buildings. Thus, if most buildings last for longer periods of time, in the context of dynamic temporary conservation, some interspersed short-term temporary buildings can allow for fast enough turnover rates to create ever new open sites. These buildings should be of high quality to be more than only provisional solutions, as well as they should be reusable and dismantlable to be ecologically and economically efficient.

5.5 Conclusions

If biodiversity is to be maintained within urban areas, temporary conservation offers the opportunity to allow both conservation management and an urban renaissance. Setting aside a proportion of land for conservation issues in a static setting results in much lower species richness and rarity than a dynamic setting. Thus, a certain proportion of built-up area is essential to cause habitat turnover due to redevelopment at one lot and abandonment at another, which is necessary to support species persistence. Temporary conservation overcomes the traditional concept of protecting isolated habitats but conceives urban green spaces in a dynamic and flexible context. Moreover, temporary buildings represent an adjustment to the short-term, fast-moving markets, and a means for keeping up with new economic trends. This combination of spontaneous, open green spaces and modern architecture can increase the ecological as well as economical value of business areas.

Acknowledgements

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5.6 Appendix

A Building species distribution models

The SDMs were built as logistic regression models (GLMs with logistic link) from species presence/absence data using the function 'logistf' for R (Heinze & Ploner, 2004) for all species with a prevalence between 10 % and 90 %. First, we performed a univariate screening of the relationship between environmental predictors and species occurrence. For further analysis only significant predictors ($p = 0.05$) with $R^2_N = 0.05$ (Nagelkerke's Pseudo- R^2) were considered. Second, for every combination of two, three, and four parameters not strongly correlated (Spearman's $\rho \leq |0.7|$) logistic regression models were built for every species. For each of the multiple models, a LR-test was performed ($p = 0.05$). Additionally, we checked if R^2_N was ≥ 0.2 and if parameter coefficients were significant ($p = 0.2$). Model averaging following the method by Burnham & Anderson (2002) was carried out if we had obtained several multivariate models for a species.

B Calculation of average brownfield site age

If the ratio of open and built-up sites is constant over time, the same number of sites that are built-up must become open per time step. Site age will be exponentially distributed if every brownfield site has the same probability to become built-up per time step independent of its age. This leads to the following equations to calculate brownfield turnover and average age:

$$n.turn.total = 2 * n.turn.brown = 2 * n.turn.built \quad (5.2)$$

$$p.turn.total = \frac{n.total}{n.turn.total} \quad (5.3)$$

$$p.turn.brown = 0.5 * \frac{p.turn.total}{p.brown} \quad (5.4)$$

$$avg.age.brown = \frac{1}{p.turn.brown} \quad (5.5)$$

with $n.turn.total$, $n.turn.brown$, $n.turn.built$: number of sites that are converted per year (total, from brownfield to built-up, from built-up to brownfield, respectively); $p.turn.total$, $p.turn.brown$: proportion of sites that are converted per year (total, from brownfield to built-up, respectively); $p.brown$: proportion of brownfield sites; $avg.age.brown$: average age of brownfield sites. From this follows that the brownfield turnover is 12.5 % and average brownfield age is 8 years, if the total turnover is for example 5 % per years and the brownfield proportion is 20 %.

C Modelled species

Table 5.2: Modelled plant (left) and insect (right) species and their rarity value and red list status (RL; for insects only); 2: critically endangered, 3: endangered, V: not yet threatened but on warning list.

Plant species	rarity	Insect species	RL	rarity
<i>Achillea millefolium</i>	1	<i>Aphrodes makarovi</i>		1
<i>Agrostis tenuis</i>	1	<i>Arocephalus longiceps</i>		2
<i>Arabidopsis thaliana</i>	1	<i>Arthaldeus pascuellus</i>		1
<i>Arenaria serpyllifolia</i>	2	<i>Athysanus argentarius</i>		3
<i>Arrhenatherum elatius</i>	1	<i>Balclutha punctata</i>		1
<i>Artemisia vulgaris</i>	1	<i>Cicadella viridis</i>		1
<i>Betula pendula B</i>	1	<i>Cicadula quadrinotata</i>		2
<i>Bromus sterilis</i>	4	<i>Cixius nervosus</i>		1
<i>Cerastium holosteoides</i>	1	<i>Dikraneura variata</i>		3
<i>Chenopodium album</i>	1	<i>Doratura homophyla</i>		4
<i>Cirsium arvense</i>	1	<i>Doratura impudica</i>	2	4
<i>Cirsium vulgare</i>	1	<i>Elymana sulphurella</i>		1
<i>Conyza canadensis</i>	1	<i>Empoasca vitis</i>		1
<i>Corynephorus canescens</i>	2	<i>Errastunus ocellaris</i>		1
<i>Dactylis glomerata</i>	1	<i>Euscelis incisus</i>		1
<i>Deschampsia cespitosa</i>	1	<i>Fagocyba cruenta</i>		1
<i>Festuca rubra</i>	1	<i>Graphocraerus ventralis</i>		2
<i>Holcus lanatus</i>	1	<i>Jassargus pseudocellaris</i>		2
<i>Hypericum perforatum</i>	1	<i>Javesella pellucida</i>		1
<i>Lolium perenne</i>	1	<i>Kosswigianella exigua</i>		3
<i>Picris hieracioides</i>	4	<i>Macropsis prasina</i>		3
<i>Plantago lanceolata</i>	1	<i>Macrosteles cristatus</i>		2
<i>Plantago major</i>	1	<i>Macrosteles laevis</i>		1
<i>Poa annua</i>	1	<i>Macrosteles ossiannilssoni</i>	3	1
<i>Poa compressa</i>	4	<i>Macrosteles quadripunctulatus</i>		1
<i>Poa pratensis</i>	1	<i>Macrosteles sexnotatus</i>		1
<i>Poa trivialis</i>	1	<i>Mocuellus collinus</i>		2
<i>Rumex acetosella</i>	1	<i>Neoliturus fenestratus</i>	3	3
<i>Saxifraga tridactylites</i>	5	<i>Neophilaenus minor</i>	V	4
<i>Senecio inaequidens</i>	5	<i>Ophiola decumana</i>		4
<i>Sisymbrium altissimum</i>	3	<i>Psammotettix confinis</i>		1
<i>Taraxacum officinale</i>	1	<i>Psammotettix excisus</i>	3	5
<i>Trifolium repens</i>	1	<i>Psammotettix nodosus</i>		3
<i>Tripleurospermum perforatum</i>	1	<i>Rhopalopyx vitripennis</i>	3	1
<i>Veronica arvensis</i>	1	<i>Ribautodelphax collina</i>		3
<i>Vicia angustifolia</i>	1	<i>Zyginidia scutellaris</i>		2
<i>Vicia hirsuta</i>	2			
<i>Vulpia myuros</i>	4	<i>Chortippus albomarginatus</i>		1
		<i>Chortippus biguttulus</i>		1
		<i>Chortippus mollis</i>	V	5
		<i>Metrioptera roeseli</i>		4
		<i>Myrmeleotettix maculatus</i>		5
		<i>Oedipoda caeruleascens</i>	3	5
		<i>Tetrix tenuicornis</i>		5

Chapter 6

Management and modelling of the biodiversity of urban brownfields

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Abstract

Urban brownfields offer habitat for many rare animal and plant species. How can the conservation of such diverse and highly dynamic habitats be managed and integrated into urban planning? We used species distribution models of 37 plant and 43 insect species to investigate the effects on biodiversity of four different planning scenarios in a business and leisure area. The concept of temporary economic use of some lots combined with simultaneous abandonment of other lots resulted in increasing ecological value and higher species richness of the study area compared to static land use.

6.1 Introduction

Urban brownfields as dynamic habitats

Cities tend to have a higher biodiversity than their agricultural surroundings. This is due to a high habitat diversity as well as to their warmer climate (Rebele, 1994). Urban brownfields often bear rich insect and plant communities (Gemmell & Connell, 1984; Eyre et al., 2003). They can be described as a spatio-temporal mosaic of a variety of dynamic habitats generated by abandonment and redevelopment.

Conservation including economic use

How can urban biodiversity be maintained and conserved? It is common practice in nature conservation to protect habitats of endangered species by static nature reserves that excludes economic use. However, this practise is not applicable here. Instead of 'conservation without use', a concept of 'conservation including use' has to be applied. The present study combines economic cycles of industrial and business areas with urban planning requirements and urban biodiversity conservation. In doing so, the conservation value of open lots at changing spatial locations is an essential part of the planning procedure in spite of being a random by-product.

Our concept also calls for a new type of architecture. Instead of being created 'for eternity', sustainable buildings should be designed for temporary use. Such buildings should bear the possibility of being disassembled, of being recycled or should be mobile. Short-term economic use can be caused by dynamic markets which result in spatial flexibility, from filling of temporarily empty building lots or from the temporary space demand of events, exhibitions or trade shows. In this context, the urban development plan can be complemented by urban planning concepts, projects and infrastructure plans as well as lease agreements with obligations to leave fixed proportions of area open within a lot.

6.2 Methods

Study area and planning scenarios

The concept of temporary buildings and temporary brownfields was applied to a study area situated in the city of Oldenburg, comprising good national and public traffic connections. According to the current urban development concept the area should be developed for sport, leisure and business land use.

Land use scenarios were created for four lots with a total area of 4.5 ha over a time period of 20 years. Two of the analysed scenarios were characterised by dynamic land use with temporary, spatially shifting buildings (Dyn 1 and Dyn 2). Every five years the land use of some of the lots changes and thus the spatial arrangement of built-up and abandoned area. These two scenarios differ in the periods of use, in turnover frequencies,

and in their building densities. Figures 6.1 and 6.2 depict the landscape layout of the two scenarios at four different time steps. As opposed to that, we developed two static scenarios (Stat 1 and Stat 2) without shifting land use but with building densities similar to those of the dynamic ones. The land use distribution of these scenarios corresponded to the one of Dyn 1 in year 5 and Dyn 2 in year 10, respectively. All four planning scenarios comprised of buildings, infrastructure, parking lots and managed green spaces. The latter structure and frame the brownfield lots, which were subject to free succession (and thus are the areas of conservational interest).

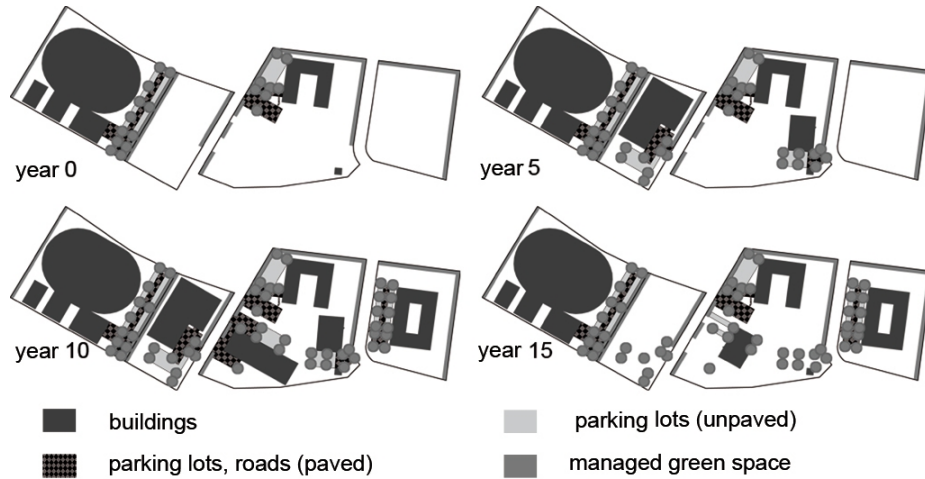


Figure 6.1: Planning scenario Dyn 1. White areas within the lots are allocated to free succession.

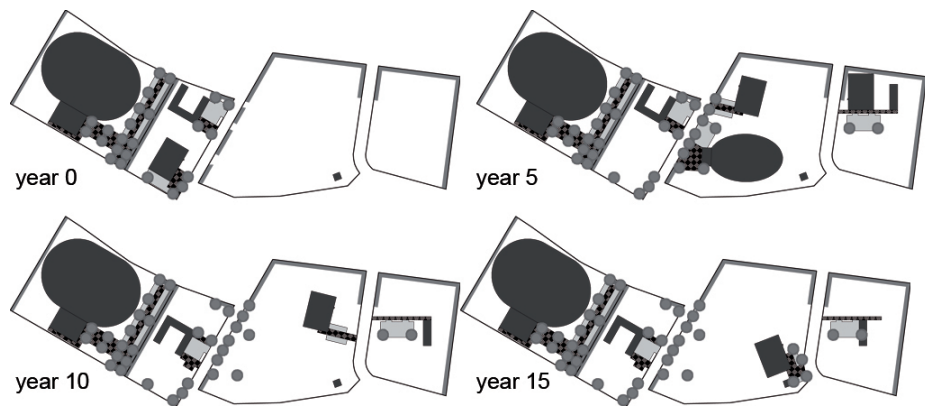


Figure 6.2: Planning scenario Dyn 2. For the legend see figure 6.1.

Species distribution models

Species distribution models (SDMs) quantify the relationship between species occurrence and environmental parameters (e.g. soil parameters, time since begin of succession) by means of statistic regression. Thus, they describe a species' realised niche. SDMs quantitatively predict the habitat quality under changed land use conditions. Hence, they allow of a forecast about increasing or decreasing incidence of a focus species.

We applied SDMs of 37 plant, 36 leafhopper, and 7 grasshopper species as indicators of biodiversity. The models were based on field data collected at business areas and abandoned railway tracks in the city of Bremen in 2003. Species presence/absence was recorded along with soil parameters, successional site age (derived from aerial photographs), the landscape context, and vegetation structure as independent environmental variables. Based on this data, SDMs were estimated using logistic regression and model averaging. A detailed description of the sampling design and the statistical model building can be found at (Strauss & Biedermann, 2006). To allow for a spatial model transfer to Oldenburg, we assumed that the study area was filled up with similar substrate as found at the study plots in Bremen (mainly nutrient poor, dry sand) during development.

