Zur Homepage der Dissertation

Insects in urban brownfields

Analyses of species occurrences, community composition, and trait frequencies along a successional gradient

Von der Fakulät für Mathematik und Naturwissenschaften
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Chapter 1

Introduction

1.1 Background

Urbanisation is proceeding throughout the world (Sandstrom et al. 2006). Cities are gradually spreading into the countryside, rural ecosystems are replaced by urban ones. How does this process affect species and communities?

On the one hand, urbanization is often considered to be one of the main causes for biodiversity decline (Kati et al. 2006; Kim & Pauleit 2005; McKinney 2002; Rouget et al. 2003). On the other hand, urban habitats are described as being diverse and species rich (Kühn et al. 2004; Rebele 1994; Ricketts & Imhoff 2003). Thus, urbanization can have both favourable and adverse effects on biotic communities (Niemelä 1999). It is time to acknowledge that urban ecosystems are not just 'reduced' forms of their rural counterparts, but complete systems with their own, distinct and typical species assemblages, and with typical processes shaping them (Gibson 1998). As urban habitats house a considerable portion of a region's biodiversity, it is crucial to understand what driving forces shape their communities, and which species find habitat under what circumstances (Helden & Leather 2004). Only with this knowledge it is possible to give planners the tools to develop cities in a way that can sustain or enlarge the biodiversity in their midst (Angold et al. 2006; Sandstrom et al. 2006).

Urban brownfields (derelict land) are urban habitats which are increasingly noticed in the light of conservation significance (Angold et al. 2006; Eyre et al. 2003; Gibson 1998). Brownfields owe their existence to strong and destructive human influence. However, once they have emerged, they undergo a rapid development that is undirected by humans (Gibson 1998). This makes them the 'wildest' among the urban ecosystems. Gaining insight into the processes shaping these dynamic habitats, like succession or the influence of patch size and patch dynamics, provides an important piece of knowledge in the understanding of urban communities. This thesis is focused on phytophagous insects, namely leafhoppers (Hemiptera: Auchenorrhyncha) and grasshoppers (Orthoptera), in urban brownfields. They colonize new habitats as soon as the first plants establish and are thus among the first animal settlers of brownfields.

1.2 Urban habitats

Urban areas offer a wide range of habitats. Most of them are managed and tended, such as gardens, parks or cemeteries. Others, like empty lots and derelict sites, are not managed and develop freely. Urban ecosystems differ from those in the surrounding countryside in several aspects. Annual mean temperatures in the centre of large towns are 0.5-1.5 °C higher than those of the surrounding rural area (Gilbert 1989). This 'urban heat island effect' permits thermophilous species to extend their range northward (Eversham et al. 1996; Klausnitzer 1995). Soils are often man-made and immature. They can be compacted from heavy machinery, whereas high contents of brick rubble result in well drained soils. Release of calcium from mortar and cement tends to elevate pH. Nitrogen is often initially deficient (Gilbert 1989). The urban flora and fauna is characterized by a high number of introduced, non-native species ('aliens') (Eversham et al. 1996; McKinney 2002; Niemelä 1999). Habitat patches are often small and isolated from each other by built-up areas (Niemelä 1999). In general, the habitat diversity is high with early successional stages being particularly common (Rebele 1994).

The heavy anthropogenic influences that operate in cities have, until recently, rendered them unattractive to ecologists who find the high proportions of exotics and the mixtures of planted and spontaneous vegetation bewildering (Gilbert 1989; McIntyre 2000; Niemelä 1999). In contrast to this, Gilbert (1989) proposed that ‘there are as many interrelationships to be uncovered in a flower bed as in a field, in a cemetery as on a sand dune. Due to the well documented history of urban sites, they are often easier to interpret than those operating in more natural areas. There is still an acute lack of knowledge about the ecology of urban areas’. McIntyre (2000) found in a review that relatively little research has been done to reveal how arthropods use urban habitats, and made a ‘call to action’.

Up to now, numerous studies have examined the urban-rural gradient. Thus, these studies investigated in which way urban communities differ from rural ones (e. g. Blair 1999; Denys & Schmidt 1998; Niemelä et al. 2002). Findings differ: Niemelä et al. (2002), summarizing the results of several studies, conclude that habitat changes commonly associated with urbanisation do not affect the ecological integrity of carabid assemblages in urban forest patches. However, they found some evidence that species richness decreases, and small-sized species become more numerous. Nagy (1997) found a rapid decrease of species numbers towards the city centre. Schwerk (2000) proposes a decline of large sized and wingless species.

Studies that reveal processes within and differences between urban communities and ecosystems remain relatively scarce. However, it is recognized that community compositions are often unusual and cannot be found elsewhere (Rebele 1994; Sanderson 1992b), forming true urban communities (Gilbert 1989).

1.3 Urban brownfields

In this thesis, I focus on the type of urban habitat that is least influenced by humans: urban brownfields. Urban brownfields, also called ‘derelict sites’ or ‘urban commons’ (Gilbert 1989), are unmanaged urban green space. They comprise empty lots within housing or industrial areas as well as industrial dumps, abandoned railyards, or landfills.

Many studies have revealed that brownfields form highly diverse habitats, and often support a rich wildlife, comprising many regionally rare, uncommon species as well as endangered species (Eversham et al. 1996; Gemmell & Connell 1984; Gibson 1998; Gilbert 1989; Sanderson 1992b; Schwerk 2000). Brownfields are considered to be analogues of semi-natural habitats such as species-rich grassland or heathland (Eversham et al. 1996; Gemmell & Connell 1984). They often present relatively undisturbed habitat-islands in an otherwise less habitable area (Sanderson 1992b).

What kind of habitat do brownfields provide for phytophagous insects? Brownfields emerge at random locations, when buildings are deconstructed or facilities (e. g. switchyards or industrial plants) are abandoned. Thus, the origin of all brownfields is man-made. During the ecological processes that follow, however, human impact is remarkably low. The newly created habitats undergo fast changes due to successional processes. Typically, four types of plant communities can be recognized along the successional gradient (Brown & Southwood 1987): (1) Ruderal, where annual plants dominate. (2) Early-successional, where annual and biennial herbs are declining but perennials and grasses are establishing. (3) Mid-successional, when grasses and perennials dominate, although tree and shrub establishment is beginning. (4) Late-successional, when shrubs and trees are dominant. Figure 1.1 depicts these vegetation changes. However, the duration of each successional stage and the course of succession vary widely between sites. The fertility of the substrate, and the existence and quality of a seed bank, are main de-

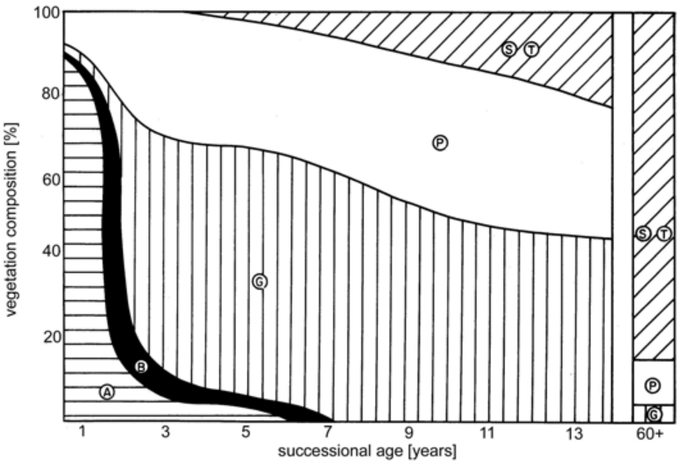

Figure 1.1: Model of vegetation change during succession in terms of plant growth form. A = annual germs and grasses, B = biennials, P = perennial herbs, G = perennial grasses, S & T = shrubs and trees. Note that the time scale can vary widely between sites. Brown & Southwood (1987), p. 323, altered.

terminants (Rebele 1992). The distance from sources and the dispersal ability of species may also influence colonization (Eversham et al. 1996).

Thus, brownfields form habitats which are highly dynamic in space (as the location of brownfield patches changes due to demolition and redevelopment), and in time (as individual brownfield patches continuously change through the course of succession) (Gibson 1998; Wood & Pullin 2002). These two processes generate a spatio-temporal mosaic of different successional stages and built-up areas. Figure 1.2 illustrates this process: Through the course of time, individual brownfield sites undergo succession. Some sites are derelict for a long time and move through all successional stages before they are redeveloped, others only see a short period of succession. Turnover rates of a site can be fast (a site is in the derelict stage and in the built-up stage twice in the example), or slow. This simple illustration demonstrates that the pace and timing of demolition and redevelopment, which are ruled by the economic situation and changing needs of industry, have large impact on the amount, quality and spatial arrangement of brownfield habitats.

An analysis of aerial photographs of six German cities, spanning 55 years, revealed

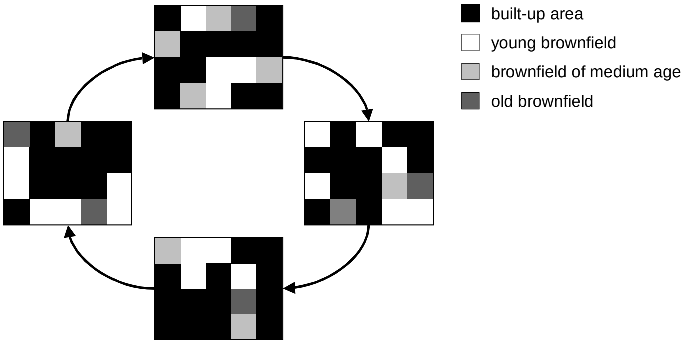

Figure 1.2: Schematic changes in the mosaic of built up sites and derelict sites of different successional stages during four time steps.

that only 40% of the analysed sites were never derelict during that time (Empter 2006). This means that most sites are available as habitat at least occasionally during the normal course of city renewal. The brownfield stage is typically short-lived, only one third of the sites undergo succession for more than 15 years in a row (Empter 2006).

Due to their dynamic nature, brownfields are challenging habitats. On the other hand, to a large extent it might be this dynamic aspect that enables high biodiversity. It is likely that many species that find suitable habitat on brownfields depend on certain successional stages. Eversham et al. (1996) proposes that the existence of early successional stages is particularly important because they are generally absent or difficult to maintain elsewhere. These early stages and the species colonizing them, rely on repeated renewal (Gibson 1998). Species find suitable habitat at changing locations (Rebele 1994), and it seems likely that the value of brownfield habitats is transient. Rather than conserving individual sites it seems to be of major importance to maintain a pattern of individually transient sites (Eversham et al. 1996; Klausnitzer 1995). There is a need for finding solutions that, on the one hand, allow derelict land to develop species rich habitats, but that, on the other hand, also maintain the cycle of its production and renewal.

Additionally, a better understanding of community dynamics for invertebrates in such artificial habitats is required (Gibson 1998). Little is known about succession of animal communities in urban ecosystems (Rebele 1994). 15 years ago, Sanderson (1992a) stated that few of the surveys of insects in urban habitats investigated derelict land. Since then, some studies have been conducted on leafhoppers and bugs (Sanderson 1992a,b, 1993) and on carabid beetles (Eyre et al. 2003; Schwerk 2000; Small et al. 2006, 2003). Overall and for most taxa, there is still little quantitative knowledge on which species occur under what conditions on brownfield sites.