The SDMs were applied to the landscape scale using a raster grid with a cell size of 2 m by 2 m. Simulations were run over a time period of 20 years. This procedure resulted in a time series of occurrence at each raster cell for each species. For scenario evaluation, we summarised these raster maps to several criteria per time step, namely the total number of predicted species within the study area and a rarity index. The latter one gave the average rarity of all predicted species. Furthermore, the number of raster cells belonging to one of five evaluation classes (1 = low value, 5 = high value) regarding species number and rarity was calculated.

6.3 Results

As opposed to the respective static scenario, a dynamic land use characterised by a spatio-temporal variable brownfield distribution had a positive effect on the number of predicted plant and insect species of the study area as well as on the rarity index (figure 6.3). All four planning scenarios yielded similar results in the first years. However, starting at the time step when a built-up lot was abandoned causing a re-initiation of succession for the first time, the evaluation criteria increased considerably (year 15 in Dyn 1 and year 10 in Dyn 2). Dyn 2, which was characterised by higher dynamic and lower building density, yielded slightly higher values for all criteria but the number of occurring insect species. Although this total number of occurring insect species decreased for the two dynamic scenarios and for Stat 1 in the last time step, the rarity index of the study area increased.

For none of the four scenarios all 37 plant and 43 insect species were predicted to be present at the same time within the study area. This was explained by the rather small size of the study area and the associated small number of different habitats.

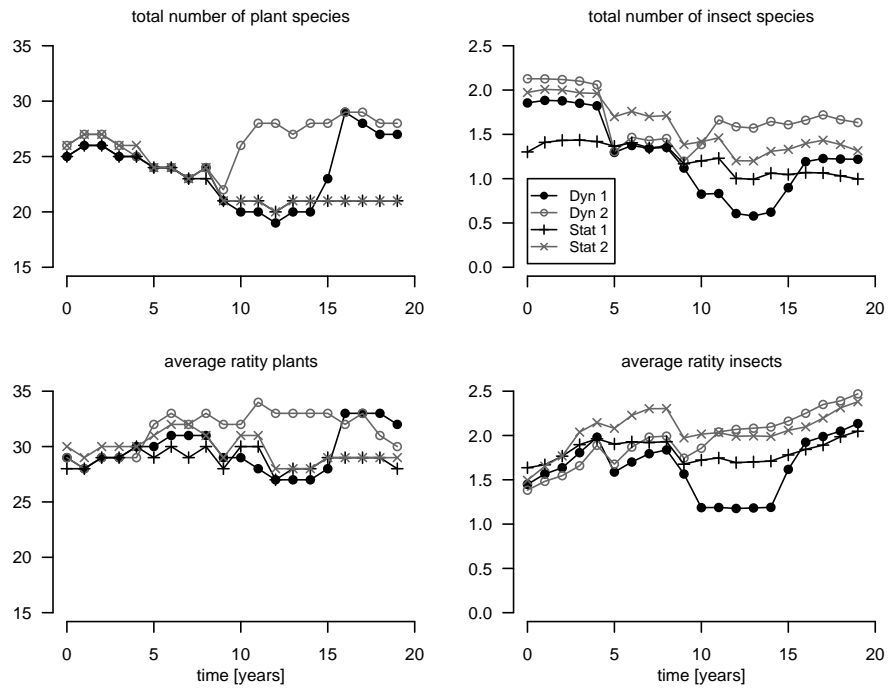


Figure 6.3: Time series of the modelling results of the four scenarios: Dyn 1 (black, closed circles), Dyn 2 (grey, open circles), Stat 1 (black, cross), and Stat 2 (grey, asterisk); from left to right: total number of predicted species and average rarity value of all raster cells; the top row shows the results for plant species, the bottom row for insect species.

The number of raster cells with many and many rare species decreased with time in the two static scenarios, resulting in raster cells of mainly class 3 for both criteria biodiversity and rarity from year 10 onwards. As opposed to that, regarding the modelled plant species about one third (biodiversity) and one fourth (rarity) of all cells were of high evaluation class (4 or 5) at the end of the modelling time span (20 years) in Dyn 1. For Dyn 2 the evaluation was even better.

With regard to the insect species, the differences between the dynamic scenarios and the respective static ones were less distinct. Furthermore, there were more raster cells of high evaluation value (class 4 or 5) with an increase at the end of the time period investigated in all four scenarios. This resulted from positive or unimodal relationships between insect occurrence probabilities and successional site age. Due to the increasing amount of older cells with time even in the dynamic scenarios, the number of suitable raster cells increased for more and more insect species. Extending the modelling time span beyond 20 years and thus further increasing the age of some cells would result in a decrease of species which are unimodally related to site age combined with a decrease of the evaluation criteria.

6.4 Discussion

Summarising the modelling results, the most dynamic scenario (Dyn 2) proved to be the best setting. Applying it to a larger planning area enables additional insect species to be maintained that rely on a higher proportion of younger succession stages in the surrounding.

The present study demonstrates the feasibility of a concept of conservation and management of biodiversity in an urban environment. The positive effect of a delayed redevelopment of abandoned lots on urban biodiversity (Angold et al., 2006) can be accelerated by specific planning actions. The resulting spatio-temporal mosaic of lots of different soil characteristics and different, especially young successional stages maintains habitat for a variety of plant and insect species, while it fits innovative urban planning and architectural concepts.

Acknowledgements

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Chapter 7

Incidence function models for grasshoppers

7.1 Introduction

In addition to the statistical modelling approach forming the basis of the first three manuscripts of this thesis, the picture of how species survive in dynamic landscapes should be completed in some aspects by a dynamic model. To this end, I used an empirical metapopulation approach based on the incidence function model (Hanski & Thomas, 1994), hoping to adapt it in a similar way as Wahlberg et al. (2002) to dynamic landscapes.

7.2 Methods

Study species

I chose the grasshoppers *Myrmeleotettix maculatus* and *Oedipoda caerulescens* as study species. *M. maculatus* inhabits scarcely vegetated, dry areas like sand dunes and heathlands, as well as infrequently calcareous dry grasslands (Bellmann, 1993). Its distribution in Germany ranges from the northern heathlands to the drought, acidic areas of South Germany. *O. caerulescens* is very xerophile, inhabiting open dry grasslands as well as gravel and sand pits. It used to be distributed throughout Germany but is endangered in many places nowadays (German red list status 3). Both species colonise anthropogenic habitats like railway tracks, pits, and mining dumps.

Study area

The study area for this subproject lay in the cargo transport centre Niedervieland in the city of Bremen and covered about 550 ha (figure 3.1). It was situated within an agricultural used matrix and thus rather isolated from other possible habitats of the analysed grasshopper species, preventing colonisation from outside the study area. The centre was established in 1985 by successively filling up mainly agriculturally used wetlands

with sandy material, but parts of the area had already been developed in 1974. Brown-field sites (mostly not yet built-up lots) made up about 45 % of the area in 2005 and comprised different successional stages ranging from bare soil to pre-forest vegetation. According to the ecological requirements of the two species, I chose all sites with at least partly scarce vegetation cover as possible habitat patches. In doing so, I defined 68 patches from aerial photographs and during the field work, ranging from 500 m² to approx. 25 ha in area (figure 7.1). These patches were sampled in late July to August in the consecutive years 2005 to 2007. To this end, *M. maculatus* was mapped by acoustic monitoring (Bellmann, 1993) over a time interval of 2 minutes at a number of random locations within each patch proportional to its area. *O. caerulescens* was recorded by visual inspection during random walks across each patch. Each patch was visited at least twice before it was recorded as unoccupied. During the time period investigated, some patches were destroyed by building activities (figure 7.1).

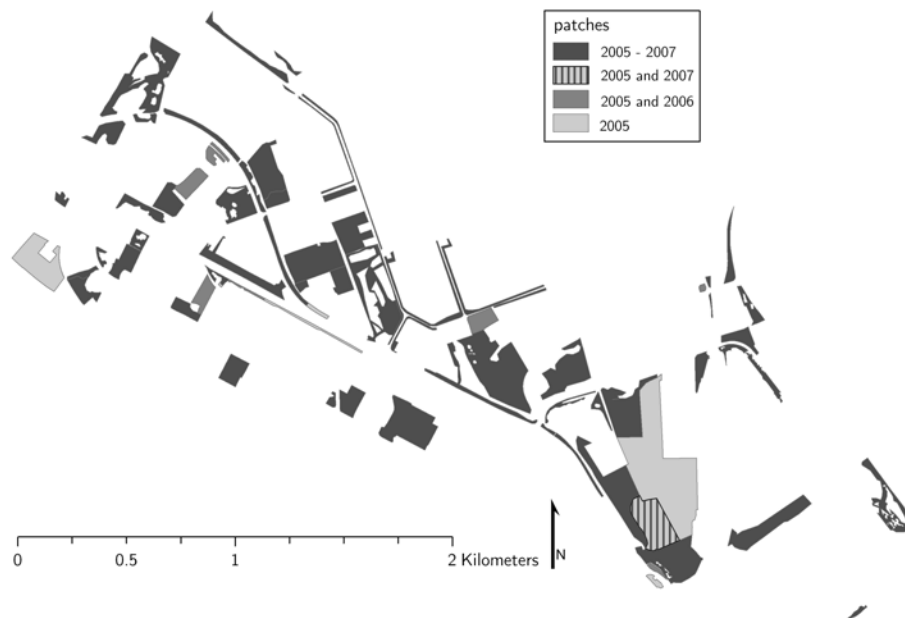


Figure 7.1: Grasshopper sampling patches for the incidence function model.

Metapopulation model

Basic assumption of all metapopulation models is that the sub-populations of a species inhabit patches which are spatially isolated from each other resulting in limited exchanges between the sub-populations. The incidence of a patch (i.e. the probability that a patch is occupied by the species) depends on extinction and colonisation events.

Assuming a positive correlation between patch area and population size, the extinction probability of a patch decreases with increasing patch area. With increasing isolation (i.e. increasing distance to other occupied patches) colonisation events become more and more unlikely. Thus, the colonisation probability depends on the patch's connectivity (S_i) to occupied patches ($p_j = 1$; 0 otherwise) of the previous year, which is calculated by

$$S_i = \sum p_j \cdot e^{-\alpha d_{ij}} \cdot A_j \quad \text{for } i \neq j \quad (7.1)$$

The parameter d_{ij} is the distance between patch i and patch j in km. $1/\alpha$ gives the average dispersal distance of a species. The distance was computed (i) from centre to centre or (ii) from edge to edge of the patches. I calculated S_i for values for α of 0.1, 0.5, 1, 1.5, 2, 3, 4, 5, 10, 20, and 50, respectively, with equivalent mean dispersal distance of 10 km to 20 m using the program *Isolator* 1.3 (Biedermann, 1999-2003). I also checked if the distance to the next occupied patch had an effect on incidence or colonisation.

7.3 Results

About 65–80 % of all patches were occupied by *M. maculatus* over the three study years, while *O. caerulescens* inhabited approx. 40–65 % of the patches (table 7.1). Much more colonisation events were recorded for both species from 2005 to 2006 than from 2006 to 2007. In agreement with that, much less extinctions took place from 2005 to 2006 than in the consecutive time step.

Table 7.1: Number of occupied patches, extinction and colonisation events in the years 2005–2007 of *M. maculatus* and *O. caerulescens* in the study area.

year	number of patches	<i>M. maculatus</i>			<i>O. caerulescens</i>		
		incidence	colonisation events	extinction events	incidence	colonisation events	extinction events
2005	68	45			26		
2006	68	54	13	4	44	17	0
2007	62	43	3	9	32	4	13

Patch area had a positive effect on incidence and a negative one on extinction probability in most years as expected ((Wilcoxon rank sum test, $p < 0.05$; table 7.2). As opposed to that, neither distance to the next occupied patch nor connectivity had the expected effect on incidence or colonisation for both species (Wilcoxon rank sum test, $p < 0.05$). Only for *M. maculatus* connectivity calculated with $\alpha = 3$ –10 had a significantly positive effect on colonisation in 2006. However, if the colonisation events for 2006 and 2007 were pooled, connectivity calculated with small α (0.1–1) significantly affected colonisation. Nevertheless, a univariate logistic regression analysis with colonisation as the dependent

and connectivity as the independent variable yielded no significant, positive relationships (Likelihood ratio test, $p < 0.05$).

Table 7.2: Effect of patch area on incidence and extinction. The table shows (x), for which years there is a significant positive correlation between patch area and incidence (inc) and a significant negative correlation between patch area and extinction (ex), respectively (Wilcoxon rank sum test, $p < 0.05$). A '-' indicates that no correlation was tested for this year (no extinction events).

year	<i>M. maculatus</i>		<i>O. caerulescens</i>	
	inc	ex	inc	ex
2005	x	-	x	-
2006	x	-	x	-
2007	x	x	x	x
pooled	x	x	x	x

7.4 Discussion

Although the investigated grasshopper species lived in patchy distributed habitats, patch isolation had no effect on occupancy or colonisation. Similar observations for populations living in clearly fragmented habitats were found for *O. caerulescens* (Maes & Bonte, 2006) and other species groups like butterflies (Rabasa et al., 2008) and beetles (Driscoll, 2008). Good dispersal abilities of the species could result in high recolonisation rates and a strong rescue effect yielding the lack of influence of connectivity on occupancy pattern.

Population turnover events are clearly unevenly distributed over the years. From 2005 to 2006 there was an increase in the number of recorded sub-populations while in 2007 much less occupied patches could be found than 2006 for both species. The number of habitat patches decreased in 2007 (table 7.1), but only 4 patches occupied by *M. maculatus* and 3 patches occupied by *O. caerulescens* were destroyed by building activity from 2006 to 2007. Thus, the strong decline particularly of *O. caerulescens* must have different reasons than destruction of occupied habitat patches.

As connectivity did not have any influence on neither patch occupancy nor colonisation, the variations could be explained by the climatic condition, which are clearly dissimilar for the summers 2005–2007. The field work period in 2005 was rather cold, rainy and cloudy, while 2006 was partly very hot and dry. The summer of 2007 was again cooler and more humid. These differences can be found in the climatic data of the time period 1st July to 31st August of the according years (figure 7.2). Maximum and mean temperature as well as sunshine hours are significantly higher in 2006 than in the two other years (Wilcoxon rank sum test, $p < 0.05$). Accordingly, humidity, cloud cover and precipitation are significantly lower in that year.

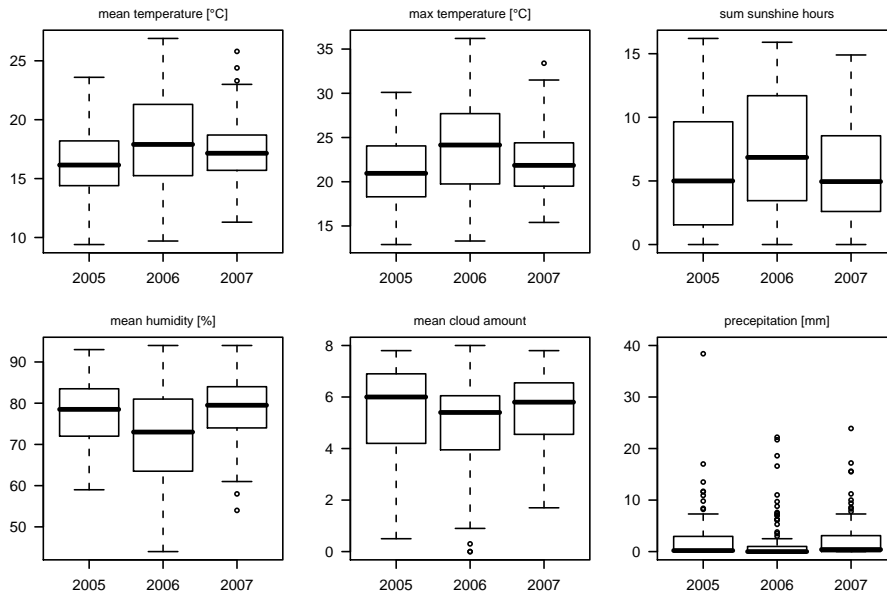


Figure 7.2: Boxplots of climatic variables of the summers (01.06.–31.08.) of the years 2005–2007.

Such climatic conditions can have two effects. First, at cooler temperatures grasshoppers are less active in terms of stridulation and also movement (Ingrisch & Köhler, 1998), which can increase the number of 'wrong zeros' (patches wrongly recorded as unoccupied). This, in turn, leads to an inflated number of colonisations in the consecutive, warmer year (from 2005 to 2006), while implying a misleading high number of extinctions in cooler years (from 2006 to 2007). Second, the climatic conditions can be the reason for more extinctions and less colonisations, as population density, survival probability, and establishment are known to be higher in dry and warm years as opposed to cool and wet ones mainly due to a lower larvae mortality (Ingrisch & Köhler, 1998).

7.5 Conclusions

I conclude that the variation in patch occupancy in the study area between the sampling years were mainly driven by the climatic conditions rather than by isolation of the patches. Thus, the data can unfortunately not be used to analyse metapopulation processes under the given assumptions and particularly not to draw conclusions about metapopulation persistence in relationship to land use (i.e. patch) configuration and turnover. I assume that the two grasshopper species studied here do not live in a metapopulation in the study area due to the lack of isolation, but that they form a spatially struc-

tured, but well connected single population.

Nevertheless, the data confirm the lower susceptibility of populations inhabiting larger patches to environmental stochasticity (here the climatic conditions) (Rabasa et al., 2008) as a lower local extinction risk was found to be clearly related to larger patch areas. This implies that even in well connected areas larger habitat patches should be preserved by conservation management. This is of particular interest for stronger climatic fluctuations as expected under climate change when species viability will depend on their ability to cope with intensified environmental stochasticity.

Especially *O. caerulescens*, which used to be very rare in the city of Bremen and which is threatened with extinction in Lower Saxony (Hochkirch & Klugkist, 1998), finds new habitats at artificially filled up building grounds of the study area. This was also observed during the sampling for the species distribution models in 2003 in the industrial park Bremen West (figure 1.1), which was also created by elevation and filling up former marshlands with sandy material and had been recorded as unoccupied by the species by Hochkirch & Klugkist (1998). These sandy, dry areas resemble the natural habitats of the species. Thus, conservation measures should take place to maintain such open patches.

During the course of development of the study area certainly more and more lots will be built-up as it was already observed during the time period investigated. The findings of this chapter imply that some large lots should be left open and unused to preserve habitat for *O. caerulescens* and *M. maculatus*. This can be achieved by either rather extensive management measures to sustain static lots at the right successional stage or by applying the TEMPO concept of temporary uses (e.g. storage areas, temporary offices, catering) and temporary conservation to maintain a dynamic mosaic of habitat patches with scarce vegetation cover.

Chapter 8

Combined effect of succession and landscape turnover on species persistence

Mira Kattwinkel, Robert Biedermann, Michael Kleyer,
ready for submission to *Oikos*.

Abstract

Dynamic landscapes are challenging habitats. Two processes generate spatio-temporal habitat transitions: stochastic disturbance and deterministic succession. Disturbance causes local extinctions by habitat destruction additional to those extinctions due to stochastic events like climatic fluctuations or demographic stochasticity. Successional changes in habitat quality further increase extinctions. How can species which rely on certain successional stages persist in such dynamic landscapes? In the present study, we used a metapopulation model to investigate species persistence in relation to landscape turnover and to species position on the successional gradient.

Our results showed that metapopulation persistence in a spatially dynamic, successional landscape depended on both landscape turnover rate and species specific successional requirements. Too slow turnover rates were insufficient to maintain species viability. Species position on the successional gradient triggered the viable range of landscape turnover rates. Furthermore, in landscapes of slower succession, a wider landscape turnover range was sufficient to maintain persistence. Species richness, scaled up from single species results, was also dependent on landscape disturbance.

Thus, disturbance was necessary to consistently re-initiate succession at some locations of the landscape and hence to maintain a spatio-temporal mosaic of different habitats. Ignoring temporal changes in habitat quality resulted in a misleading evaluation of landscape turnover on both single species and species richness level. For application in urban biodiversity management our findings imply that development and conservation can go hand in hand. Species persistence is maintained by habitat destruction at one location and creation at another forming a pattern of individually temporary sites.

Chapter 8: Effect of succession and landscape turnover on species persistence

keywords: metapopulation, dynamic landscape, habitat quality, succession, disturbance, simulation study, urban brownfields

8.1 Introduction

In recent years, much insight has been gained into the mechanisms affecting metapopulation survival in dynamic landscapes (Fahrig, 1992; Keymer et al., 2000). Landscape dynamics, emerging from natural disturbances like fire, wind, and flooding, or from management (Stelter et al., 1997; Wahlberg et al., 2002; Akçakaya et al., 2004), results in habitat destruction. This, in turn, yields deterministic local extinctions additional to those induced by stochastic events like climatic fluctuations or demographic stochasticity. Colonisation of the remaining patches or of newly emerging ones created by disturbance has to compensate for extinction to guaranty metapopulation persistence. Succession which converts suitable habitat patches to unsuitable ones further increases local extinctions (Amarasekare & Possingham, 2001). To sustain single species viability as well as species richness, the effect of landscape turnover and of species specific, succession dependent habitat requirements needs to be known.

Empirical studies showed the pronounced effect of habitat quality on metapopulation dynamics (Fleishman et al., 2002; Franken & Hik, 2004). Insect occurrences for instance are often directly linked to the successional stages of the vegetation (Steffan-Dewenter & Tschardt, 2002). Hence, shifts in vegetation structure, the establishment and later disappearance of host plants or changing micro-climatic conditions cause temporal changes in habitat quality (Wahlberg et al., 2002; Biedermann, 2004). Thus, disturbance and succession generate a mosaic cycle of spatial and temporal shifts in habitat quality (Kleyer et al., 2007). Species can only persist in such landscapes, if they are able to track these spatio-temporal habitat transitions.

Recently, a few studies explored metapopulation fate in dynamic landscapes that also included successional processes (Stelter et al., 1997; Boughton & Malvadkar, 2002; Bossuyt & Honnay, 2006; Wimberly, 2006). However, the combined effect of stochastic disturbances (habitat destruction and regeneration) and deterministic succession affecting metapopulation survival remained unexplored. Little is known about the role of species' niche position on the successional gradient and of the pace of succession for persistence in dynamic landscapes. Furthermore, most studies only focus on single species persistence instead of multiple species and species richness of a landscape. Thus, the question arises as to how several species with different habitat requirements can be maintained best within a dynamic landscape.

In the present study we used a simulation model to analyse metapopulation persistence of virtual insect species in relation to both landscape dynamics as well as species niche position and breadth. As a study system we chose urban brownfields (derelict land), which have been shown to offer habitat for a variety of insect species that depend on different successional stages e.g. leafhoppers, grasshoppers, and butterflies (Strauss & Biedermann, 2006; Angold et al., 2006). In this context, abandonment of lots opens new habitat patches, while rebuilding destroys habitat and the inhabiting populations. Open patches undergo succession with changes in vegetation structure (Schadek et al., 2008) as well as shifts in insect community assembly (Strauss & Biedermann, 2008).

Thus, habitat patches of changing quality and shifting location form a spatio-temporally fragmented landscape.

By means of this modelling study, we aimed to: (1) assess the role of species niche position and niche breadth; (2) understand how the pace of succession influences the effect of landscape turnover rate; (3) investigate how species richness responds to spatio-temporal landscape dynamics. Furthermore, we show how conservation planning can maintain metapopulation viability and species richness by management of a mosaic of temporary habitat patches.

8.2 Methods

Model overview

We used a patch based, spatially explicit stochastic metapopulation model. Without loss of generality rectangles with fixed boundaries defined the patches. Each patch could be either unsuitable (built-up in the context of our urban study system) or open. Open patches were potentially suitable for a species depending on its niche position and breadth, and could be either occupied or unoccupied.

Each time step, the population of an occupied patch could go locally extinct depending on the patch's area and habitat quality. Subsequently, unoccupied, open patches were colonised with a colonisation probability related to their distance to the occupied patches of the previous time step and to habitat quality as well as area of those patches. After these two processes, open patches grew one year older, thus changing their habitat quality. At the last step in the sequence, landscape turnover converted open patches to unsuitable (built-up) ones and also created new open patches by abandonment of built-up ones.

Metapopulation dynamics

Habitat quality. Assuming a correlation between population size and patch area (A) as well as habitat quality (hq), hq modifies the effective patch area (Moilanen & Hanski, 1998). In the present study, hq of patch i was only determined by the patch's successional age (t_i) as the time since its emergence as an open patch. We assumed that every species had an optimum position (no) and a certain niche breadth (nb) on the successional gradient. Using a Gaussian distribution with maximum ($hq = 1$) at no and standard deviation nb we described habitat quality as (figures 8.1 and 8.2):

$$hq_i = \exp\left(\frac{1}{2} \cdot \frac{(t_i - no)^2}{nb^2}\right). \quad (8.1)$$

Extinction. A patch's extinction probability (E_i) is related to its area (A_i) and its habitat quality (hq_i) due to the relationship of population size to these two parameters. We expressed E_i as:

$$E_i = \min\left(\frac{n}{(hq_i \cdot A_i)^x}, 1\right). \quad (8.2)$$

Here, x reflects the population's susceptibility to environmental stochasticity. The parameter n determines the minimum effective patch area $A_0 = n^{1/x}$; E_i equals 1 for patches with $A_0 \leq n^{1/x}$. The smaller x and the larger n the higher is the extinction risk of a population even if inhabiting large, high quality patches.

Colonisation. Colonisation probability (C_i) depends sigmoidally on the patch's connectivity (S_i) to occupied patches ($p_j = 1$; 0 otherwise):

$$S_i = \sum p_j \cdot e^{-\alpha d_{ij}} \cdot (hq_j \cdot A_j)^{0.5} \quad \text{for } i \neq j \quad (8.3)$$

$$C_i = \frac{1}{1 + \left(\frac{y}{S_i}\right)^2}. \quad (8.4)$$

The parameter d_{ij} is the distance between patch i and patch j . The survival rate of migrants over this distance is scaled by α , with $1/\alpha$ giving the average dispersal distance of a species. The parameter y describes the colonisation ability of a species; the smaller y the less affected is the species by isolation.

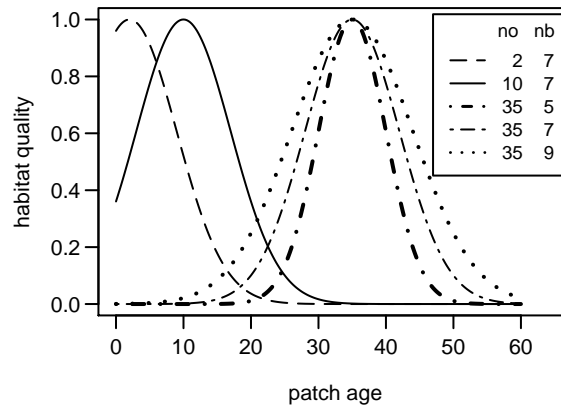


Figure 8.1: Habitat quality as a function of successional patch age for different niche optima (no) and niche breadths (nb).

Landscape initialisation and dynamics

The two dimensional landscape of size 200 by 200 was generated by dividing it into 400 patches, whose geometry was constrained by minimum patch area, width, and height

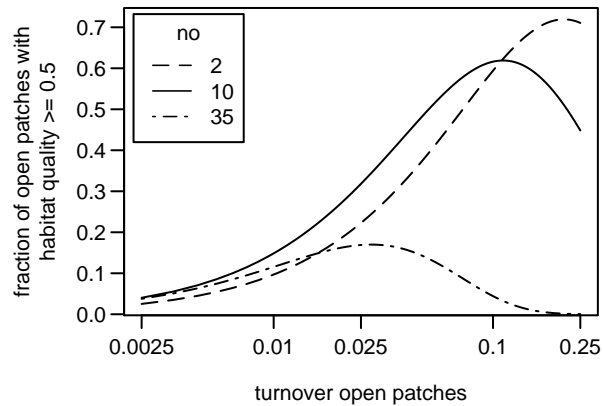


Figure 8.2: Average fraction of open patches with habitat quality > 0.5 as a function of landscape turnover for three different niche optima. $nb = 7$.