Thus, in this thesis, I want to shed some light on these questions by quantifying species-environment relationships for leafhoppers and grasshoppers, based on a large sample size and on two geographically different study areas. I will look at the issue from two sides. First, I will take a more species centred point of view and quantify species' environmental needs by the use of habitat models. Second, I will substitute species by their biological traits and will analyse the changes in traits during succession.

1.4 Habitat models

Habitat models analyse and quantify the relationship between species abundance or occurrence and habitat factors (Guisan & Zimmermann 2000). Moreover, they can yield predictions of species abundance or occurrence for given environmental conditions. The latter makes them a predictive tool than can be used to assess the consequences of environmental change.

Habitat models have come a long way from their beginning in the 1980s, where the U.S. Fish & Wildlife Service used expert knowledge to formulate general rules for the habitat preferences of species (Schröder). Increasing computer power made statistical methods widely available. This gave raise to the widespread use of multivariate and regression techniques, such as CCA (Canonical Correspondence Analysis), DCA (Detrended Correspondence Analysis), classification trees, artificial neuronal networks, GAMs (generalised Additive Models), or GLMs (generalised Linear Models) with different link functions (Guisan & Zimmermann 2000). None of these techniques proved to be clearly superior for all species and situations (Block et al. 1998; Guisan et al. 1999;

Manel et al. 1999b; Olden & Jackson 2002). In this work, I chose to use logistic regression, which is the most frequently used of the GLM techniques (Engler et al. 2004). This approach is robust, and results can be interpreted easily (Hirzel & Guisan 2002; Schröder).

Beyond describing the species-habitat relationships, I want to assess the magnitude of the influence of different environmental factors. Multivariate ordination methods such as CCA are helpful in describing how factors structure communities (Olden 2003); for examples see Cherrill & Rushton (1993), Eyre et al. (2004) or Small et al. (2003). However, ordination methods do not provide a quantitative background to predict community composition under given environmental conditions. For this reason, hierarchical partitioning, which combines both goals, sees increasing attention (e. g. Heikkinen et al. 2005; Mac Nally 2002). However, hierarchical partitioning software can so far only deal with a limited number of variables. Moreover, and this is more important, there is no straightforward way to consider other than sigmoid responses (Heikkinen et al. 2004).

To overcome this problem, I used a third way: model averaging as proposed by Burnham (2002), which has been used in species modelleing by Gibson et al. (2004a,c). It combines the advantages of GLMs with the option to assess the magnitude of factor impact. In addition, model averaging avoids the choice of a 'single best model', a process with numerous pitfalls and doubtful, even spurious outcomes, especially if stepwise selection methods are used (Mac Nally 2000).

1.5 Species traits

Habitat models give valuable information on the species level. By simultaneously applying models of many species, large parts of a community can be modelled. This helps to answer the question how single species or a whole community reacts to environmental conditions. However, this approach does not reveal *why* species react the way they do, and which biological features (traits), reflecting life strategies, are common to species that show similar behaviour. Analysing the frequency of biological traits within a species pool rather than the occurrence of single species, sheds light on this issue.

In the framework of studies on urban brownfields, this trait centered approach is particularly appealing. As outlined above, succession is a dominant, characteristic feature of brownfields. Successional processes have stimulated decades of research on traits and how their frequencies change within a community during the course of succession (Brown et al. 1992; Brown & Hyman 1986; Brown & Southwood 1983; Hollier et al. 1994; Steffan-Dewenter & Tscharntke 1997). For instance, 40 years ago, observations of changes in traits during succession led to the r-K concept (MacArthur & Wilson 1967). In general, variations in life history traits across successional gradients are of special interest to determine the mechanisms of succession (Steffan-Dewenter & Tscharntke 2001). Many structural and functional attributes of the community change during its successional development. Hence, succession provides one of the cardinal axis along which ecological strategies of communities may be organized (Southwood et al. 1979).

Moreover, analyses of traits reveal if a particular habitat favours or delimits certain biological traits and thus certain groups of species. For urban habitats, it has been proposed that body size decreases, whereas flight ability increases with respect to rural habitats (Schwerk 2000).

1.6 Outline of the thesis

In this thesis, I will first give an introduction to the study areas, and to the data I collected (**Chapter 2**). All further analyses base on these data.

Chapters 3 to 6 move from approaches centering around single endangered species to very general approaches beyond the species level. In **Chapter 3**, I chose a few typical brownfields species that are listed in the red data book. For these individual species, well-groomed habitat models are developed that give a detailed description of the species needs. I demonstrate how such models can be applied to produce habitat suitability maps that can be of great value for nature conservation. In **Chapter 4**, I model the species community by means of habitat models for each individual species. I demonstrate that changes in species numbers along the successional gradient are little compared to changes in species composition. **Chapter 5** shows the need to validate species models with independent data before drawing general conclusions from them. In **Chapter 6**, I leave the species-based level and move to the analyses of the biological traits associated with leafhopper species. I show how traits are related to the successional gradient, and how the brownfield species pool and the occurrence of species is biased towards species with pioneer traits.

Chapter 7 provides a synthesis of the leafhopper and grasshopper species and communities in urban brownfields, of the driving factors shaping them, and of the biological characteristics that make species prosper and perish during succession. I discuss the advantages and drawbacks of the approaches I used, and draw conclusions about conditions that are needed to maintain a large and diverse species pool on urban brownfields.

1.7 Contributions to the thesis

This thesis was part of the TEMPO project (temporary building and biodiversity). It was financed by the German Ministry of Education and Research (BMBF, grant 01LM0210). The extensive data collection would not have been possible without the assistance of students. Ute Schadek, working on the vegetational counterpart of my subproject (Schadek 2006), provided the data on plant species coverage and the soil data. The work on chapters three to six was done in collaboration with Robert Biedermann. All the writing was done by myself. Robert Biedermann contributed the *Verdanus bensoni* study in Chapter 3.

Chapter 2

Study sites & experimental design

2.1 Study sites

Data were collected in two cities, Bremen and Berlin (Figure 2.1). Both cities are located in Northern Germany at a distance of approximately 300 km. Within these cities, work was restricted to derelict sites. These sites differed widely in their successional stage and origin (Figure 2.2).

The sites comprised small lots within the city centres as well as abandoned railyards and large vacant areas within industrial and logistics centres. All brownfields were not managed or used in a commercial way. However, most of them were accessible to the public. People quickly found ways to make use of these scarce spots of open space. Thus, depending on their location, brownfield sites were used to a smaller or greater

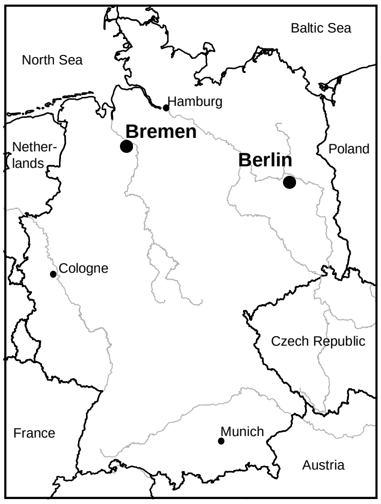

Figure 2.1: Study sites were located in Bremen and Berlin, Germany.

Figure 2.2: Study plots spanned all successional stages and comprised very scarce pioneer vegetation (upper left) as well as stages dominated by herbs (upper right) and grasses (lower left), and pioneer forests (lower right).

extent for various activities. Walking dogs and children's play were the most common, but we observed kite surfing, horse riding or motocrossing just as well.

Bremen

The Free Hanseatic City of Bremen (53°05' N, 8°44' E) spreads over an area of 327 km^2 along the river Weser. The city has 550,000 inhabitants. Bremen has a long tradition as a port and trading city. Even though the port lost importance, the city gained influence as a reloading centre for trucks and trains, making Bremen one of Germany's major foreign trade and industrial centre.

The climate of Bremen is maritime with a mean annual temperature of 8.8 °C. Winters are mild, with the mean temperature for January at 0.8 °C, summers are cool (July 16.8 °C) (weather station at Bremen airport, mean values 1961-1990, Wetterdienst 1996-

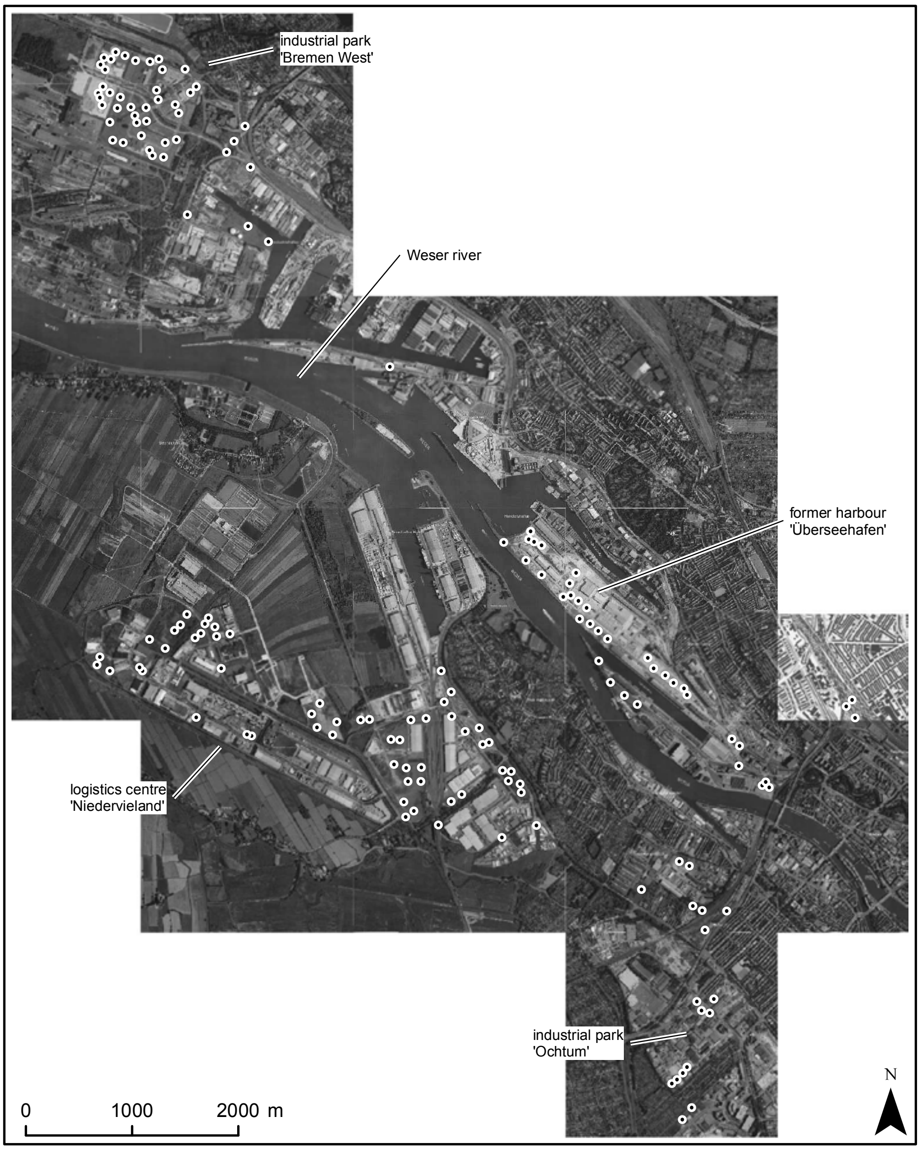

Figure 2.3: Location of study plots in Bremen. Aerial pictures 1:10,000, March 2002, Geoinformation Bremen.