(table 8.1). We performed the simulations on a torus to avoid edge effects. After landscape generation, a fraction of patches according to the scenario settings were randomly chosen to be open and thus potentially suitable for colonisation (figure 8.3). The remaining patches were defined as unsuitable resembling the inhabitable matrix. Initial age of the open patches had a geometric distribution (see below). For initialisation, landscape turnover took place for 500 time steps which included (i) destruction of open patches (ii) emergence of new ones, and (iii) ageing of the patches. Subsequently, a random 50 % of the open patches were occupied by each species at the beginning of each simulation run.

Landscape turnover was spatially and temporally uncorrelated; each patch had the same independent probability to become built-up or open, respectively, at each time step. We chose the two turnover rates (open to built-up and built-up to open) such that the overall proportion of open patches stayed constant on average, to exclude the effect of habitat loss. The number of open patches fluctuated stochastically. This parameter setting resulted in a geometric distribution of patch ages with mean $1/(\text{turnover open to built-up})$ (Boughton & Malvadkar, 2002).

Simulation experiments

All species specific parameters except for niche optimum (no) and niche breadth (nb) were constant (table 8.2). For all scenarios, we tested the effect of different landscape turnover rates (turnover from open to built-up between 0.0025 and 0.25) at a fraction of open patches of 25 %. We assessed the relationship between species persistence at different turnover rates and niche position by setting no to 2, 10, and 35, respectively, while fixing nb to 7 (figure 8.1). By fixing no to 35 and setting nb to 5, 7, and 9, respectively, we explored the role of niche breadth. We defined different paces of succession of the

Table 8.1: Parameters of landscapes with different variances in patch area. Number of patches = 400; maximum, median, and variance of 500 repetitions. The setting for medium variance is the default one for all other simulations.

	no variance	medium variance (default)	high variance
min patch area	100	49	9
min patch width and height	10	7	3
max patch area	100	715	1566
median patch area	100	90	75
variance in patch area	0	1844	6937

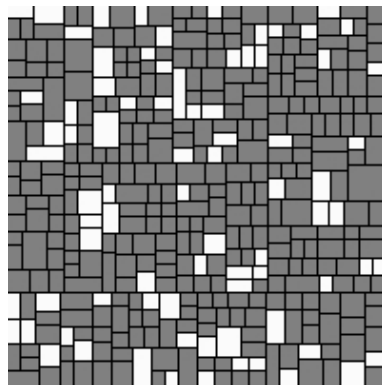


Figure 8.3: Generated landscape with a proportion of open patches (white) of 0.25; total number of patches is 400, minimum patch size is 49.

habitats for a rather late successional species by increasing and decreasing the value of nb by two units, and increasing or decreasing no by the according factor. In doing so, we compared fast succession ($no = 25$, $nb = 5$), with a medium pace of succession ($no = 35$, $nb = 7$), and slow succession ($no = 45$, $nb = 9$).

Furthermore, we assessed the effect of variability in patch area by comparing three settings: (i) quadratic patches all of the same size (no variance in patch area), (ii) medium variance in patch area (default), and (iii) high variance in patch areas (table 8.1). Additionally, we investigated how the way disturbance affects the landscape influences metapopulation persistence. For that purpose, we contrasted the random disturbance described above with a disturbance algorithm, where at each time step exactly the same number of patches became open as became built-up. In a third setting, the same patches stayed open over the whole simulation run, while disturbance re-initiated their succession. Thus, the second setting had always a fixed number of open patches, while in the latter one additionally the location of patches was fixed.

Table 8.2: Parameter values of species properties defining local extinction risk (n , x) and colonisation ability (y , α).

Parameter	Value
n	11.1803
x	1.5
y	75
α	0.02

The model used 1-year time steps and simulations were run over 100 time steps. We calculated the survival probability as the proportion of surviving metapopulations in 500 repeated simulation runs. As a measure of species richness, we aggregated the modelling results of three species with different niche optima (2, 10, and 35) and identical values for all other species specific parameters. To this end, we summed their survival probabilities at the different paces of turnover and additionally at different fractions of open patches, respectively (Nicholson & Possingham, 2006).

8.3 Results

In our spatio-temporal dynamic landscape the position of habitat patches shifted due to destruction and creation, while succession caused changes in their quality over time. In such a landscape, species could not persist at very low turnover rates (figure 8.4 a). The survival probability in relation to landscape turnover was subject to the position of the habitat quality optimum (niche optimum n_0) on the successional gradient. Mid successional species ($n_0 = 10$) outperformed early and late successional ones with metapopulation persistence over the widest range of turnover rates. Compared to that, early successional species ($n_0 = 2$) could persist only if turnover was high enough, whereas late successional species ($n_0 = 35$) were at high risk of extinction at increased turnover rates.

Reducing niche breadth (nb) by only 2 units could result in completely unviable populations under the simulated landscape settings (figure 8.4 b). Likewise, increasing nb clearly enhance metapopulation persistence and enlarged the range of sustainable turnover rates. Thus, generalist species had a higher viability than specialists.

Likewise, the pace of succession, defined by different combinations of niche optimum and niche breadth, influenced metapopulation persistence (figure 8.4 c). The faster succession, the higher was the viable turnover rate and the smaller its range for species survival.

The variance in patch area had a considerable influence on metapopulation persistence. If all patches were of the same size, survival probability was significantly higher over a wide range of turnover rates compared to the default setting (pairwise comparison of the

number of surviving metapopulations, χ^2 – test, $p \leq 0.05$; figure 8.4 d). Similarly, if patch areas varied stronger, species survival decreased significantly. As opposed to that, the way disturbance acts on the landscape had no effect on metapopulation persistence.

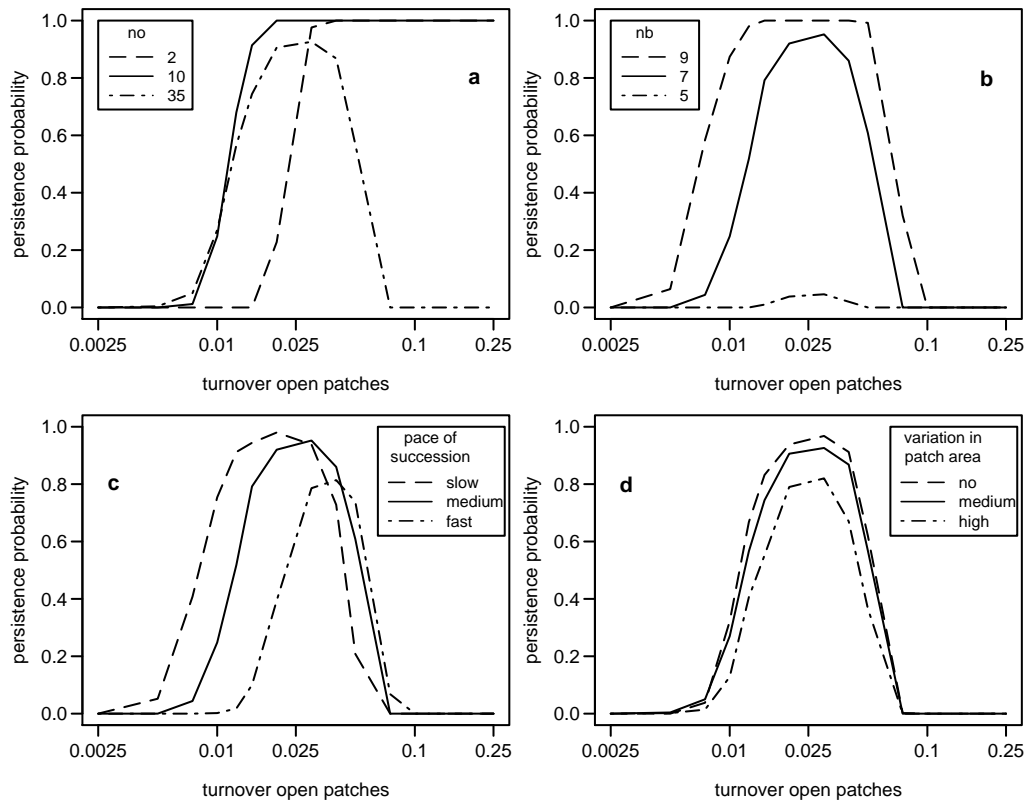


Figure 8.4: Metapopulation persistence as a function of landscape turnover; a: in relation to niche optimum, $nb = 7$; b: in relation to niche breadth, $no = 35$; c: in relation to the pace of succession (slow succession: $no = 45$, $nb = 9$, medium pace of succession: $no = 35$, $nb = 7$, fast succession: $no = 25$, $nb = 5$); d: in relation to the variance in patch areas (no variance: all patches have size = 100, medium variance: minimum patch area = 49, high variance: minimum patch area = 9), number of patches = 400, $no = 35$, $nb = 7$. The fraction of open patches is 0.25 for all simulations.

Apart from the above mentioned effects on single species, landscape dynamics and configurations had a strong effect on species richness (figure 8.5). The pace of turnover triggered the cumulative survival probabilities of three species with different niche optima. The fraction of open patches (i.e. the number of potentially suitable ones) determined the range of turnover rates at which all three species had a high survival probability. For the species modelled here, intermediate turnover rates resulted in the highest species richness in the whole study area expressed as the sum of persistence probabilities.

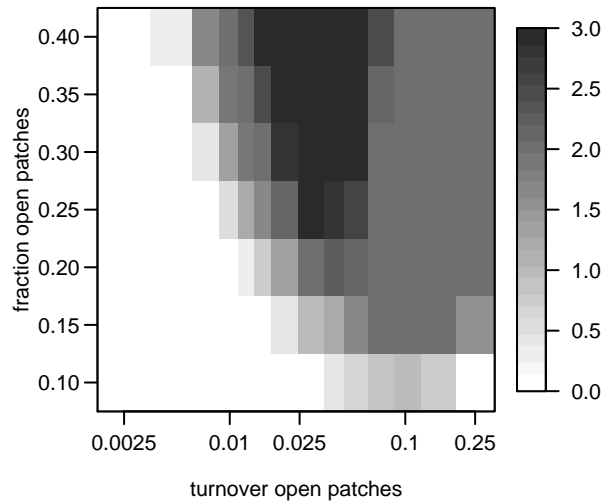


Figure 8.5: Species richness as a function of landscape turnover and fraction of open patches. The graph shows the sum of species' persistence probabilities for three species with different niche optima (2, 10, 35), $nb = 7$.

8.4 Discussion

We investigated metapopulation persistence in dynamic landscapes subject to two processes influencing the spatio-temporal configuration of habitats: spatially stochastic patch disturbances and deterministic succession altering habitat quality. For species relying on certain successional stages, landscape turnover was essential for persistence because it was needed to re-initiate succession. Thus, landscape turnover influenced the amount of suitable habitat (Johnson, 2000; Amarasekare & Possingham, 2001).

Our results showed that different landscape turnover rates maintained persistence dependent on species' niche position on the successional gradient. Consistent with the findings of Ellner & Fussmann (2003) viability thresholds depended on which successional stage a species required. At first glance one would expect that species persistence arranges along the turnover gradient in order of their position on the successional gradient. Late successional species should benefit most from low turnover rates, early successional ones would be sustained by high turnover rates and mid successional species in between. However, mid successional species outperformed both early and late successional ones by high persistence probabilities from low to high turnover rates. For early successional species, this is due to the fact that the left side of the Gaussian habitat quality curve is cut off (figure 8.1) resulting in a smaller area under the curve. On the other hand, there are always much more young patches than old ones due to the geometric distributed patch ages in such a randomly disturbed landscape. Thus, the number of suitable patches for

a late successional species is low even at low turnover rates (figure 8.2). If disturbance was patch age dependent like habitat quality, the age distribution and thus habitat quality distribution would be different. For instance, older lots could be less likely to be built-up again due to higher development costs, or, as an example of natural disturbances, fire resistance could be related to forest stand age (Syphard & Franklin, 2004).

The breadth of the successional niche of a species strongly affected species persistence as it influences the proportion of suitable habitat patches in a dynamic landscape. Plant species turnover generally declines over the course of succession (Cook et al., 2005; Anderson, 2007), associated with a decrease of the pace of changes in vegetation structure. Thus, species inhabiting late successional stages might find their host plants or appropriate vegetation structure over a wider span of patch ages than those relying on early successional stages. From that follows that late successional species, which suffer from less suitable habitat in dynamic landscapes as outlined above, might compensate for this disadvantage by a wider niche on the patch age gradient.

The pace of succession that characterised the landscape also had a remarkable effect on species persistence probability in relation to turnover rate. We defined slow succession by a later but wider peak in habitat quality compared to fast succession. In our simulation study, landscapes of slower succession maintained high survival probabilities over wider ranges but at lower turnover rates than landscapes of fast succession. Opposed to our findings, higher patch growth rates (corresponding to the pace of succession) increase population viability if habitat quality (expressed as carrying capacity) increases sigmoidally with time (Johst et al., 2002). Hence, results strongly depend on the assumptions made about the way succession affects habitat quality. The pace, direction, and climax stage of plant succession are driven by climatic conditions, nutrient availability, and soil moisture (Otto et al., 2006; Prach & Rehoukova, 2006). They should be taken into consideration in conservation of species depending on a certain vegetation structure or host plant availability.

Variance and location of landscape turnover did not affect species persistence as long as on average the same number of potential habitat patches stayed open. Thus, habitat destruction and regeneration can occur at random locations, or the restart of succession could even be maintained by management activities. However, as spatial correlated disturbances reduce metapopulation persistence (Johst & Drechsler, 2003; Vuilleumier et al., 2007), habitat destruction and redevelopment should be rather randomly distributed. With respect to our urban study system, this meets the requirements of spontaneous urban development. For patch areas, an equality is favourable, because it prevents fluctuations in total suitable habitat area.

Species richness also responded to the pace of landscape turnover. Our findings are similar to those of Roy et al. (2004): species richness of communities of competing species inhabiting spatially dynamic but non-successional landscapes likewise depends on landscape turnover rate. In biodiversity conservation, the succession dependent habitat requirements of each species might be unknown and therefore the exact optimum landscape turnover remain indeterminable. Moreover, landscape dynamics can usually

no be controlled to the point. Therefore, the lower dependency of species richness on a certain turnover rate at higher fractions of open patches gives another motivation to allocate more area to conservation.

Our study system were habitat patches within urban business areas. The need of landscape turnover for species persistence offers a new perspective of urban conservation. In line with the concept of dynamic nature reserves (Bengtsson et al., 2003), urban biodiversity management should not be restricted to stationary areas within cities but should be maintained in a spatio-temporal mosaic of moving habitat patches. Locally 'temporary conservation' provides the opportunity to react on economic needs in time by keeping open lots ready for development, while simultaneously maintaining urban biodiversity.

8.5 Conclusions

In dynamic landscapes, species persistence strongly depends on life history and dispersal traits (Brachet et al., 1999; Keymer et al., 2000; Johst et al., 2002; Bossuyt & Honnay, 2006). In the present study we showed that under succession depended habitat quality, as it can be found in many ecosystems (Thomas, 1994; Eber & Brandl, 2003; Perry & Millington, 2008), metapopulation viability is additionally determined by species position on the successional gradient and by the pace of succession of the landscape. While ignoring landscape dynamics can lead to an overestimation of species persistence (Hastings, 2003; Akçakaya et al., 2004), here we discovered that ignoring successional dynamics would result in a misleading evaluation of landscape turnover on both single species and species richness level. Disturbance can have a positive influence on temporal habitat connectivity and thus enhance metapopulation persistence (Keymer et al., 2000; Roy et al., 2004; Wimberly, 2006). In a successional landscape, landscape turnover is additionally needed to continuously re-initiate succession at certain locations of the landscape.

Acknowledgements

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Chapter 9

Synthesis

9.1 General remarks

Brownfields, as a special case of urban green spaces, provide wildlife habitat, water and micro-climate regulation as well as social and cultural values. In modern cultural landscapes they represent the wildest and least anthropogenic influenced habitats. Moreover, urban brownfields can contribute considerably to urban biodiversity. Nevertheless, they have been integrated into urban conservation planning very rarely (Herbst & Herbst, 2006). Despite their recognition as valuable habitats by ecologists (Gibson, 1998; Maurer et al., 2000; Angold et al., 2006), they are rather perceived as undesirable by urban planners, associated with despair and emptiness (Harrison & Davies, 2002; Herbst, 2003). Hence, there is a need to investigate their potential for urban conservation and to translate the findings into recommendations for urban planners.

In this thesis, I analysed the species-environment relationships of multiple species based on extensive field data. From this data, I built species distribution models (SDMs) to identify the main drivers of species occurrence. Furthermore, I developed a landscape model to extrapolate the plot based SDMs to the landscape scale to investigate different scenarios. By this means and by a second modelling approach (the metapopulation model), I derived general rules for species persistence and recommendations for urban conservation planning regarding the spatio-temporal arrangement of urban brownfields. Furthermore, the concept of temporary conservation was applied in an exemplary planning study.

9.2 Driving forces of biodiversity on urban brownfields

The most important finding of this thesis is that species which find habitat on urban brownfields rely on landscape turnover, i.e. habitat destruction by redevelopment and habitat regeneration by abandonment. These species depend on different successional stages. Thus, landscape turnover maintains a spatio-temporal mosaic of transient habitats, which offers a variety of habitats for different species on the landscape scale.

On single species level, the two modelling approaches revealed distinct responses of species occurrence and persistence to the landscape turnover rate, which determines average site age. By scaling up SDMs to the landscape scale I identified species, that

benefited from many young sites (i.e. a fast turnover), others that depended on a sufficient number of older sites, and some that exhibited a unimodal relationship to landscape turnover rate (chapter 4, figures 4.4 and 4.5). A fourth, small group was independent of the pace of turnover. Thus, for most species the pace of turnover influenced the amount of suitable habitat depending on species specific requirements (Johnson, 2000; Amarsekare & Possingham, 2001).

An increase of the proportion of brownfields and therefore of the potential habitat area had a positive effect on the species richness and the rarity index of the landscape as well as on metapopulation persistence. On the one hand, a higher proportion of brownfield sites increased the chance to meet the habitat requirements of a multitude of species. Moreover, it reduced the risk of global extinctions by providing habitat for more or larger local populations. Thus, the more area was left open over a certain period of time, the higher was the conservational value of the whole area. Additionally, a higher brownfield proportion allowed a faster turnover. This is due to the fact that it increases the probability of a single patch to run through the whole course of succession and thus to provide habitat for even late successional species. However, in the context of the TEMPO concept, a certain proportion of built-up area is necessary to maintain site dynamics by abandonment and redevelopment with feasible periods of economic use of the sites.

In addition to the spatio-temporal structure of the landscape, which was defined by the turnover rate, species responded strongly to abiotic site conditions, landscape context and, in the case of insect species, to the present vegetation. Likewise, metapopulation persistence is considerably influenced by the pace of vegetation succession, which is driven by soil properties, the present seed bank and biological interactions (Rebele, 1994; Gibson et al., 2005). Thus, although this study focuses on spatio-temporal factors, local habitat conditions should be kept in mind in urban conservation planning. For instance, xerophile species like *Oedipoda caerulescens* will not be found at open but moist patches with high groundwater tables. The importance of both local and landscape factors as well as abiotic conditions and landscape dynamics requires the implementation of urban conservation on the landscape scale. This fact has been recognised but is nevertheless often neglected (Flores et al., 1998; Mörberg et al., 2007).

9.3 Advantages of a multi-species approach

Due to varying habitat requirements and susceptibilities (Bastin & Thomas, 1999; Garden et al., 2006), species responded differently to the environmental conditions and spatio-temporal parameters. Although it is impossible to model all species of a landscape, an approach that focuses only on single or few species is unsuitable for biodiversity management (Chase et al., 2000).

Likewise, the prediction of diversity indices in response to environmental parameters is often misleading. Such approach neglects the fact, that local species richness may be similar at different locations or remain constant over the course of succession, whereas

species composition varies considerably in space and time (Brown et al., 2001; Strauss & Biedermann, 2006). Therefore, in both modelling approaches I scaled up single species simulation results to biodiversity indices for the whole study area (Olden, 2003). Such a multi-species approach can be further improved by assigning weights according to the species' status of endangerment (Early & Thomas, 2007). The rarity index I used to evaluate the SDMs simulation results is an example of such a species specific weighting.

9.4 Species distribution models

SDMs in biodiversity conservation

If SDMs are applied to derive guidelines for conservation management for a multitude of species, the question arises whether the pool of modelled species is considerably biased and thus not representative for all species living in urban brownfield environments. Another point is that SDMs are based on an equilibrium assumption, which might not hold in such a dynamic environment (Rebele, 1994). Hence, another question is, if species are actually able to track the spatial habitat transitions.

One considerable limitation of SDMs is their restriction to the more common species if no special sampling scheme is applied (Engler et al., 2004). This is due to the fact that a minimum prevalence is required for statistical model building. The pool of species is further limited to those species that are responsive to the considered environmental parameters. At the study plots, out of 231 recorded vascular plant species, only 64 had a prevalence of $\geq 10\%$. Only 37 out of these were modelled by SDMs. Likewise, out of 146 leafhopper and 11 grasshopper species, 41 and 8, respectively, met the prevalence criterium. Of these, 36 leafhopper species and 7 grasshopper species could be modelled by SDMs. To verify the representativeness of these species they were investigated with regard to their functional traits.

Analyses of functional traits

Functional trait data collected by Schadek (2006) describing dispersal abilities and seed characteristics of those plant species with a prevalence of at least 10 % at the study plots (table 9.1, left) was analysed. I assessed whether dispersal limitations influenced species responsiveness to the considered environmental parameters. Dispersal limited species are assumed to be associated with older brownfield sites as it takes them a longer period of time to reach suitable habitats. Therefore, I investigated whether the trait values had an effect on the role of the parameter site age (as time since initiation of succession) on species occurrence. Additionally, I analysed functional traits of all recorded leafhopper species (table 9.1, right) collected by Strauss (2007). By this means, I gained insight into the bias of the pool of leafhopper species which can be described by the SDMs approach. For grasshoppers no trait data was available. In detail, it was explored whether

- i) the responsive plant species (37 out of 66) were different regarding their traits compared to the non-responsive ones,
- ii) the leafhopper species with a sufficient prevalence for model building ($\geq 10\%$) were different regarding their traits compared to the more infrequent ones.

Additionally, it was investigated if there was a relationship between

- iii) species traits and model performance,
- iv) species traits and the form of the statistical relationship between species occurrence and site age (sigmoidal positive, sigmoidal negative, unimodal or none),
- v) plant species dispersal traits and responsiveness to the parameter site age as well as the model weight of this parameter.

Table 9.1: Plant species traits analysed for all species with prevalence $\geq 10\%$ (left) and leafhopper species traits analysed for all recorded species (right).

trait	data type	trait	trait categories
terminal velocity	numerical	hibernation	egg, nymph, adult
wind dispersal potential	categorical	host plant type	herbs, grasses, herbs & grasses, woody plants
seed number (whole plant)	numerical	phagy	monophagous, oligophagous, polyphagous
seed weight (single seed)	numerical	volinism	1 generation/year, 2 generations/year
seed longevity	index		

The analyses showed the following results:

- i) Plant species responsiveness to the environmental parameters was not significantly related to any of the investigated traits (Wilcoxon rank sum test, $p \leq 0.05$).
- ii) All analysed leafhopper traits except from hibernation strategy had a strong effect on leafhopper prevalence (Wilcoxon rank sum test, $p \leq 0.05$). Leafhoppers that occurred at a sufficient number of plots for model building were associated with (1) being faster in reproduction (two generations per year), (2) were more likely to be oligophagous or polyphagous than monophagous, and (3) more frequently fed on herbs and grasses or only herbs than on grasses or woody plants than the more infrequent species.
- iii) There was no relationship found between any plant or leafhopper trait value and model performance (AUC_{cor} , R_{Ncor}^2 , CCR, sensitivity, and specificity; Spearman's $\rho < |0.5|$ for plant traits; Wilcoxon rank sum test, $p \leq 0.05$ for insect traits).
- iv) Regarding the form of the relationship between species occurrence probability and site age there was no significant association to plant species dispersal traits

or seed characteristics (Wilcoxon rank sum test, $p \leq 0.05$). Likewise, the form of the relationship was independent of leafhopper trait values (Fisher's exact test, $p \leq 0.05$).

- v) There was no relationship between plant dispersal traits and the the responsiveness to site age or the model weight of the parameter site age (Spearman's $\rho < |0.5|$).

The pool of modelled species

As opposed to the plants species, nearly all (36 out of 41) leafhopper species with a prevalence of at least 10 % were responsive to the environmental parameters. The pool of sufficiently common species for statistical modelling was, however, seriously biased compared to all recorded leafhopper species. Generalist species, with fast development were clearly more likely to be common than specialists with slower development or depending on later successional stages (i.e. feeding on woody plants). Nevertheless, the modelled leafhopper species showed no preference for habitats of young site age.

Plant species responsiveness to the environmental parameters was independent of dispersal limitations and seed characteristics. Moreover, dispersal ability did not affect model performance. Likewise, the effect of the parameter site age was not related to the trait values and seed longevity did not affect model performance or species responsiveness. As opposed to that, Verheyen et al. (2004) found a clear trend of limited dispersal ability and a transient seed bank for species responding to site age. Thus, in the present study site age in the SDMs is rather a proxy of the successional stage of a site in terms of e.g. soil development or competition than one of dispersal limitation of the plant species (opposed to the assessment of Bastin & Thomas (1999)).

A reason for the slightly lower model performance of plant species compared to the insects and also for the lower proportion of responsive species might be due to different seed banks among the sampling plots. Furthermore, competition might be more important among plants than insects. Hence, the lack of a seed bank or the presence of a superior competitor could result in absences of otherwise suitable plot which yield a lower responsiveness and performance.

Concluding, for the plant species dispersal limitations seem to be negligible in the study area or are captured by the landscape context variables. Furthermore, neither plant nor leafhopper model performance was related to the values of the tested traits. SDMs performance was of satisfying quality and within the range of comparable studies (Pepler-Lisbach & Schröder, 2004; Wintle et al., 2005). With respect to urban conservation planning the SDMs approach seems capable of identifying the main drivers of species occurrence. Moreover, it is applicable and sufficiently reliable to find optimal brownfield turnover rates and configurations. Nevertheless, one should still keep in mind that mainly leafhoppers of rather early successional stages were modelled and that it is unknown if the plant species pool is likewise biased. Furthermore, no dispersal traits were investigated for the insect species and only for the more common plant species. It

might be that scarce species depend on well connected habitat networks (Rudd et al., 2002; Bryant, 2006; Sandström et al., 2006). For these species, it is particularly important that a sufficient density and connectivity of habitat patches i.e. a high fraction of brownfield sites is maintained.

9.5 Metapopulation modelling

To complement the statistical SDMs approach by one that includes dynamic processes like colonisation and extinction, I additionally applied a metapopulation approach. By this means, further insight was gained into species response to landscape dynamics (turnover as well as changes in habitat quality). The underlying assumptions here were that (i) local extinctions are less likely on larger habitat patches and (ii) colonisation events are positively related to patch connectivity (Hanski & Thomas, 1994).