2006). Annual precipitation amounts to 694 mm (Deutscher Wetterdienst 1996-2006).

The study plots were located in the Weser river marsh, north and north-west of the city centre, spreading over 100 km^2 (Figure 2.3). In order to make this marshland suitable for industrial use and building, it has been elevated and filled with several meters of sand. The sand has mostly been dug or sucked up from the Weser riverbed. Thus, the former wet meadows today are mostly not within the reach of groundwater. The study sites are mostly characterized by sandy soils, on older industrial sites high amounts of building rubble are commonly found (Schadek 2006).

In Bremen, a number of sites have not seen any commercial use so far, especially those in the logistics centre ‘Niedervieland’ and in the industrial park ‘Bremen Nord’. After the dumping of sand was finished, these areas have undergone succession for a number of years, some for decades. Other sites have been repeatedly built-up and abandoned, especially in the industrial park ‘Ochtum’. In the area of the former harbour ‘Überseehafen’, an entire port basin was filled, and kilometres of rails and many warehouses were removed.

Berlin

Berlin (52°30’ N, 13°28’ E, 892 km^2) is the German capital. With 3.4 million inhabitants it is the largest German city. Berlin has a more continental climate than Bremen. Annual precipitation amounts to 584 mm at Berlin Airport Tempelhof (mean values 1961-1990, Deutscher Wetterdienst 1996-2006). Mean annual temperature at the Tempelhof weather station is at 9.4 °C, mean temperatures for January and July are at -0.2 °C and 18.8 °C, respectively. Berlin weather stations show a clear trend from the cooler suburbs (Lichtenrade: annual mean 8.9 °C, January -0.6 °C, July 17.6 °C) to the warmer city centre (Alexanderplatz: 9.8/0.3/19.2) (Wetterdienst 1996-2006).

Study plots in Berlin spread over a large area of 370 km^2. A number of study sites was situated along the former ‘Berlin Wall’. In many places, its former course is still accompanied by derelict sites, e. g. along the road ‘Bernauer Straße’, or east of the ‘Potsdamer Platz’ (Figure 2.4). Other study sites comprised abandoned railyards, the former military training area ‘Parks Range’, and empty lots.

The parent material on most sites is strongly altered by anthropogenic influence. Building rubble from houses that were destroyed during World War II can be found on the majority of Berlin sites (Blume & Runge 1978; Runge). Like in Bremen, sites are characterized by sandy anthrosols (Schadek 2006) which resemble natural loose lithosols and regosols (Finnern et al. 1996). Groundwater level in Berlin is mostly low with depths of more than 10-30 m (Sukopp 1990).

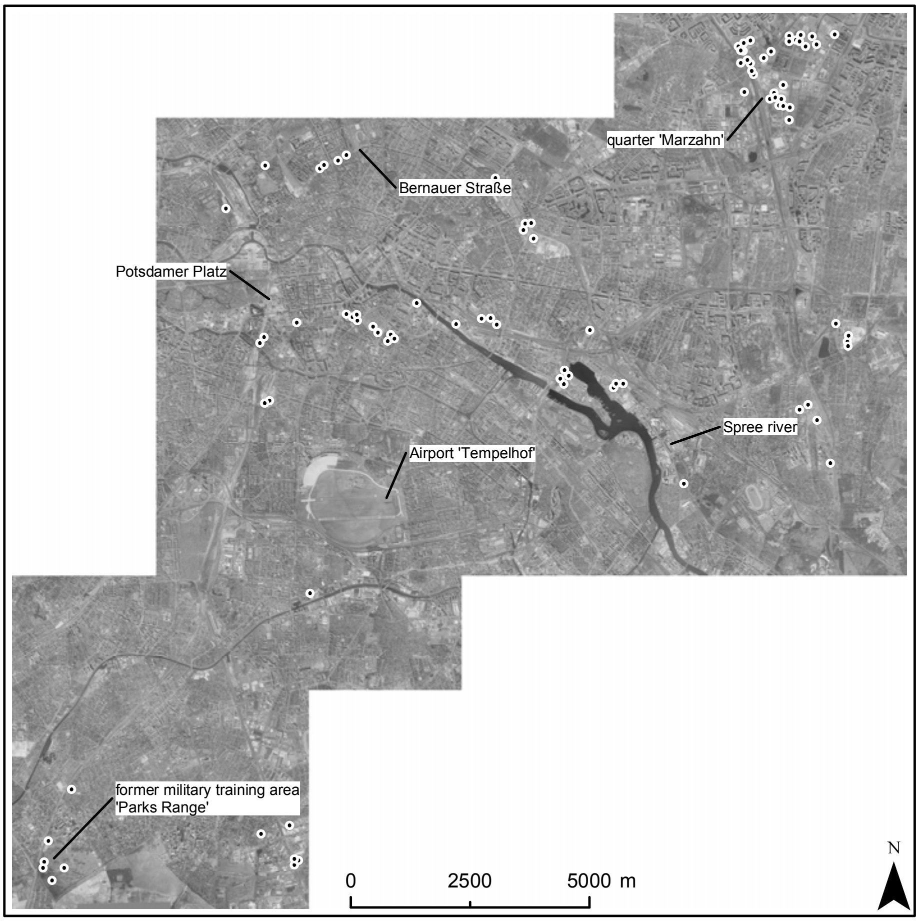

Figure 2.4: Location of study plots in Berlin. Aerial pictures 1:10,000, March 2002, Senatsverwaltung für Stadtentwicklung Berlin.

2.2 Data collection

In Bremen, data were collected during two years (2003 and 2004), in Berlin during one year (2004).

Plot selection

Study plots covered the whole gradient of successional stages and environmental conditions. The plots were chosen in a random stratified way (Guisan & Zimmermann 2000; Hirzel & Guisan 2002; Maggini et al. 2002), covering three gradients: site age, site size, and soil moisture.

To this end, first all brownfield sites suitable for the study were stratified. They were mapped in the field and categorized according to site age (4 categories, obtained from a time series of aerial photographs, see Table 2.1), site size (small = smaller than the median of all sites, large = larger than the median), and soil moisture (dry vs. moderately dry to moist). Soil moisture was estimated from visually inspecting the sites in early spring. Puddles of backed up rainwater due to compressed soil, as well as the presence of plants associated with moist habitats (e. g. rushes), were indicators of moderately dry to moist conditions.

Table 2.1: Stratification of study plots over three gradients: site age, site size, and soil moisture. Br = Bremen, Be = Berlin.

site age [years]	'small' (< 2.3 ha (Br) / < 1.5 ha (Be))				'large' (> 2.3 ha (Br) / > 1.5 ha (Be))			
	dry		moderately dry / wet		dry		moderately dry / wet	
	Br	Be	Br	Be	Br	Be	Br	Be
0-2	12	-	6	2	19	14	2	2
3-5	20	9	6	1	14	10	10	5
4-10	3	5	10	3	8	11	2	6
>10	17	9	5	3	20	6	3	3

Thus, all sites were assigned to one of 16 combinations (Table 2.1). Next, for each combination, a minimum of five points was randomly chosen within a GIS. Minimum distance between plots was 80 m, minimum distance from the site edge 20 m, as far as site size allowed. Some combinations were too rare for five points to be placed – in this case, the maximum possible number was used. Where possible, more points were placed, to a maximum of 20. This procedure resulted in a set of 154 points in Bremen and 89 in Berlin (Table 2.1).

Species data

Grasshoppers

Grasshoppers (Orthoptera) were recorded in a 15 m × 15 m quadrat north-east of the randomly selected sample point (Figure 2.5). I recorded grasshopper presence/absence once per year in late July or early August, when all species are present as adults (Ingrisch & Köhler 1998). To this end, acoustic monitoring (Bellmann 1993a,b) was used. I recorded all singing grasshoppers for two minutes at six distinct points per plot (Figure 2.5). *Oedipoda caerulescens*, which does not produce sounds, was detected by carefully searching the whole plot. The large species has a characteristic habitus and bright blue wings, making it easy to spot. However, all *Tetrix* species, which also do not sing, cannot be detected in this way. Thus, they could not be considered. The same was true for the *Tettigonia* species and for *Meconema thalassinum*, which are mainly active in the evening and during night.

I detected a total of 17 grasshopper species, 11 in Bremen and 15 in Berlin (Appendix 2, p. 134). Nine species were present in both cities. Species numbers per plot ranged between 0 and 9 with a median of 5. Six species are listed in in Germany's red data book (Maas et al. 2002), four as near threatened, one as vulnerable, and one as endangered.

Leafhoppers

Leafhoppers (Hemiptera: Auchenorrhyncha) were recorded in a 15 m × 15 m quadrat north-west of the random point (Figure 2.5). For leafhoppers, sweepnet sampling was carried out four times per year, at monthly intervals between early June and early September. Leafhopper species occur at different times of the year, thus four sampling periods were required to sample all species in the adult stage. Each sampling procedure consisted of 100 sweeps covering the entire plot. The catch was killed with ethyl acetate and frozen. All male adult individuals were determined to species level (Biedermann & Niedringhaus 2004). Female adults were only considered for species where determination of females is possible.

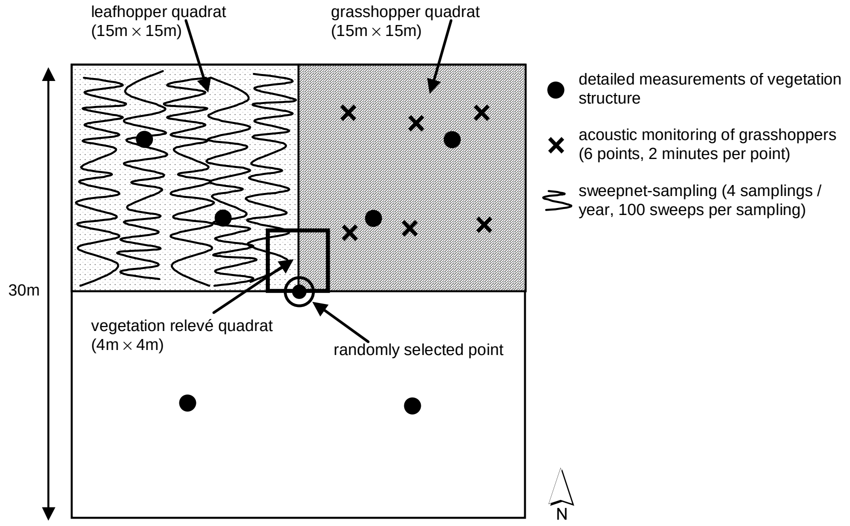

Figure 2.5: Data collection at each random point. Leafhopper sampling in the north-western quadrat (15 m × 15 m), grasshopper sampling in the north-eastern quadrat (15 m × 15 m), vegetation structure measurements at six points, 4 m × 4 m vegetation relevé quadrat.