The first, empirical approach was to map patch occupancy of the two grasshoppers *Myrmeleotettix maculatus* and *Oedipoda caerulescens* in an industrial area in Bremen over three consecutive years. However, no metapopulation structure was found. The incidence of the two species was not influenced by isolation but seems to be mainly determined by habitat quality. Similar results have been found e.g. in butterflies inhabiting urban areas (Wood & Pullin, 2002; Angold et al., 2006). Nevertheless, data analysis revealed that larger habitat patches are more likely to be occupied by the two studied species. This proved at least one underlying principle of patch occupancy models. Furthermore, the study also showed that the two grasshopper species do indeed find habitat on urban brownfields, which is particularly relevant for the Red listed one *O. caerulescens* (Maas et al., 2002).

Thus, not all species inhabiting patchy environments form metapopulations (Driscoll, 2008). However, there are numerous empirical examples emphasising the role of patch area and connectivity additional to local habitat quality on species persistence. For instance, lower habitat quality can be compensated by higher patch connectivity in butterfly metapopulations (Binzenhöfer et al., 2008). Similarly, the positive effect of connectivity on occupancy was found for multiple species (e.g. Snäll et al., 2004; Cousins, 2006; Maes & Bonte, 2006). In urban areas of isolated, often small habitat patches, connectivity can be of special importance (Rudd et al., 2002; Helden & Leather, 2004).

Therefore, in a second, theoretical approach, I developed a metapopulation simulation model to investigate species persistence in landscapes subject to both stochastic disturbances and deterministic succession. The virtual species of this simulation study can be regarded e.g. as grasshoppers related to certain succession stages of the vegetation. I investigated the persistence of an early successional species, a mid, and a late successional one. Examples for such species could be, the Blue Sand-Grasshopper (*Sphingonotus caerulans*), which is an early successional species depending on bare sand or gravel. It colonises secondary habitats like railroad tracks and abandoned industrial sites (Bellmann, 1993). The Lesser Field Grasshopper (*Chorthippus mollis*) for instance is

a mid-successional species associated with dry grasslands and heathlands, whereas e.g. the Oak Bush-cricket (*Meconema thalassinum*) inhabits sparse woods and hedges as a late successional species (Bellmann, 1993).

The simulation study revealed that species persistence depended on landscape turnover (see above, chapter 9.2). Furthermore, it was shown that landscapes of slower succession sustained species over a wider range of turnover rates. Thus, nutrient poor sites, that show retarded succession might be particularly important for maintaining populations on urban brownfields (Small et al. 2006).

Obviously, this model contained some considerable simplifications. In contrast to the SDMs approach, habitat quality was only determined by the successional site age of a patch. All other factors shaping species occurrence were ignored. As succession is the change of community composition with time, it is obviously related to site age (Steffan-Dewenter & Tscharrntke, 1997; Prach & Rehoukova, 2006). However, other factors like soil properties, the present seed bank, surrounding source habitats, and micro-climatic conditions shape the course and pace of succession remarkably (Rebele, 1994; Gibson et al., 2005; Rehoukova & Prach, 2006). Likewise, species life history and dispersal traits, which play a key role in metapopulation persistence in dynamic landscapes (Brachet et al., 1999; Keymer et al., 2000; Johst et al., 2002; Bossuyt & Honnay, 2006), were not assessed. I assumed a rather high dispersal ability according to the fact that virtual grasshoppers were modelled ($\alpha = 0.02$, corresponding to a mean dispersal distance of 500 m in a landscape of 2000 m by 2000 m if one unit length in the model equals 10 m). Species limited in their dispersal will presumably have smaller viable landscape turnover ranges and depend on higher proportions of brownfield i.e. more potential habitat.

However, the modelling results emphasised the importance of disturbance by habitat destruction and regeneration for species persistence. An example of a species relying on similar spatio-temporally dynamic habitats is the Pink-winged grasshopper (*Bryodema tuberculata*) which inhabits temporary gravel bars along braided rivers. Its persistence depends on a certain frequency of flood events to re-initiate succession (Stelter et al., 1997). In the current study, species viability could be similarly guaranteed over a certain range of landscape turnover rates depending on species successional requirements.

9.6 Brownfields in urban biodiversity management

Urban habitats, particularly brownfields, are suitable only for a limited pool of species (Kark et al., 2007; Strauss & Biedermann, 2008) but they comprise true urban communities, which cannot be found elsewhere (Alberti et al., 2003). Species that do find habitat on brownfields are often restricted to a certain part of the successional gradient. Thus, they depend on the repeated re-initialisation of succession at some locations of the landscape.

The strong effect of the spatio-temporal landscape configuration on both single species and species richness offers an opportunity for conservation management by means of

urban planning. As it can control site age and size, urban management can significantly influence the biodiversity of brownfields (Muratet et al., 2007). However, it is difficult to give exact recommendations for urban planning, as the optimum turnover rate strongly depends on which species are considered and how they are weighted against each other. This influences both single species results as well as aggregated indices like species richness and rarity. For the pool of species modelled by SDMs an intermediate turnover resulting in an average site age of 15 years was found to be optimal. The metapopulation model likewise predicts the highest species richness for rather low landscape turnovers. However, in praxis it might be impossible to control the turnover rate exactly. Still, if planners keep in mind that abandoned sites should be left untouched for some time, they can create a network of great ecological value. Additionally, some brownfields should be allowed to grow quite old. By this means also habitat for late successional species can be provided.

With respect to legal regulations of temporary conservation and temporary buildings there exist some building codes that are applicable to the TEMPO-concept (Scheele & Malz, 2007). For instance a temporary use can be defined in the development plan ('Bebauungsplan', BauGB) and likewise in projects and infrastructure plans ('Vorhabens- und Erschließungspläne'). However, just the legal protection of species can prevent a temporary re-building. If protected species are found at a site, the destruction of this certain habitat combined with a regeneration at a different location might be impossible, even if the species is a pioneer.

Regarding architectural design and infrastructure of temporary buildings already several approaches can be found in praxis (Draeger, 2008). Common features of such buildings should be that they are recyclable, modular, and easy to assemble. For instance container systems, pneumatic and tent constructions as well as wooden structures are in use. They are employed for manufacturing, logistics, the services sector, trading, and recreational uses.

I suppose, the best opportunity to apply the TEMPO-concept of temporary conservation and temporary buildings are newly planned business parks. In such business parks it is possible to plan for intended abandonment right from the beginning. Furthermore, temporary brownfield sites can be directly integrated as ecological compensation area and thus allow for rather high proportion of open green space. The practical application in our case study at the city of Oldenburg demonstrated the feasibility of the concept in a real planning situation. Moreover, it met interest among the municipality and the development company of the study area. The metapopulation study showed that the location of the re-initiation of succession is irrelevant although disturbances should be spatially uncorrelated (Johst et al., 2002; Vuilleumier et al., 2007). Hence, it is possible to combine several rather constant economic uses with some very short-term ones. Such a low-density business parks would also provide contact to nature at people's workplaces thus enhancing human well-being (Matsuoka & Kaplan, 2008).

Another application are shrinking cities that face the problems of population and economic decline (Haase, 2008). In that context, the active incorporation of brownfields into

urban development can help to sustain and improve real estate value.

However, if urban biodiversity is to be maintained by the TEMPO-concept, it is important to improve the acceptance and the reputation of temporary brownfields among residents as well as property holders. This can be achieved for instance by managed green spaces that frame and structure the brownfield lots to overcome the public feeling of despair and lack of control. Furthermore, people should be invited to use brownfields for recreational activities (Stadt Leipzig, 2005). On the other hand, landowners must be ensured that their development rights are preserved and that a permanent exclusion from economic use is not intended (Gibson, 1998).

The strong anthropogenic impact on urban habitats results in additional factors shaping species occurrence. Alongside environmental parameters, social, economic, and cultural factors influence urban biodiversity (Pickett et al., 2001; Hope et al., 2003; Kinzig et al., 2005). In such fragmented landscapes spatio-temporal habitat dynamics are of remarkable importance for species occurrence and persistence and should therefore be considered in conservation planning (Bastin & Thomas, 1999; Garden et al., 2006). In this thesis, I tried to shed light on the factors that drive species occurrence and persistence on urban brownfields and aimed at finding optimum spatio-temporal configurations to maintain habitat for a variety of species.

Despite all the mentioned constraints, I think that the concept of temporary conservation is valuable for urban biodiversity management. Obviously, urban brownfields offer species rich habitats which cannot be maintained by the common practice in nature conservation, i.e. by excluding some sites permanently from economic use. Integrating temporary brownfields into urban planning can preserve a network of sites of different successional stages without the need for heavy management. It dissolves the conflict between urban redevelopment and conservation interests and allows people to experience wild nature within cities.

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Appendix

Table A: Explanatory variables of the species distribution models.

symbol	description
soil properties	
brick.rubble	soil contains brick rubble (yes / no)
kf	soil coefficient of permeability [cm/d]
lk	soil air capacity [mm]
fk	field capacity [mm]
nfk	plant available field capacity [mm]
kak	effective cation exchange capacity [cmol/kg]
ph	pH (CaCl ₂)
ln.caco3	ln CaCO ₃ [ln kg/ha]
p	plant available phosphorus [kg/ha]
k	plant available potassium [kg/ha]
aw	plant available water [mm]
site age and disturbance	
site.age	site age in 2003 from aerial photographs [years]
age.area	average development age of the area (1, 2, 3)
disturb	current disturbance (Schadek, 2006)
landscape context	
brownf	proportion of brownfield
s	proportion of sparsely vegetated brownfield
d	proportion of dense vegetated brownfield
hi	proportion of brownfield with high vegetation
low	proportion of brownfield with low vegetation
age1	proportion of brownfield 0 - 4 years
age2	proportion of brownfield 0 - 6 years
age3	proportion of brownfield 0 - 8 years
age4	proportion of brownfield 0 - 11 years
age5	proportion of brownfield 6 - 11 years
age6	proportion of brownfield 10 - 20 years
age7	proportion of brownfield 15 - 25 years
age8	proportion of brownfield 25 - 30 years
age9	proportion of brownfield > 25 years
vegetation	
pls1, pls2	1st and 2nd PLS vegetation parameter
L	Ellenberg light indicator value
F	Ellenberg moisture indicator value
R	Ellenberg pH indicator value
N	Ellenberg nitrogen indicator value

Appendix

Table B: Plant species distribution models built by logistic regression and model averaging and some performance measures. The symbols are given in table A. Landscape context variables were calculated in radii of 25, 50, 75, 100, and 200 m, indicated by .25, .50, .75, .100, and .200, respectively. Ellenberg indicator values were multiplied with the respective plant occurrence probability at the plot and summed over all species ('sum_') or only for those with an indicator value > 4 ('index_').

species	species distribution model	AUC	R2N
Achillea millefolium	-2.649 -0.0003 * kf + 0.001 * lk 0.0008 * lk^2 + 0.001 * fk + 0.004 * nfk + 0.15 * ph -0.014 * ph^2 + 0.08 * site.age -0.002 * site.age^2 + 0.022 * aw -3.095 * age1.100 + 0.853 * age8.100 -1.593 * age8.100^2 -0.726 * brach.50	0.87	0.38
Agrostis tenuis	-6.902 + 0.001 * kf 0.001 * kf^2 + 0.003 * lk + 38.335 * kak -38.964 * kak^2 -0.68 * ph -0.068 * disturb + 0.017 * disturb^2	0.87	0.43
Arabidopsis thaliana	-24.447 + 0.077 * ph + 0.0004 * p -0.081 * site.age + 2.836 * age4.100 -3.348 * age4.100^2 + 57.372 * brach.50 -36.682 * brach.50^2	0.88	0.34
Arenaria serpyllifolia	-5.192 -0.001 * lk -0.001 * fk -0.002 * nfk + 0.885 * ph + 0.000003 * p -0.029 * aw	0.79	0.3
Arrhenaterum elatius	2.603 + 0.369 * brick.rubble -0.002 * kf + 0.106 * site.age + 0.048 * age4.25 -0.061 * age4.25^2 + 0.26 * age8.25 -0.227 * age8.25^2 + 0.297 * age7.50 -0.318 * age7.50^2 -7.284 * brach.25	0.96	0.61
Artemisia vulgaris	-17.074 -0.005 * kf - 0.003 * lk + 5.276 * ph -0.402 * ph^2	0.83	0.33
Betula pendula	-18.995 + 0.59 * ph -0.062 * ph^2 -0.131 * ln.caco3 + 0.005 * site.age -1.508 * age4.100 + 2.068 * age8.100 + 20.259 * brach.50 -12.769 * brach.50^2 + 30.639 * brach.200 -29.773 * brach.200^2	0.98	0.56
Bromus sterilis	-17.629 + 2.949 * ph -0.231 * ph^2 + 0.0002 * p + 8.482 * age.area -2.097 * age.area^2 -0.034 * aw	0.84	0.36
Cerastium holosteoides	1.068 -0.004 * kf -2.749 * brach.100	0.76	0.22
Chenopodium album	-4.119 + 0.218 * ph + 0.003 * p -0.000001 * p^2 + 0.003 * ln.caco3 -0.254 * site.age + 3.378 * age1.25 -2.748 * age1.25^2	0.91	0.42
Cirsium arvense	-100.683 + 0.542 * brick.rubble -0.001 * kf -0.004 * lk + 0.002 * kak + 31.284 * ph -2.471 * ph^2 + 0.0002 * p + 0.002 * k -0.0000004 * k^2 + 0.184 * age.area -0.044 * age.area^2 -0.006 * disturb -0.002 * disturb^2	0.9	0.46
Cirsium vulgare	-1.784 + 0.164 * site.age -0.007 * site.age^2 + 11.646 * age8.100 -20.47 * age8.100^2	0.74	0.21
Conyza canadensis	-4.92 -0.001 * site.age + 5.384 * age.area -1.404 * age.area^2 -0.043 * aw + 0.807 * age3.25 -0.412 * age6.25 + 5.699 * age2.200 -6.727 * age2.200^2 + 0.177 * brach.100	0.83	0.4
Corynephorus canescens	-9.689 -1.531 * brick.rubble + 0.033 * lk - 0.004 * lk^2 + 3.462 * ph -0.33 * ph^2 -0.003 * p -0.002 * k -0.038 * aw	0.89	0.44
Dactylis glomerata	-5.72 -0.003 * kf + 0.002 * fk + 0.003 * nfk - 0.000004 * nfk^2 + 0.001 * p - 0.0000001 * p^2 + 0.046 * site.age -0.001 * site.age^2 + 0.212 * aw -0.003 * aw^2 + 2.109 * age4.25 -2.497 * age4.25^2	0.88	0.38
Deschampsia cespitosa	2.546 + 3.467 * kak -0.571 * ph -1.17 * age.area	0.81	0.32
Festuca rubra	-0.528 -0.001 * kf + 0.067 * site.age + 0.005 * aw -0.137 * age2.25 -0.241 * brach.25	0.75	0.25
Holcus lanatus	5.016 -0.909 * ph + 0.0004 * aw + 0.062 * age5.25 + 7.96 * age4.50 -8.306 * age4.50^2 + 0.557 * age9.100 -0.714 * age9.100^2	0.79	0.33
Hypericum perforatum	-2.759 -0.005 * kf + 0.00005 * k + 0.057 * site.age -0.002 * site.age^2 + 1.985 * age.area -0.512 * age.area^2 + 13.316 * age8.50 -12.869 * age8.50^2 + 0.052 * age8.100 -0.065 * age8.100^2	0.88	0.48
Lolium perenne	-14.095 -2.543 * brick.rubble + 0.00005 * kf - 0.0000009 * kf^2 + 0.023 * fk - 0.00007 * fk^2 + 0.219 * nfk -0.001 * nfk^2 -0.235 * ph -0.001 * k -0.047 * site.age + 11.197 * age1.25 -8.148 * age1.25^2 -2.314 * age6.25 -2.515 * age9.25	0.96	0.65

Table B: continued.

species	species distribution model	AUC	R2N
Tripleurospermum perforatum	$-2.379 + 0.01 * ph + 0.028 * \ln.caco3 - 5.659 * age6.25 + 3.101 * age1.100 - 3.699 * age1.100^2 + 5.139 * age3.100 - 6.022 * age3.100^2$	0.83	0.32
Picris hieracioides	$-15.013 + 0.058 * site.age - 0.079 * age4.25 - 0.232 * age4.50 + 0.154 * age7.50 + 7.028 * age4.100 - 19.716 * age4.100^2 + 2.227 * age7.100 - 1.758 * age7.100^2 + 0.228 * age8.100 - 0.158 * age8.100^2 + 12.425 * brach.25$	0.96	0.57
Plantago lanceolata	$-1.735 + 0.018 * brick.rubble - 0.003 * kf - 0.003 * lk + 0.211 * site.age - 0.004 * site.age^2 - 0.149 * age3.25 - 0.359 * brach.25$	0.85	0.36
Plantago major	$-24.729 + 0.237 * brick.rubble - 0.005 * kf + 9.027 * ph - 0.762 * ph^2 - 0.343 * site.age - 1.692 * age7.25 - 1.692 * age8.25$	0.92	0.5
Poa annua	$-5.66 + 0.439 * ph - 0.296 * site.age + 2.901 * age.area - 0.538 * age.area^2 - 0.039 * aw + 0.164 * age1.25 - 0.097 * age1.25^2 - 1.468 * age7.25 - 1.468 * age8.25 + 2.437 * age1.50 - 1.996 * age1.50^2$	0.94	0.63
Poa compressa	$-10.758 - 0.016 * site.age + 7.391 * age3.25 - 5.952 * age3.25^2 - 0.098 * age7.25 - 0.1 * age8.25 - 0.098 * age7.50 - 0.102 * age8.50 + 0.094 * brach.50 + 22.838 * brach.100 - 14.958 * brach.100^2$	0.82	0.31
Poa pratensis	$-16.708 + 0.908 * brick.rubble - 0.001 * kf - 0.005 * lk + 5.518 * ph - 0.468 * ph^2$	0.78	0.23
Poa trivialis	$-4.565 + 0.175 * ph + 0.0000008 * p + 0.096 * \ln.caco3 + 0.136 * site.age - 0.005 * site.age^2 + 2.116 * age.area - 0.56 * age.area^2 + 1.888 * age3.50 - 1.617 * age3.50^2$	0.8	0.29
Rumex acetosella	$-15.384 - 1.223 * brick.rubble + 6.001 * ph - 0.57 * ph^2 + 0.0003 * k + 0.014 * site.age - 0.0004 * site.age^2 + 0.638 * age1.50 - 0.823 * age1.50^2 + 2.985 * age2.50 - 4.287 * age2.50^2 + 1.675 * age9.50$	0.85	0.42
Saxifraga tridactylites	$-52.266 - 0.012 * kf - 0.003 * lk + 12.057 * ph - 0.891 * ph^2 + 0.076 * \ln.caco3 - 0.001 * \ln.caco3^2 + 0.998 * age.area - 0.183 * age.area^2 + 10.076 * brach.25$	0.96	0.56
Senecio inaequidens	$-1.425 + 0.137 * site.age - 0.007 * site.age^2 + 2.457 * age4.100 - 3.219 * age4.100^2 + 2.623 * brach.100$	0.8	0.34
Taraxacum officinale	$-1.306 + 0.156 * ph + 0.0004 * p + 0.042 * \ln.caco3 - 0.026 * site.age - 0.027 * aw + 0.095 * age1.25 + 0.576 * age3.25$	0.77	0.29
Trifolium repens	$-4.43 + 0.542 * ph - 0.021 * site.age - 0.014 * aw + 1.647 * age1.25 - 1.359 * age1.25^2 + 2.506 * age3.25 - 2.017 * age3.25^2 - 1.808 * age7.25 - 1.762 * age8.25$	0.83	0.37
Veronica arvensis	$-29.125 + 8.929 * ph - 0.714 * ph^2 + 0.055 * site.age - 0.001 * site.age^2 - 1.088 * age2.25$	0.79	0.21
Vicia angustifolia	$-17.828 - 0.00007 * kf + 0.004 * fk + 0.001 * nfk + 0.708 * kak - 0.511 * kak^2 + 4.002 * ph - 0.35 * ph^2 + 0.142 * site.age + 0.006 * aw - 0.474 * disturb - 0.074 * disturb^2 + 15.201 * age4.25 - 12.865 * age4.25^2$	0.9	0.52
Vicia hirsuta	$-7.294 + 0.001 * kf - 0.000001 * kf^2 + 0.0004 * fk + 0.002 * nfk + 20.731 * kak - 18.81 * kak^2 + 0.167 * site.age - 0.003 * site.age^2$	0.83	0.33
Vulpia myuros	$-8.874 - 2.095 * brick.rubble + 0.237 * ph + 7.456 * age.area - 1.976 * age.area^2 - 0.219 * age6.25$	0.83	0.33

Appendix

Table C: Leafhopper species distribution models built by logistic regression and model averaging and some performance measures. Symbols and descriptions in tables A and B.

species	species distribution model	AUC	R2N
Aphrodes makarovi	-14.438 + 0.229 * pls1 + 0.247 * brick.rubble + 0.055 * lk - 0.0002 * lk ² + 0.0003 * nfk - 0.000001 * nfk ² + 0.047 * aw - 0.001 * aw ² - 2.989 * s.25 + 0.052 * d.75 - 0.047 * d.75 ² - 1.784 * age9.25 + 0.334 * age3.50 - 0.315 * age3.50 ² + 3.686 * age1.100 - 3.68 * age1.100 ² + 0.752 * index_R - 0.015 * index_R ²	0.92	0.53
Arocephalus longiceps	-9.173 + 2.325 * pls1 - 0.021 * ph + 0.051 * ln.caco3 - 0.004 * ln.caco3 ² + 2.976 * s.75 - 3.558 * s.75 ² + 1.648 * hi.100 - 0.032 * age2.50 + 0.422 * age6.50 - 0.712 * age6.50 ² + 0.008 * sum_L - 0.00007 * sum_L ² + 0.006 * sum_F - 0.00008 * sum_F ² + 0.227 * sum_R - 0.004 * sum_R ² + 0.006 * index_L - 0.00005 * index_L ² + 0.008 * index_F - 0.0003 * index_F ² + 0.406 * index_R - 0.008 * index_R ² + 0.003 * index_N - 0.0000606 * index_N ²	0.85	0.48
Arthaldeus pascuellus	-2.59 + 0.353 * pls1 + 0.025 * brick.rubble + 0.002 * fk + 0.001 * nfk + 0.246 * kak + 0.117 * ph - 0.011 * ph ² + 0.238 * site.age - 0.006 * site.age ² + 0.028 * aw - 2.055 * s.75 - 0.533 * s.100 - 0.795 * low.100 + 0.163 * index_F - 0.006 * index_F ²	0.88	0.53
Athysanus argentarius	-5.946 + 0.375 * pls1 + 0.802 * brick.rubble - 0.00001 * kf + 0.004 * fk + 0.001 * nfk + 2.313 * kak - 1.327 * kak ² + 0.007 * aw - 0.051 * s.25 + 2.238 * d.50 + 0.859 * d.75 - 1.286 * low.50 - 0.488 * age2.25 - 0.345 * age2.100 + 0.078 * sum_R - 0.002 * sum_R ² + 0.197 * index_R - 0.005 * index_R ²	0.88	0.48
Balclutha punctata	-2.47 + 0.348 * pls1 + 0.376 * age.area + 8.356 * s.50 - 19.704 * s.50 ² + 0.067 * d.75 + 0.091 * age2.100 - 0.198 * age2.100 ² - 3.348 * age5.200	0.87	0.36
Cicadella viridis	-1.178 + 0.069 * pls1 + 0.393 * site.age - 0.011 * site.age ² + 0.098 * disturb - 0.024 * disturb ² - 0.337 * s.25 - 0.253 * s.75 + 3.685 * low.25 - 5.631 * low.25 ² - 0.34 * low.75 + 0.284 * age5.25 + 5.029 * age4.50 - 3.576 * age4.50 ² + 0.056 * sum_F - 0.001 * sum_F ²	0.9	0.53
Cicadula quadrinotata	-5.454 + 1.112 * pls1 - 0.00003 * kf + 0.00004 * lk - 0.0000002 * lk ² + 0.028 * site.age - 0.001 * site.age ² + 0.006 * aw - 0.00009 * aw ² + 0.114 * disturb - 0.033 * disturb ² + 1.041 * hi.100 - 1.238 * hi.100 ² + 3.347 * age6.25 - 3.948 * age6.25 ² + 0.112 * age6.50 - 0.156 * age6.50 ² + 0.015 * age2.100 - 0.02 * age2.100 ² + 0.006 * sum_L + 0.008 * sum_F - 0.00009 * sum_F ² + 0.007 * index_L + 0.419 * index_F - 0.015 * index_F ² + 0.105 * index_R - 0.002 * index_R ²	0.85	0.41
Cixius nervosus	-0.45 + 0.291 * pls1 + 0.005 * lk - 0.0000002 * lk ² - 0.324 * ph + 1.53 * d.50 + 0.047 * s.75 - 0.076 * s.75 ² + 6.942 * s.100 - 18.664 * s.100 ² - 0.848 * low.100 + 0.037 * age8.25 + 0.745 * age2.50 - 1.557 * age2.50 ² + 0.051 * age8.50 - 4.738 * age2.100 - 0.001 * sum_L + 0.049 * sum_R - 0.001 * sum_R ² - 0.001 * sum_N + 0.041 * index_R - 0.001 * index_R ²	0.91	0.50
Dikraneura variata	-2.726 + 2.015 * d.25 - 3.059 * d.25 ² + 0.456 * hi.50 - 0.698 * hi.50 ² + 1.076 * age7.25 + 2.405 * age1.50 - 3.81 * age1.50 ² + 11.691 * age1.100 - 24.675 * age1.100 ²	0.88	0.32
Doratura homophyla	-3.077 + 3.655 * pls1 + 0.423 * pls2 - 0.006 * lk + 0.004 * fk - 0.00002 * fk ² + 0.035 * nfk - 0.0002 * nfk ² - 0.00003 * p - 0.001 * k + 0.098 * d.75 + 0.012 * hi.75 + 0.007 * hi.100 + 1.438 * age4.100 + 0.005 * index_N - 0.0002 * index_N ²	0.88	0.55
Doratura impudica	-6.496 + 0.568 * pls1 + 1.03 * pls2 + 0.00002 * p - 0.00002 * k + 24.876 * hi.50 - 32.123 * hi.50 ² + 13.298 * age2.50 - 20.662 * age2.50 ² - 6.874 * age5.50 + 16.081 * age5.50 ²	0.97	0.71

Table C: continued.