I found a total of 214 leafhoppers species, 173 in Bremen and 130 in Berlin. 89 species occurred in both cities. Of the Bremen species, 44 occurred only in 2003 and 26 species only in 2004, resulting in a total of 147 species in 2003 and 129 species in 2004 (Appendix 1, p. 131). Species numbers per plot ranged between 0 and 32 with a median of 15. 46 species are listed in the German red data book (Remane et al. 1998). The conservation status of these is near threatened (9 species), vulnerable (28 species), endangered (8 species), and critically endangered (1 species).

Environmental Variables

At each site, I recorded a number of environmental variables. These variables described four main driving factors: site age, vegetation structure, soil parameters and landscape context. With the exception of site age, these driving factors comprised several variables (Table 2.2). For further analyses, only variables with at least 10% of non-zero values were considered.

Site Age

Site age was derived from a time series of aerial photographs, provided by 'GeoInformation Bremen' and by 'Senatsverwaltung für Stadtentwicklung Berlin'. For an example, see Figure 2.6.

Vegetation structure

Vegetation structure was assessed by two different methods. First, I estimated horizontal vegetation density, vegetation height, cover of moss and tree layer, litter cover, and cover of bare soil. For each parameter, I estimated an average value characterizing the entire 15 m × 15 m plot.

Second, at six points per plot (Figure 2.5), I conducted detailed measures, using a white screen (width: 50 cm, height: 150 cm) (Sundermeier 1999). The screen was

Table 2.2: Environmental data recorded for all plots. These were used as explanatory variables within habitat models.

successional age [years]
time since demolition of buildings or any other severe disturbance that reset succession;
derived from a series of aerial photographs

vegetation structure

- vegetation density [%]
  - horizontal density: density estimated from looking down on the vegetation
  - vertical density (measured with screen; Sundermeier 1999, Zehm et al. 2003)
    - average density at 4 different layers: 0-5 cm above ground, 5-15 cm,15-50 cm, 50-100 cm
    - average vertical density
    - variation of vertical density
- vegetation height [cm]
  - estimated height: height estimated from looking down on the vegetation
  - height measures (using screen) (Sundermeier 1999, Zehm et al. 2003)
    - 50%-height (height below which 50% of the total vertical vegetation cover is located), 75%-height, 90%-height
    - standardized vegetation height: height, at which vertical density has dropped to 25% of the value directly above the ground (Kuhn and Kleyer 1999/2000)
    - average height
- moss cover [%], litter cover [%], proportion of bare soil [%]
- cover of shrub & tree layer [%]
- cover of host plants [%] (for mono- and oligophagous leafhoppers), as specified by Nickel (2003)

soil parameters

- pH ($CaCl_2$), Ellenberg pH-values (calculated from vegetation data) (Ellenberg 1992)
- P [kg/ha], K [kg/ha], ECEC [$cmol_c$/kg] (Finnern et al. 1996), Ellenberg N-values (calculated from vegetation data) (Ellenberg 1992)
- available water capacity (AWC) [mm] (Finnern et al. 1996), air porosity [Vol%] (Finnern et al. 1996), Ellenberg moisture values (calculated from vegetation data) (Ellenberg 1992)
- gravel and stone content of topsoil [content classes] (Finnern et al. 1996)

landscape context [%]
proportion of brownfield types within 25, 50, 75, 100, 125 m

- open brownfields (< 10% vegetation cover)
- moderately dry to dry brownfields
  - brownfields with grassy vegetation (divided into scarce/dense and low/high)
  - brownfields with herbaceous vegetation (divided into scarce/dense and low/high)
- moist to wet brownfields
- brownfields covered with pre-forest stages or forests
- sum of all brownfield types

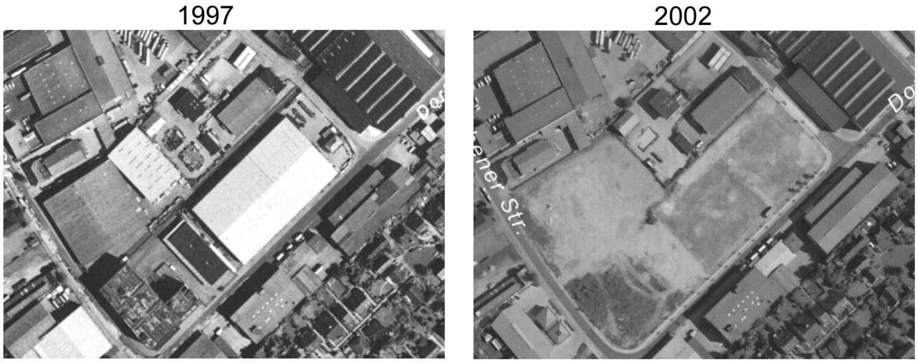

Figure 2.6: Site age was derived from a series of aerial photographs. The left picture shows one site when it was built up in 1997, the right picture shows the same site when it was derelict for about one year in 2002. Photographs provided by GeoInformation Bremen.

divided horizontally in eight layers: 0-5 cm, 5-10, 10-15, 15-25, 25-50, 50-75, 75-100, and 100-150. Each layer was divided vertically in strips, each 10 cm wide (Figure 2.7). I looked at the screen through a 10 cm wide stand of vegetation. Vegetation at distances further than 10 cm I pressed down with a board. For each rectangle on the screen, I estimated the vertical vegetation cover using the Londo scale (Dierschke 1994).

From these cover estimates, I calculated the average densities for each layer. These layer densities I used to calculate a number of height and density measures, following Sundermeier (1999) and Zehm et al. (2003) (see Table 2.2).

Weighted height (WH) and **weighted density** (WD) were calculated as follows:

$$WH = \frac{\sum_{i=1}^{k} h_i d_i}{\sum_{i=1}^{k} d_i} \qquad WD = \frac{\sum_{i=1}^{k} d_i (u_i - l_i)/t}{k}$$

with
d_i: vegetation density in layer i
h_i: mean height of layer i
k: number of layers
u_i: height of upper boundary of layer i
l_i: height of lower boundary of layer i
t: total height of all layers (150 cm)

In the same way, I calculated weighted **densities for four different layers**: 0-5 cm, 5-15 cm, 15-50 cm, and 50-100 cm. The **50%-height** was calculated as the height below which 50% of the vegetation is situated. Since this was usually somewhere within one layer, I calculated the height by interpolation. As an example, lets assume that from the ground up to the 10-15 cm layer, 40% of the vertical vegetation cover are situated. Up to the 15-25 cm layer, 60% are situated. Thus, the 50%-height is above the 10-15% layer, and within the 15-25% layer. It is interpolated between the heights (upper boundaries) and accumulated percent vegetation covers of these two layers. These are 15 cm and 40% for the 10-15 cm layer vs. 25 cm and 60% for the 15-25 cm layer. In this example, the 50% height is at 20 cm. **75%- and 90%-heights** were calculated the same way.

Another height measure was the **'standardized vegetation height'** (Kuhn & Kleyer 1999/2000). It represents the height where the vertical density has dropped to 25% of the value directly above the ground. As an example, let the vertical density be 80% above the ground, i. e. in the 0-5 cm layer. The standardized vegetation height is, where vertical density has dropped to 25% of this value, which is 20%. Again, I interpolated between layers as described above for the 50%-height. However, in this case I used the mean heights of layers instead of the upper boundaries (e. g. 2.5 cm for the 0-5 cm layer). This takes into account that the density usually decreases within a layer from bottom to top. To assess the degree of small-scale **variation in vertical densities**, I used the weighted densities for each vertical 10 cm wide stripe and calculated their standard deviation.

For all measures of vegetation structure that were derived from the screen measurements, six values were available per plot, since the screen was erected at six points. In all further analyses, the arithmetic means of these six values were used to characterize each plot.

Cover of all **plant species** was recorded within a 4 m × 4 m vegetation relevé quadrat north of the random point (Figure 2.5) by Schadek (2006). From these data, I extracted the cover of the host plants of mono- and oligophagous leafhopper species. I considered host plant specialisation as specified by Nickel (2003) for German leafhoppers.

Figure 2.7: White screen, divided in rectangles, used for detailed measures of vegetation height and density at six points per plot. Vegetation cover in front of each rectangle was estimated looking through a 10 cm wide stand of vegetation.

Soil parameters

Soil data were provided by Schadek (2006). Soil samples had been taken 0.5 m south of each random point. I used data on pH, soil nutrients (P, K, effective cation exchange capacity = ECEC), soil moisture (available water capacity = AWC, air porosity), and gravel and stone content of the topsoil (Finnern et al. 1996). As an alternative way to characterize soil conditions, I used Ellenberg indicator values for pH, N, and moisture (Ellenberg 1992). Those I calculated from the vegetation relevé data. I only calculated the Ellenberg indicator values for those plots where a minimum of five plant species was present which had assigned an indicator value .

Landscape context

To assess landscape context, I used a map of brownfield types. Types were (1) open brownfields with less than 10% vegetation cover, (2) brownfields dominated by herbaceous vegetation, (3) brownfields dominated by grasses, and (4) brownfields dominated by shrubs or trees (Table 2.2). For the herbaceous and grassy brownfields, further distinctions were made between scarce and dense vegetation, and between low and high vegetation.

Landscape context I expressed as proportions of each of these brownfield types in the surroundings of a plot (Figure 2.8). I used circles with five different radii between 25 m and 125 m. For each circle, I calculated the proportions of all brownfield types (Holland et al. 2004; Steffan-Dewenter 2003).

Figure 2.8: Landscape context was based on a map of brownfield types. Around each plot, this map was overlaid with circles of different radii (here: 100 m). The proportions of each brownfield type within the circle was calculated. In this example, the proportion of open brownfields is 9%, grassy brownfields and herbaceous brownfields account for 18% each.

Chapter 3

The use of habitat models in conservation of rare and endangered leafhopper species (Hemiptera, Auchenorrhyncha)

B. Strauss & R. Biedermann, Journal of Insect Conservation (2005) 9: 245-259.

Abstract

For conservation of leafhopper species, the knowledge of their habitat requirements is essential. However, for most species there is no ‘quantitative’ knowledge that would allow e. g. spatially explicit predictions. Such predictions can be made by habitat models, which quantify the relationship between the environment and the occurrence of species. In two plot-based case studies – the endangered leafhopper *Verdanus bensoni* in mountainous grasslands and four endangered leafhoppers in urban brownfields – we used habitat models to quantify the habitat requirements of these five species and to exemplify their use for creating habitat suitability maps. In the first case study, the multivariate model showed that occurrence probabilities of the leafhopper *V. bensoni* increase with both decreasing nitrogen indicator values and decreasing tree cover. On urban brownfields, successional age was a driving factor for species’ occurrence. Site age largely determines a range of vegetation characteristics, which, in multivariate models, often replaced the variable age. Internal validation showed the robustness of all models. The models allow predictions of habitat quality under different management regimes (e. g. response to fertilization or abandonment for *V. bensoni*, or to different turnover rates on brownfield sites). We discuss the application of habitat models in the conservation of leafhoppers, especially the use of habitat suitability maps.

3.1 Introduction

In cultural landscapes, habitat quality for leafhoppers (Hemiptera, Auchenorrhyncha) is often determined by habitat management. In grasslands, management type and intensity (e. g. mowing, grazing, fertilization) are of great importance (Morris 1981; Nickel & Hildebrandt 2003; Sedlacek et al. 1988). For instance, intensively used grasslands may exhibit different plant species composition and vegetation structure than largely undisturbed ones. The presence of certain host plants is a major habitat requirement of many leafhopper species. The actual quality of host plant patches may be largely determined by the amount, architecture and physiology of the host plant (e. g. Moon et al. 2000; Prestidge 1982). For many leafhopper species, additional factors like vegetation structure, microclimate or landscape context may be relevant (e. g. Claridge 1986; Denno & Roderick 1991; Haynes & Cronin 2003).

For conservation of leafhopper species, the knowledge of their habitat requirements is essential. However, for most species there is no ‘quantitative’ knowledge that would allow e. g. spatially explicit predictions. Nickel (2003) presents a comprehensive review of habitat requirements and host plants of Auchenorrhyncha species in Germany. However, the information is qualitative and descriptive rather than quantified. For instance, *Neophilaenus minor* is described to prefer ‘sparse cover of vegetation’. Since exact figures are not provided, it remains unclear whether the optimum is at 20 % vegetation cover, or if 50 % are still tolerated. For this reason, data-based predictions of habitat suitability, especially at the landscape level, are not feasible.

Such predictions can be made with habitat models. The aims of habitat models are twofold (e. g. Guisan & Zimmermann 2000; Scott et al. 2002). First, habitat models analyse and quantify the relationship between species’ abundance or occurrence and habitat factors. Second, they yield predictions of species’ abundance or occurrence given certain environmental conditions. The latter makes habitat models a potentially powerful tool in nature conservation: models are able to predict the probability of occurrence for sites or landscapes where species distribution data are not available (Wilson et al. 2005). They can also be used to assess the effects of land use changes or succession on habitat quality (Rudner et al. 2004). Habitat suitability maps which can be obtained from habitat models identify potential core habitats of species and form the basis for the planning of nature reserves (e. g. Cabeza et al. 2004). Such predictions of spatial distribution are essential, since conservation planning has to deal with the whole landscape (Wilson et al. 2005).

Here, we use presence-absence data of leafhopper species and environmental data to build habitat models based on logistic regression. In two case studies – the rare leafhopper *Verdanus bensoni* in mountainous grasslands and four endangered leafhopper species in urban brownfields – we (1) demonstrate the procedure of model building, including variable selection, classification and internal validation, (2) quantify habitat requirements of selected species, (3) exemplify the construction of habitat suitability maps, and (4) discuss the application of habitat models in the conservation of Auchenorrhyncha, especially to rare and endangered species. Rare here is understood as locally restricted due to rare habitat; the species can well build up considerable densities in their habitats.

3.2 Methods

Study sites

Case study 1: Leafhopper *Verdanus bensoni*

The first case study investigated habitat requirements of the leafhopper *Verdanus bensoni* (China, 1933). It was conducted in the mountain ranges of Dreisessel (1332 m; 48°47' N, 13°48' E) and Arber (1456 m; 49°06' N, 13°08' E) in the Bavarian Forest, Germany. The climate is characterized by mean annual temperatures between 5 and 6 °C with annual precipitation between 900 mm (low altitudes) and 2000 mm (high altitudes). For details on climate, geology and soil types see Hofmann (1984). The area is largely covered by forests. While at altitudes up to approx. 1200 m mixed forests (mainly beech, fir and spruce) are predominant, above this altitude only spruce forests are found. In the valleys and at lower altitudes land use is characterized by a mix of forests, pastures and fields. At higher altitudes only few patches of grassland are scattered within the forests, mainly small pastures ('Schachten', see Hofmann 1984) and ski runs.

Verdanus bensoni has a scattered range and is restricted to European mountain ranges (Nickel 2003). Up to now, it has been recorded from the German Alps, Scotch Highlands, Swiss and French Jura, Bavarian and Bohemian Forest, Giant Mountains, and Ural Mountains. In Germany, *Verdanus bensoni* is a rare species in the Alps and in the Bavarian Forest. It is listed in the Red Data Book (Remane et al. 1998). In the study area, the Bavarian Forest, *V. bensoni* was recorded above approx. 800 m a.s.l. (Biedermann unpubl.). *V. bensoni* was found in montane and alpine grasslands, probably feeding on grasses (Biedermann 1998; Nickel 2003). However, the specific habitat requirements have not been studied yet in detail.

Case study 2: Endangered species in urban brown-fields

The second case study was carried out on brownfield sites in the city of Bremen, located in the lowlands of northwest Germany (8°44'N, 53°05'E, mean temperature 8.8 °C, mean annual precipitation 694 mm). Urban brownfields, previously-developed land within cities, often support a rich wildlife and house a whole range of rare and endangered species (Eyre et al. 2003; Gibson 1998). They can provide habitat for stenotopic species from semi-natural habitats like dry sandy grasslands (Eversham et al. 1996). Brownfields form highly dynamic habitats (Gibson 1998; Gilbert 1989) which are continuously being generated, quickly changed by successional processes, and destroyed by redevelopment. We assume that, within this cycle, each species finds a limited period of time where its habitat requirements are met. In this study, we investigated four endangered leafhopper species found on brownfield-sites: *Kelisia sabulicola* (W. Wagner, 1952), *Macrosteles quadripunctulatus* (Kirschbaum, 1868), *Rhopalopyx vitripennis* (Flor, 1861), and *Neophilaenus minor* (Kirschbaum, 1868). They are listed as 'threatened' or 'potentially threatened' (*N. minor*) in Germany's Red Data Book (Remane et al. 1998).

Sampling design

Case study 1

For the *Verdanus bensoni* study, 42 plots (5 m × 5 m) were chosen at altitudes between 542 m and 1453 m a.s.l., depending on the availability of grasslands or forests with grass layer. In each grassland or forest the plots were chosen randomly. In each plot the following parameters were measured: total plant cover and cover of the predominant grass species in the herb layer, tree cover, slope, and altitude. Additionally, the mean Ellenberg indicator values (Ellenberg 1992) for moisture and nitrogen were calculated from the plant species composition. The occurrence of *Verdanus bensoni* was recorded by sweep-netting. At each plot, 20 sweeps were taken covering the entire plot. The sweep-netting was repeated three times.

Case study 2

We investigated urban brownfields within 100 km^2 in the city of Bremen. On the brownfield sites, 157 sample plots of 225 m^2 were set up in a random stratified way (Guisan & Zimmermann 2000; Hirzel & Guisan 2002; Maggini et al. 2002). Minimum distance between plots was set to 80 m. To ensure that all characteristic types of brownfields got sampled, the plots covered three gradients: site size, age of brownfields (duration of abandonment), and soil moisture. In 2003, sweep-net sampling was carried out four times between early June and early September, with 100 sweeps each time.

At each study plot we collected a set of environmental parameters. These included several parameters describing vegetation structure, cover of host plants (as specified by Nickel 2003), soil parameters and landscape context. Site age, as time since demolition of buildings or any other severe disturbance that put succession back to zero, we derived from a time series of aerial photographs. Landscape context was assessed using a map of vegetation types. For examples of these vegetation types see Table 3. Within a GIS, we calculated the proportion of each of these types within a certain distance around every plot (Strauß et al. 2004). We tested radii between 25 m and 125 m.

For detailed measures of vertical vegetation structure, we used a white screen, divided in rectangles, that was erected perpendicular to the ground (see Sundermeier 1999). At six points per plot, vertical cover was estimated for each rectangle looking through a 10 cm wide stand of vegetation. From these estimates, height and density parameters were calculated (Table 3) (Sundermeier 1999; Zehm et al. 2003). 50%-height refers to the height, below which 50% of the total vegetation cover are located. 75%-height and 90%-height are defined respectively.

Statistical methods of habitat modeling

Logistic regression

We used species' presence/absence data for model building. A popular approach for modelling such data is using logistic regression (i. e. generalised linear models (GLM) with a logistic link) (Guisan & Zimmermann 2000; Harrell 2001; Hosmer & Lemeshow 2000; Morrison et al. 1998; Reineking & Schröder 2003). Logistic regression has been successfully used in numerous studies on species-habitat relationships (e. g. Guisan et al. 1999; Manel et al. 1999a; Peeters & Gardeniers 1998). Metric variables can be handled along with nominal ones. The shape of the response curve can be either sigmoid or unimodal ('bell-shaped'), the latter by including second order terms (Hosmer & Lemeshow 2000; Peeters & Gardeniers 1998). The outcome of a logistic regression model is the occurrence probability at given parameter values. To distinguish between predicted presence and absence, a threshold probability needs to be defined. Predictions should stay restricted to the range of parameter values that has been covered by the study.

Measures of model performance

Numerous measures assessing performance of logistic regression models are available (Hosmer & Lemeshow 2000; Manel et al. 2001; Pearce & Ferrier 2000b). All of them can only describe certain aspects of model performance. Therefore, we used a set of criteria, threshold-independent as well as threshold-dependent (Manel et al. 1999b).

The difference between predicted and observed values (model calibration) was measured by R_N^2 (Nagelkerke 1991). Like R^2 in linear regression, it ranges from 0 to 1. On an univariate level, we used R_N^2 to compare the relative influence single predictor variables had on species' presence. Model discrimination was assessed with AUC (Hanley & McNeil 1982), the **a**rea **u**nder the receiver operating characteristic **c**urve. AUC values ≥ 0.7 are regarded as acceptable, ≥ 0.8 as excellent, and ≥ 0.9 as outstanding (Hosmer & Lemeshow 2000).

Sensitivity (proportion of correctly predicted presences), specificity (proportion of correctly predicted absences) and CCR (**c**orrect **c**lassification **r**ate) are classification threshold dependent measures. CCR is easy to interpret, however largely dependent on the rather arbitrary choice of a threshold (Reineking & Schröder 2003) and should be handled with care. As a threshold, we chose P_{fair}, where specificity and sensitivity are equivalent (Hosmer & Lemeshow 2000). Since the species under study are rare and their prevalence is low, P_{fair} ensures that a reasonable proportion of presences will be predicted correctly. On the other hand, this may result in a lower total number of correct predictions (lower CCR) and, in particular, more predicted presences for observed absences (lower specificity) than with other thresholds. For nature conservation, where often the aim will be to correctly predict as many relevant habitats patches as possible (Morrison et al. 1998), we believe that the advantages of P_{fair} outrun these disadvantages.