species	species distribution model	AUC	R2N
Elymana sulphurella	-1.976 + 0.227 * pls1 + 0.002 * fk + 0.003 * nfk + 0.034 * site.age -0.001 * site.age ² + 0.011 * aw -2.359 * low.50 -3.573 * low.100 -1.55 * age8.25 + 1.583 * age5.50	0.87	0.37
Empoasca vitis	-2.126 + 0.976 * pls1 + 0.351 * age.area -1.495 * low.50 -2.763 * age5.25 -0.739 * age5.50	0.82	0.25
Errastunus ocellaris	-1.092 -0.017 * s.100 -3.846 * low.50 + 5.227 * age5.100	0.80	0.30
Euscelis incisus	2.846 + 3.5 * pls1 -0.000008 * kf + 0.0003 * nfk + 0.0001 * p + 0.011 * site.age - 0.0004 * site.age ² + 3.991 * low.75 -5.498 * low.75 ² + 4.12 * age5.100 -5.809 * age5.100 ² + 0.00006 * sum_L + 0.0001 * sum_F -0.081 * sum_R + 0.0001 * sum_N + 0.00007 * index_L + 0.003 * index_F -0.009 * index_N	0.86	0.44
Fagocyba cruenta	-3.69 + 0.024 * pls1 -0.005 * kf + 1.701 * kak -1.492 * kak ² + 0.0003 * site.age + 3.769 * s.100 -8.868 * s.100 ² -0.018 * age4.25 + 0.568 * age7.50 -0.433 * age7.50 ² -0.057 * age4.100 + 15.113 * age8.100 -14.028 * age8.100 ²	0.92	0.50
Graphocraerus ventralis	-2.852 + 1.321 * pls1 -0.103 * age3.50 + 0.317 * age6.50 -0.078 * age3.100 + 3.078 * age5.100	0.82	0.33
Jassargus pseudocellaris	-1.063 + 0.582 * pls1 + 1.404 * pls2 + 0.004 * lk -0.00002 * lk ² + 0.001 * fk -0.102 * ph + 0.003 * site.age + 0.059 * age.area + 0.021 * aw -0.312 * brownf.200 -0.187 * s.25 -0.04 * s.100 + 1.525 * GW.25 -2.037 * GW.25 ² + 0.173 * age7.25 -0.131 * age7.25 ² -0.342 * age4.50 -1.777 * age4.100 + 0.005 * age8.100 -0.004 * age8.100 ² -0.005 * index_N	0.88	0.46
Javesella pellucida	-0.815 + 0.156 * pls1 + 0.706 * brick.rubble + 0.062 * site.age -0.002 * site.age ² + 0.00005 * aw -0.994 * s.25 -0.688 * s.50 -1.365 * low.25 + 0.159 * low.50 -0.356 * low.50 ²	0.83	0.33
Kosswigianella exigua	-3.603 + 0.222 * pls1 + 0.04 * lk -0.0001 * lk ² + 0.05 * ph -0.004 * ph ² + 0.008 * site.age -0.0002 * site.age ² -0.56 * age1.50 -1.239 * age1.100 -0.001 * index_N	0.78	0.24
Macropsis prasina	-3.445 + 3.156 * pls1 -0.308 * kak + 12.41 * low.75 -36.9 * low.75 ² + 0.064 * low.100 -0.22 * low.100 ² -1.098 * age1.100 + 4.324 * age4.100 -3.807 * age4.100 ² + 3.082 * age5.100 -10.023 * age5.100 ² + 0.95 * age9.100 -0.815 * age9.100 ² + 0.043 * index_N -0.001 * index_N ²	0.92	0.54
Macrosteles cristatus	-25.13 + 0.761 * pls1 -0.00004 * kf + 6.396 * ph -0.511 * ph ² + 0.0005 * ln.caco3 + 1.026 * age.area + 0.402 * s.25 -0.465 * s.25 ² + 0.128 * hi.75 -0.225 * hi.75 ² + 0.046 * hi.100 -0.08 * hi.100 ² + 8.614 * age1.25 -7.534 * age1.25 ² + 7.841 * age5.50 -13.952 * age5.50 ² + 1.516 * age9.50 -2.231 * age9.50 ² + 0.576 * age4.100 -0.59 * age4.100 ² + 0.02 * sum_F -0.0003 * sum_F ²	0.89	0.49
Macrosteles laevis	-7.51 + 1.037 * pls1 + 1.18 * hi.50 -0.748 * GW.25 + 0.243 * age3.25 -0.216 * age3.25 ² + 0.783 * age8.100 -0.887 * age8.100 ² + 0.057 * sum_L -0.0005 * sum_L ² + 0.118 * sum_F -0.002 * sum_F ² + 0.141 * index_L -0.001 * index_L ² + 0.051 * index_F -0.002 * index_F ²	0.74	0.24
Macrosteles ossiannilssoni	-0.747 + 1.466 * pls1 + 4.269 * d.25 -6.143 * d.25 ² + 0.476 * s.50 -0.578 * s.50 ² + 0.304 * age3.25 -0.277 * age3.25 ² + 8.692 * age6.50 -14.51 * age6.50 ² + 0.278 * age3.100 -0.283 * age3.100 ² + 0.751 * age7.100 -1.627 * age7.100 ² + 0.001 * sum_N + 0.001 * index_N	0.81	0.36
Macrosteles ossiannilssoni	-0.747 + 1.466 * pls1 + 4.269 * d.25 -6.143 * d.25 ² + 0.476 * s.50 -0.578 * s.50 ² + 0.304 * age3.25 -0.277 * age3.25 ² + 8.692 * age6.50 -14.51 * age6.50 ² + 0.278 * age3.100 -0.283 * age3.100 ² + 0.751 * age7.100 -1.627 * age7.100 ² + 0.001 * sum_N + 0.001 * index_N	0.81	0.36

Appendix

Table C: continued.

species	species distribution model	AUC	R2N
Macrosteles quadripunctulatus	$-0.909 + 2.207 * pls1 + 0.019 * ph - 0.001 * aw + 5.558 * low.75 - 7.789 * low.75^2 + 0.157 * age3.25 - 0.102 * age3.25^2 + 0.09 * age3.50 - 0.078 * age3.50^2$	0.85	0.47
Macrosteles sexnotatus	$-8.45 + 0.002 * pls1 + 0.176 * brick.rubble + 0.0005 * p + 6.815 * low.50 - 8.979 * low.50^2 + 1.303 * age6.50 - 2.362 * age6.50^2 + 4.623 * age5.100 - 13.103 * age5.100^2 + 0.432 * sum_F - 0.007 * sum_F^2 + 0.008 * sum_R - 0.0002 * sum_R^2 + 0.041 * sum_N - 0.001 * sum_N^2 + 0.022 * index_R - 0.001 * index_R^2$	0.78	0.32
Mocuellus collinus	$-5.77 + 5.123 * pls1 + 0.348 * ph - 0.037 * ph^2 - 0.000006 * p - 0.0002 * k + 0.16 * ln.caco3 + 13.572 * age3.50 - 16.032 * age3.50^2 + 0.868 * age5.100 - 0.008 * index_F$	0.91	0.46
Neoaleturus.fenestratus	$-14.285 + 2.771 * pls1 - 0.001 * lk + 9.849 * s.25 - 6.098 * s.25^2 - 0.703 * d.100 + 0.092 * low.25 - 0.066 * low.25^2 - 1.655 * hi.100 - 1.46 * age3.100 + 0.623 * sum_R - 0.013 * sum_R^2 + 0.37 * index_R - 0.009 * index_R^2$	0.9	0.57
Neophilaenus minor	$-3.388 + 0.873 * pls1 + 0.909 * pls2 + 0.005 * nfk - 0.0002 * p + 0.007 * site.age - 0.0002 * site.age^2 + 0.047 * age.area + 1.947 * low.25 - 0.368 * hi.100 + 0.357 * hi.100^2 - 0.345 * age1.25 + 0.978 * age6.25 + 0.635 * age6.50 - 1.669 * age1.100 - 0.002 * sum_F - 0.002 * sum_R - 0.002 * index_R$	0.94	0.56
Ophiola decumana	$0.025 + 1.682 * pls1 - 0.019 * site.age - 0.318 * age.area + 0.077 * age.area^2 - 0.009 * aw + 0.069 * s.25 + 2.056 * hi.100 - 0.01 * age6.25 + 0.072 * age3.50 - 0.059 * age3.50^2 + 0.393 * age8.50 + 0.099 * age3.100 - 0.096 * age3.100^2 - 0.086 * index_N + 0.002 * index_N^2$	0.83	0.40
Psammotettix confinis	$-1.533 + 1.286 * pls1 + 0.187 * site.age - 0.006 * site.age^2 + 0.249 * s.100 - 0.293 * s.100^2 + 2.459 * hi.75 + 0.034 * age4.25 - 0.025 * age4.25^2 + 0.384 * age9.50 + 0.062 * age1.100 - 0.069 * age1.100^2 + 0.372 * age5.100 + 0.768 * age9.100 + 0.03 * sum_N$	0.84	0.40
Psammotettix excisus	$-11.271 + 6.541 * pls1 + 1.104 * pls2 + 0.00005 * kf - 0.00000005 * kf^2 + 0.002 * lk - 0.000005 * lk^2 + 0.006 * ph - 0.001 * ph^2 + 0.000004 * p - 0.00003 * k - 0.015 * ln.caco3 - 0.014 * aw + 0.837 * s.50 + 2.331 * low.50 + 1.47 * low.75 + 0.006 * age9.50 - 0.161 * age1.100 + 0.163 * sum_R - 0.015 * index_F + 0.12 * index_R$	0.97	0.70
Psammotettix nodosus	$-1.301 + 2.726 * pls1 - 0.011 * brick.rubble + 0.0001 * lk - 0.000005 * k - 0.003 * ln.caco3 + 0.099 * site.age - 0.003 * site.age^2 - 0.018 * age.area - 0.001 * aw + 0.778 * s.50 + 0.425 * hi.50 + 1.764 * age4.100 - 2.126 * age4.100^2 + 0.162 * age9.100$	0.84	0.46
Rhopalopyx vitripennis	$-18.414 + 0.87 * pls1 + 3.81 * kak - 3.328 * kak^2 + 5.943 * ph - 0.501 * ph^2 + 0.057 * site.age - 0.001 * site.age^2 + 0.002 * aw - 0.039 * disturb - 1.818 * brownf.25 - 0.08 * brownf.50 - 0.002 * s.75 + 2.537 * d.75 - 3.227 * d.75^2 + 0.152 * d.100 - 0.239 * d.100^2 + 0.843 * hi.50 - 0.848 * hi.50^2 + 0.013 * age6.25 - 0.017 * age6.25^2$	0.87	0.45
Ribautodelphax collina	$-1.711 + 2.04 * pls1 + 4.686 * pls2 - 0.826 * ph + 0.079 * ph^2 - 0.000002 * k - 0.0005 * ln.caco3 + 0.01 * site.age - 1 * s.75 + 0.585 * d.75 + 0.29 * age9.50 + 0.033 * sum_F + 0.039 * sum_N - 0.00005 * index_N$	0.85	0.43
Zyginidia scutellaris	$-4.634 + 0.373 * pls1 + 0.003 * site.age - 0.00009 * site.age^2 + 0.09 * disturb - 0.014 * disturb^2 - 0.537 * s.75 - 0.52 * s.100 + 1.473 * age6.25 - 1.203 * age6.25^2 + 0.743 * age9.25 - 0.616 * age9.25^2 - 0.338 * age1.50 + 0.458 * sum_R - 0.009 * sum_R^2$	0.78	0.32

Table D: Grasshopper species distribution models built by logistic regression and model averaging and some performance measures. Symbols and descriptions in tables A and B.

species	species distribution model	AUC	R2N
Chortippus albomarginatus	$-2.014 + 0.809 * pls1 + 1.795 * kak - 0.002 * disturb - 1.668 * brownf.50 + 0.339 * d.50 - 0.43 * d.50^2 - 0.123 * low.25 + 3.086 * hi.50 - 2.307 * hi.50^2 + 3.444 * hi.75 - 2.798 * hi.75^2 + 0.277 * age3.25 - 0.279 * age3.25^2$	0.82	0.33
Chortippus biguttulus	$6.116 + 0.921 * pls1 + 0.049 * brick.rubble - 0.008 * kf - 0.001 * lk - 0.018 * kak - 0.018 * ph + 0.105 * site.age - 0.003 * site.age^2 + 0.001 * age.area - 0.081 * disturb - 0.097 * s.100 - 0.216 * d.100 + 0.446 * low.100 - 0.761 * low.100^2 + 12.471 * hi.75 - 12.608 * hi.75^2 - 0.264 * age1.25 - 0.076 * age1.50 - 0.794 * age1.100 - 0.015 * sum_L - 0.018 * index_L - 0.032 * index_F$	0.96	0.71
Chortippus mollis	$-2.998 + 0.329 * pls1 + 0.031 * lk - 0.0001 * lk^2 + 0.044 * ph - 0.004 * ph^2 + 0.192 * site.age - 0.005 * site.age^2 + 1.849 * d.50 - 2.051 * d.50^2 - 0.01 * age1.100$	0.77	0.27
Metrioptera roeseli	$-5.657 + 0.024 * pls1 + 0.001 * kf - 0.000002 * kf^2 + 0.003 * fk + 0.005 * nfk + 0.36 * kak + 3.871 * age.area - 0.922 * age.area^2 + 0.005 * aw - 1.757 * s.25 + 0.002 * d.50 - 1.653 * s.100 + 0.013 * index_F$	0.87	0.38
Myrmeleotettix maculatus	$-2.769 + 1.613 * pls1 + 2.697 * pls2 - 0.001 * p + 0.0002 * k + 0.267 * site.age - 0.005 * site.age^2 + 0.024 * age9.50$	0.87	0.47
Oedipoda caerulescens	$-2.648 + 0.677 * pls1 - 0.183 * brick.rubble + 0.0003 * lk - 0.001 * p - 0.001 * k - 0.294 * disturb - 0.192 * low.100 + 0.356 * hi.75 + 0.887 * hi.100$	0.88	0.41
Tetrix tenuicornis	$-3.545 + 0.69 * pls1 + 0.0003 * lk + 0.015 * ph - 0.0002 * p + 2.399 * d.50 - 2.568 * low.50 - 4.69 * low.75 + 0.032 * hi.25 + 0.368 * hi.100 - 0.388 * hi.100^2 - 0.47 * age8.50 + 12.138 * age3.100 - 13.08 * age3.100^2$	0.92	0.51

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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 und den Änderung der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften vom 16.12.2005.

Hiermit erkläre ich, dass ich eine Promotion zum Dr. rer. nat. anstrebe. Es soll der Grad eines Doktors verliehen werden.

Des Weiteren erkläre ich, die vorliegende Arbeit in allen Teilen selbstständig und nur mit den angegebenen Hilfsmitteln angefertigt zu haben.

Außerdem erkläre ich, dass die Dissertation weder in ihrer Gesamtheit noch in Teilen einer anderen wissenschaftlichen Hochschule zur Begutachtung in einem Promotionsverfahren vorliegt oder vorgelegen hat.

Chapter 4 dieser Arbeit wurde bereits veröffentlicht:

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