Since CCR, sensitivity and specificity are highly dependent on the species' prevalence (Manel et al. 2001), we used Cohen's $Kappa(\kappa)$ (Cohen 1960) as another, less sensitive threshold-dependent measure (Fielding & Bell 1997). $Kappa$ ranges from 0 to 1 with values between 0.40 and 0.55 indicating fair, values between 0.55 and 0.70 good agreement between observed and predicted values (Monserud & Leemans 1992). For comparison between models we used the information criterion AIC_c, a version of AIC (**A**kaike's **I**nformation **C**riterion) modified for small samples (Buckland et al. 1997). AIC indicates how well a model performs the trade-off between model fit and model complexity.

Model building

As recommended by Hosmer & Lemeshow (2000), we performed careful univariate analyses prior to building of multivariate models. For each species, we tested univariate models of all variables. Only significant variables ($p \leq 0.05$) with $R_N^2 \geq 0.05$ were considered for further analysis.

A popular approach for building multivariate models are stepwise procedures for variable selection. Pearce & Ferrier (2000a) recommend the stepwise backward procedure, which we used for the *Verdanus bensoni* study. In general, all stepwise procedures have some disadvantages (Reineking & Schröder 2004). They might not find the best model, or selection is unstable and does not hold for slightly different data. With a large number of predictor variables, like in the brownfield study, stepwise procedures perform poorly. Therefore, in that study, we followed a different approach: we calculated models for all combinations of four, three and two parameters, using Splus 6.1 functions glm and stepAIC (MASS library). Since the ratio 'number of observations'/'predictor variables' should not fall much below 10 (Guisan & Zimmermann 2000; Morrison et al. 1998), more than four variables per model are not a sound choice for the available data sets.

Strong correlations between predictor variables will lead to abnormally high coefficients and standard errors (Neter et al. 1989). Therefore, maximum Spearman rank correlation between predictor variables within one model was allowed to be 0.7 (Fielding & Haworth 1995). Since height and density parameters in the brownfield study showed strong correlations, only one of each group was chosen for multivariate modelling.

Model validation

Performance criteria are usually over-optimistic if they are calculated on the same data set that was used for parameter estimation (Reineking & Schröder 2003). Since independent data were not available to correct for this optimism, we used the bootstrap as an internal validation method (Efron & Tibshirani 1993; Verbyla & Litaitis 1989) for evaluating the models. According to Steyerberg et al. (2001) and Harrell (2001), it outperforms other internal validation procedures and allows nearly unbiased estimates of model performance. We performed the bootstrap with Splus 6.1, doing 300 iterations, resulting in corrected measures of model performance.

Habitat suitability maps

Habitat suitability maps can be obtained by applying the regression equations of habitat models to maps of the relevant environmental data within a GIS. These maps spatially explicit predict the probability of occurrence of the focal species (Austin 2002; Joy & Death 2004; Osborne et al. 2001). Models used for such spatially explicit predictions are restricted to parameters being available area-wide. In the brownfield-study, these were age of brownfield sites, and all landscape context parameters. For *N. minor*, we calculated a model from these parameters and applied it to part of the study area.

3.3 Results

Univariate models

Case study 1

The univariate logistic regression analysis revealed a number of significant habitat parameters being related to the incidence of *Verdanus bensoni* (Table 3.1). The occurrence of *V. bensoni* was positively related to altitude and moisture indicator and negatively to nitrogen indicator and tree cover. The habitat parameters slope and total plant cover

Table 3.1: Case study 1: Univariate responses of the leafhopper *Verdanus bensoni* to various habitat parameters. -S: sigmoid response, occurrence probability decreases with increasing values of predictor variable; +S: sigmoid, occurrence probability increases with increasing values of predictor variable.

Parameter	**Range**	**Response of *V. bensoni***	
		R^2_N	**shape**
Altitude	542-1453 m	0.43	+ S
Nitrogen indicator	2-6	0.41	– S
Moisture indicator	5-7	0.34	+ S
Tree cover	0-100%	0.14	– S

showed no effect on the occurrence of *V. bensoni*. Likewise, the cover of single grass species had no positive influence on the occurrence of *V. bensoni*.

Case study 2

For the brownfield study, univariate responses for all relevant variables are listed in Table 3.3. A total of 29 predictor variables passed the performance criteria. Age was a strong predictor for all four species. *M. quadripunctulatus* showed a sigmoid response, occurrence probability decreased with increasing age (Figure 3.1), whereas the other species showed unimodal responses with peaks between 13 and 20 years.

Vegetation height did not play an important role for *M. quadripunctulatus*. *K. sabulicola*, *N. minor* and *R. vitripennis* showed similar, mostly unimodal responses to vegetation height and density parameters. *R. vitripennis* made an exception in preferring high density in the lowest layer. For *M. quadripunctulatus*, high overall density decreased occurrence probability, whereas it preferred moderate densities within the lower vegetation layers.

Most species exhibited strong relationships with moss cover, litter cover and bare ground. As with density and height, *K. sabulicola* was negatively correlated with moss and litter cover, whereas the other species preferred medium to high values for these parameters. In general, high covers of the respective host plants strongly enhanced occurrence probabilities. PH was the most important among the soil parameters. *M. quadripunctulatus* preferred high, *N. minor* and *R. vitripennis* medium levels.

Overall, the influence of landscape context was comparatively weak with two exceptions. Occurrence of *N. minor* increased with rising proportions of brownfields with grassy, sparse vegetation. *M. quadripunctulatus* showed an unimodal response to the

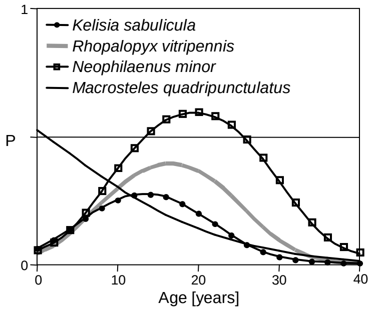

Figure 3.1: Univariate response curves for the variable ‘age’.

Table 3.2: Case study 2: Univariate responses: R_N^2 and shape of response curves. R_N^2 of variables included in best multiple models printed bold. -S: sigmoid response, occurrence probability decreases with increasing values of predictor variable; +S: sigmoid, occurrence probability increases with increasing values of predictor variable; U: unimodal response.

Variable/Parameter	Range	*M. quad.*		*K. sabul.*		*N. minor*		*R. vitrip.*	
		R^2_N		R^2_N		R^2_N		R^2_N	
Age [years]	0-33	0.16	-S	**0.13**	U	0.19	U	**0.21**	U
Vegetation height [cm]									
Veg. Height	0-110							0.22	U
Weighted height	0-24			0.09	U	0.10	U	0.18	U
Max. height	0-117			0.05	+S			0.20	U
50%-height	0-10					**0.14**	U		
75%-height	0-28					0.11	U	0.08	U
90%-height	0-63			0.06	U			0.13	U
Vegetation density [%]									
Veg. cover (horizontal)	0-90	0.05	-S	0.14	U			0.22	U
Veg. density (vertical)	0-21	0.08	-S					0.22	U
Veg. dens. 0-5cm	0-92	0.16	U	**0.14**	U	0.07	U	0.18	+S
Veg. dens. 5-15cm	0-66	0.14	U	0.13	U	0.07	U		
Veg. dens. 15-50cm	0-28	0.06	-S					0.13	U
Veg. dens. 50-100cm	0-20							0.07	U
Density variation	0-7							0.11	U
Other vegetation parameters [%]									
Moss cover	0-100	0.23	-S	0.05	+S	0.05	+S	**0.23**	U
Litter cover	0-100	**0.27**	-S			**0.08**	U	0.18	+S
Bare ground	0-100	0.20	U	0.12	-S	0.06	-S	0.18	-S
Cover of host plants [%]									
Festuca rubra/ovina	0-88					0.05	+S	**0.40**	+S
Carex arenaria	0-19			**0.20**	+S				
Corynephorus canescens	0-38					**0.29**	+S		
Soil									
Effective cation exchange capacity	2-15			0.09	U			0.07	U
pH	3.4-7.7	**0.24**	+S			0.18	U	0.12	U
Stone content (topsoil)	0-6	0.08	+S	0.07	U	0.17	-S		
Available water capacity	4-193					0.08	+S	0.05	+S
Landscape context:									
Proportion of brownfields, covered with a certain structural vegetation type, within a radius of 75m [%]									
Open (<10% veg. cover) ('BO75')	0-100	**0.14**	U					0.05	-S
Grassy, sparse veg. ('BGS75')	0-100			0.07	+S	**0.36**	+S		
Grassy, dense veg.	0-82	0.06	-S					0.07	U
Herbaceous, sparse veg.	0-98	0.09	U					0.06	-S
Bushes/hedges	0-22							0.08	U

proportion of open brownfields with $< 10\%$ vegetation cover. For all species, R_N^2 of landscape context was highest for the 75 m-radius.

Multivariate models

Case study 1

The multivariate habitat model for *V. bensoni* contained two significant habitat parameters (Table 3.3). The model showed that with both decreasing nitrogen indicator values and decreasing tree cover the incidence of *V. bensoni* increased (Figure 3.2). Model discrimination was good (Table 3.3): in 85% of the plots occurrence of *V. bensoni* was correctly classified.

Table 3.3: Case study 1: Multiple habitat model of the leafhopper *Verdanus bensoni*. Model parameters, model performance and classification using the threshold P_{fair}

Model parameters & coefficients	
Nitrogen indicator	-1.94218
Tree cover	-0.05667
Intercept	7.33042
Model performance	
Significance	$p < 0.001$
R^2_{Ncorr}	0.56
AUC_{corr}	0.88
Classification P_{fair}	
P_{fair}	0.48
κ	0.72
Sensitivity	0.88
Specificity	0.85
CCR	0.85

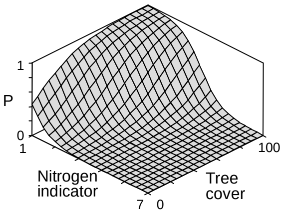

Figure 3.2: Multiple habitat model for *Verdanus bensoni*. Probability of occurrence (P) is plotted against nitrogen indicator and tree cover.

Case study 2

The final multivariate models for the brownfield species contained three or four (*N. minor*) explanatory variables (Table 3.5). Model performance measures are given in Table 3.5, coefficients, standard errors and p-values in Table 3.4.

The model for *R. vitripennis* included the parameters age, moss cover and cover of *Festuca rubra/ovina*. Occurrence probabilities were highest at medium levels of age and moss cover (Figure 3.3). With increasing cover of *Festuca*, the influence of these parameters became negligible, occurrence probabilities always exceeded the threshold.

Table 3.4: Case study 2: Model performance of multiple models. All performance measures corrected by bootstrapping. (+ˆ2) indicates that the second order term is included to model an univariate response.

Species	pres./abs.	Model parameters	Threshold independent		Threshold dependent: P_{fair}				
			R^2_N	AUC	P_{fair}	κ	Sensitivity	Specificity	CCR
Rhopalopyx vitripennis	33/124	Age(+^2) + Moss%(+^2) + Festuca.rubra/ovina%	0.42	0.85	0.21	0.49	0.77	0.81	0.80
Neophilaenus minor	25/132	50%-height(+^2) + Litter%(+^2) + Corynephorus.canescens% + BGS75	0.50	0.90	0.15	0.43	0.75	0.81	0.80
Neophilaenus minor	25/132	Age (+^2) + BGS75	0.38	0.83	0.13	0.36	0.73	0.78	0.77
Macrosteles quadripunctulatus	58/99	Litter% + pH + BO75(+^2)	0.41	0.84	0.41	0.52	0.76	0.78	0.77
Kelisia sabulicola	30/127	Age(+^2) + Veg.dens.0-5cm(+^2) + Carex.arenaria%	0.29	0.77	0.17	0.28	0.67	0.72	0.70

Table 3.5: Case study 2: Coefficients and p-values of the multiple models.

	Coeff.	S.E.	P
Macrosteles quadripunctulatus			
Intercept	-5.0951	1.3283	<0.01
BO75	0.0492	0.0334	0.14
BO75^2	-0.0008	0.0004	0.04
Litter	-0.0382	0.0100	<0.01
ph	0.8739	0.2120	<0.01
Rhopalopyx vitripennis			
Intercept	-3.9712	0.7500	<0.01
Age	0.2096	0.1184	0.08
Age^2	-0.0070	0.0035	0.04
Moss.cover	0.0938	0.0363	0.01
Moss.cover^2	-0.0010	0.0004	0.01
Festuca rubra/ovina	0.0678	0.0160	<0.01
Neophilaenus minor			
Intercept	-9.8063	3.2662	<0.01
50%-height	3.1886	1.6546	0.05
50%-height^2	-0.4859	0.2231	0.03
Litter.cover	0.1483	0.0490	0.00
Litter.cover^2	-0.0014	0.0005	0.01
Corynephorus canescens	0.2307	0.1194	0.05
BGS75	0.0617	0.0163	<0.01
***Neophilaenus minor* (suitability map)**			
Intercept	-3.4064	0.5709	<0.01
Age	0.0644	0.0266	0.02
Age^2	-0.0020	0.0012	0.11
BGS75	0.0563	0.0106	<0.01
Kelisia sabulicola			
Intercept	-4.6136	0.9552	<0.01
Age	0.2059	0.1027	0.05
Age^2	-0.0043	0.0029	0.14
Veg.dens.0-5cm	0.1005	0.0449	0.03
Veg.dens.0-5cm^2	-0.0012	0.0005	0.02
Carex arenaria	0.6490	0.2458	0.01

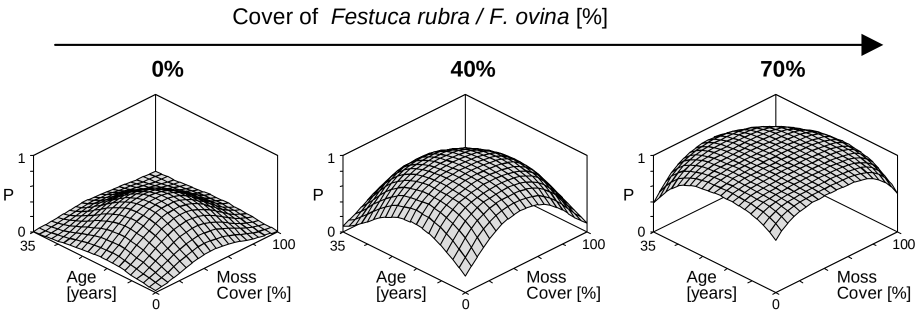

Figure 3.3: Best habitat model for *Rhopalopyx vitripennis*. Occurrence probability (P) on the z-axis, against age and moss cover. Three levels of *Festuca rubra/ovina*-cover are represented in the three diagrams.

Occurrence of *N. minor* could be explained best with a four-parameter model. Occurrence probabilities above the threshold were restricted to low, but non-zero 50%-heights, regardless of the other parameter values (Figure 3.4). Medium litter covers were preferred in combination with low cover of *Corynephorus canescens* and low proportions of BGS75. With increasing values of either or both of these parameters, the modifying influence of litter cover decreased.

The shape of the response surface of *K. sabulicola* strongly depended on the cover of *Carex arenaria* (Figure 3.5). High values of 10% led to occurrence probabilities close to one, regardless of the other two factors (Figure 3.5). At low cover of *Carex*, presence depended on medium levels of age and vegetation density in the 0-5 cm layer. *M. quadripunctulatus* reached high occurrence probabilities only at moderate to high pH-levels and in combination with both little to no litter cover and medium proportions of BO75 (Figure 3.6).

Model performance was better for *R. vitripennis*, *N. minor* and *M. quadripunctulatus* ($R_N^2 > 0.41$, AUC>0.84) than for *K. sabulicola* ($R_N^2 = 0.29, AUC = 0.77$) (Table 3.4).

Habitat suitability map

The habitat suitability map for *N. minor* (Figure 3.8) was based on a two-parameter model with age and BGS75. Occurrence probability steeply raised with increasing proportions of BGS75, in particular in combination with medium age (Figure 3.7). As the threshold was low (0.13), most of the response surface was above the threshold. Nevertheless, large proportions of the brownfield sites (62%) have low values for BGS75 combined with young age, resulting in occurrence probabilities below the threshold, shown as white regions on the map. The model yielded poorer performance than the best model for the species (Table 3.5), with R_N^2 at 0.38 and AUC at 0.83. Sensitivity and specificity were at 0.76 and 0.77, respectively. Out of the 28 plots within the section shown in the map (Figure 3.8), all nine presences were predicted correctly, six of the 19 absences were classified incorrectly as presences.

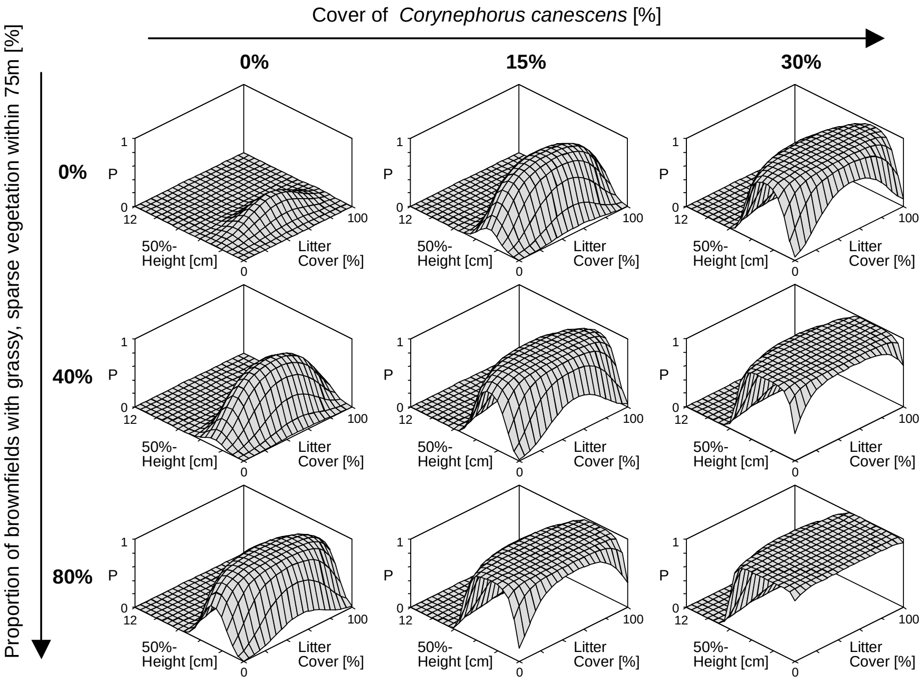

Figure 3.4: Best habitat model for *Neophilaenus minor*. In each diagram, P is plotted against 50%-Height and litter cover. Columns represent different levels of *Corynephorus canescens*-cover, rows different proportions of BGS75.

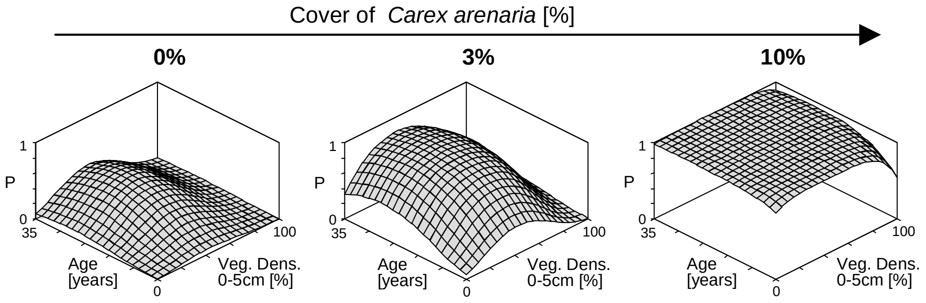

Figure 3.5: Best habitat model for *Kelisia sabulicola*. P is plotted against age and vegetation density 0-5 cm, diagrams represent different levels of *Carex arenaria* cover.

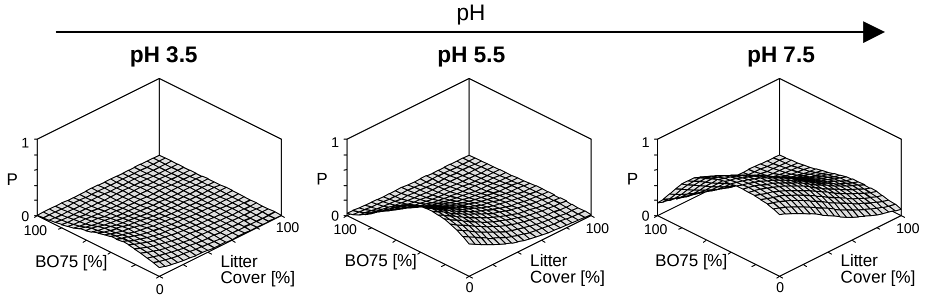

Figure 3.6: Best habitat model for *Macrosteles quadripunctulatus*. P is plotted against BO75 and litter cover, diagrams represent different levels of pH.

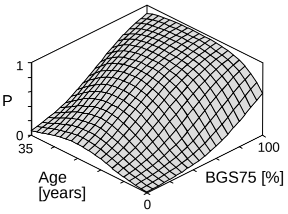

Figure 3.7: Model used to calculate a habitat suitability map for *Neophilaenus minor*. P is plotted against age and BGS75.

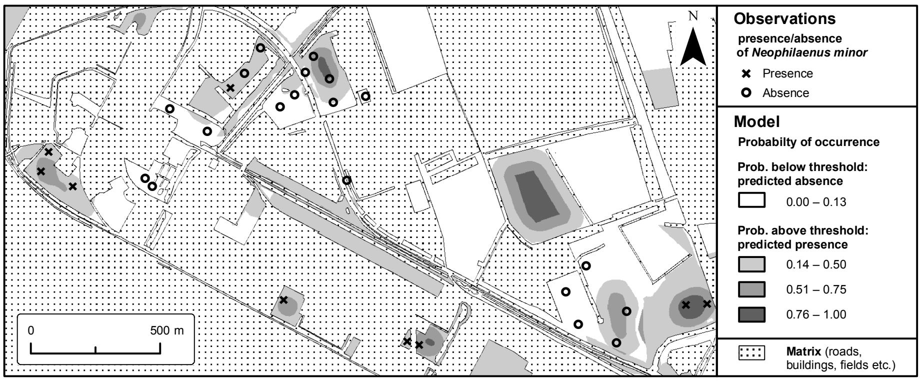

Figure 3.8: Habitat suitability map for *Neophilaenus minor*. Non-brownfields sites (sealed areas: e. g. roads, buildings, container parks; farmland: mostly wet grassland) are considered per se as unsuitable habitats (matrix) and are dotted on the map.

3.4 Discussion

Case study 1

For *V. bensoni*, the most important habitat factor was found to be the fertility of the grassland sites. *V. bensoni* was restricted to low productivity sites. Consequently, agricultural intensification and fertilization of the low productivity habitats would pose a threat to *V. bensoni*. Further, the occurrence of *V. bensoni* would decrease if the tree cover of grassland sites increased, for instance after abandonment of mowing or grazing. There was no relationship between the occurrence of *V. bensoni* and the cover of single grass species. It is known from literature that *V. bensoni* lives on grasses, and it has been argued that *V. bensoni* may use several grass species as host plants (Biedermann 1998; Nickel 2003). Our results confirm that *V. bensoni* obviously is not a host plant specialist like, for instance, *Neophilaenus minor*.

Case study 2

Within our dataset, age of brownfield sites was the most important single factor determining species' occurrence. This agrees with the results of Small et al. (2003) for carabid assemblages, who found that time since the last disturbance has a significant influence on species' occurrence. In the study of Brown et al. (1992), successional age had a strong effect on leafhopper assemblages. Characteristic stages of brownfield succession strongly depend on time (Gilbert 1989), but substrate can modify succession rates considerably (Gilbert 1989; Small et al. 2003). The main difference between successional stages lies in their vegetation structures (Hollier et al. 1994). This might be the reason why in two of the ‘best’ multivariate models, age was substituted by vegetation parameters. They probably represent the specific conditions of a particular site more accurately.

Vegetation structure is known to strongly affect species composition of Auchenorrhyncha communities (Achtziger 1995; Denno & Roderick 1991; Murdoch et al. 1972). We assume that vegetation structure is also an indirect measure for a site’s microclimate. Sparse vegetation causes more extreme conditions in terms of temperature and moisture (Biedermann; Geiger et al. 2003). Soil conditions influence both plant species composition and food quality of plants (Schoonhoven et al. 1998). The effect of soil conditions on leafhoppers was shown by Sanderson et al. (1995).

Landscape context we believe to indirectly represent several factors. First, it is a measure for site isolation. If proportions of favoured habitat types are low or those of unsuitable habitat are high, the site is likely to be isolated and is thus less likely to be occupied (Biedermann 2004; Haynes & Cronin 2003). Second, landscape context is an indicator for patch size: large proportions of favourable habitat types represent large patch sizes. Large patches have a higher probability to be occupied (e. g. Biedermann 2002a). The positive correlation between *N. minor* and the proportion of brownfields with grassy, sparse vegetation is probably due to either of these two factors. Third, surrounding vegetation influences a site’s microclimate. Bushes and hedges slow down wind and thus provide more balanced, warmer and moister conditions. Sparse vegetation does the contrary. The comparatively small influence of landscape context might be due to two factors. First, most leafhopper species seem to not need large sites to build up viable populations (Biedermann 2002a, 2004; Cronin 2004). Second, it is likely that for leafhoppers, most brownfield sites are not truly isolated. Small patches of potential habitat are found along most roads and tracks and connect the larger sites.

Overall, univariate responses of all four species corresponded well to habitat requirements described by Nickel (2003). For instance, *M. quadripunctulatus* is regarded to be a pioneer species preferring sandy, sparsely vegetated and moderately dry to dry sites. This agrees with our results that the species was restricted to young sites with very scarce vegetation.

The use of habitat models in conservation

Internal validation showed the robustness of habitat models within our studies. However, in perspective, it would be desirable to validate these models externally, i. e. apply them to independent data sets from other landscapes. In this respect, it would be interesting to test whether the habitat model of *Verdanus bensoni* from the Bavarian Forest is applicable to Alpine populations. The transfer of habitat models has been successfully demonstrated in other insects (Biedermann 2005; Bonn & Schröder 2001; Kuhn & Kleyer 1999/2000; Schröder & Richter 1999/2000). Unfortunately, up till now there have been no attempts with leafhoppers. However, transferability is regarded as a prerequisite towards a broad application of habitat models in the conservation of leafhoppers.

The habitat models presented here are able to predict the quality of habitats under different management. In the leafhopper *Verdanus bensoni*, the habitat model predicts the response to fertilization or abandonment. In the urban brownfield study, the effects of different turnover rates became obvious. Models are able to predict the occurrence of species along a temporal gradient of succession. This quantitative information may be essential for the conservation of species in brownfields. It was shown that the species under study are restricted to the early or intermediate stages of brownfield succession. Once sites become too old, these species are likely to disappear. Small et al. (2003) found for carabid beetles that the most species rich assemblages are found on early successional sites that can be between 6 and 20 years old. For conservation, this implies, that protection of existing brownfield-sites without management will cause many species to disappear over time. In order to preserve high biodiversity, one should focus on the duration of the brownfield stage within the cycle of emergence, succession and demolition of brownfields sites. A constant stock of brownfields of young and intermediate age within an industrial area preserves the typical species assemblage.

The case studies also showed, that in some species it is possible to build habitat models with good performance using only a few habitat parameters. For instance, in *Verdanus bensoni* two parameters were sufficient to reach a high correct classification rate. For conservation purpose, those habitat models may be a tool to identify potential habitat relying on only a small number of environmental parameters. Even though a large number of parameters might be necessary to detect the driving forces and build well performing models, once these parameters are known, models can easily be applied to other regions, provided availability of parameters. In the light of increasing availability of area-wide environmental data (e. g. from satellite imagery or public GIS databases) this prerequisite will be easier to meet in future. However, some variables, like the ones describing aspects of vegetation structure in a detailed way, cannot be obtained area-wide by these methods. Still, these variables are of great importance when studying a species' ecological needs. Hence, for habitat suitability maps, these variables have to be substituted by ones that are available area-wide.

The application of habitat suitability maps in conservation may easily identify and map areas for protection (e. g. Cabeza et al. 2004). However, there are some issues to consider when applying habitat models and habitat suitability maps. First, species' absences can never be recorded with the same certainty as species' presences. Kleyer et al. (1999/2000) suggest to understand presence and absence as a species-specific characteristic. Second, false-positive predictions not necessarily indicate a poor model fit, since plots recorded as non-use are not always unsuitable habitat (Capen et al. 1986). This is particularly true in declining populations, where many false-positive predictions might result (Wilson et al. 2005): due to an increased extinction rate, suitable habitat might not be inhabited. Thus, habitat suitability maps may help to identify areas for the reintroduction of endangered or rare species by showing potentially suitable habitat.

In conclusion, this study demonstrated the building and application of habitat models for leafhoppers. Although further research is needed, especially on the generality of single species habitat models, the value of habitat models for conservation seems obvious. The use of habitat suitability maps could find a broad application in future.

Acknowledgements

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Chapter 4

Urban brownfields as temporary habitats: Driving forces for the diversity of phytophagous insects

B. Strauss & R. Biedermann. Ecography (in press).

Abstract

In urban brownfields (derelict sites), we studied the influence of local factors (successional age, vegetation structure, soil) and landscape context (spatial arrangement of brownfields of different successional stages) on the diversity of phytophagous insects, grasshoppers and leafhoppers (Orthoptera and Hemiptera: Auchenorrhyncha). The study was conducted on a total of 246 plots in the cities of Bremen and Berlin, Germany. We used a habitat modelling approach, enabling us to predict the community from single species models (30 species in Bremen, 28 in Berlin).

The results revealed that communities were predominantly determined by vegetation structure, followed by landscape context, soil parameters and site age. For most species, local factors were the most important. Only few species were strongly influenced by landscape context, even though some showed clear negative reactions to low proportions of brownfields in the surroundings.

Along a successional gradient of vegetation structure, from scarce and low to dense and high vegetation, the insect community was not static. Even though species numbers remained comparatively constant, species composition changed considerably. Many species showed clear preferences for certain successional stages. Thus, maintaining the regional species pool of a city requires a mosaic of all successional stages.

4.1 Introduction

Urban brownfields as habitats

Urban areas tend to have a higher biodiversity than their agricultural surroundings. This might be due to high habitat diversity and a wide range of environmental conditions found in urban habitats (Rebele 1994; Schwerk 2000) as well as to their warmer climate. The latter is known as the urban heat island effect (Gilbert 1989). Urban brownfields (derelict sites) are one of the many habitat types found in urban areas. Brownfields, comprising previously-developed land as well as landfills, industrial dumps or abandoned railyards, form an important type of urban habitat. They often support rich communities and considerable portions of the biodiversity of a city (Eyre et al. 2003; Gibson 1998; Rebele 1994). Even though created by humans, they represent largely undisturbed, semi-natural habitats (Sanderson 1992b), and are home to true urban communities that might not be found elsewhere.

Brownfields are continuously being generated, quickly changed by successional processes (Brown & Southwood 1987), and destroyed by redevelopment. Thus they form habitats which are highly dynamic in space (as the location of brownfield patches changes due to redevelopment and demolition) and time (as individual brownfield patches continuously change through the course of succession) (Gibson 1998; Wood & Pullin 2002). These two processes generate a spatio-temporal mosaic of different successional stages and built-up areas. Species that are restricted to certain successional stages will find suitable habitat at changing locations (Rebele 1994).

In order to preserve biodiversity within cities, it is crucial to understand how these dynamic aspects influence habitat quality, and which driving factors shape the rich urban communities (Wood & Pullin 2002). Urban ecosystems, which have been largely neglected by ecological research for a long time (Niemelä 1999), start to receive increasing interest. Recently, much work has been done on species assemblages along urban-rural gradients (e. g. Niemelä et al. 2002; Sadler et al. 2006). However, processes on, and differences within, urban sites have not yet seen much attention. Even though some studies surveyed insects in urban brownfields, e. g. carabid beetles (Eversham et al. 1996; Eyre et al. 2003; Schwerk 2000; Small et al. 2006, 2003) and leafhoppers (Sanderson 1992b), quantitative knowledge linking presence or abundance to environmental mechanisms remains scarce for most taxa.

Modelling species communities

In order to preserve species diversity, it is crucial to know which species occur under certain environmental conditions. Olden (2003) proposes that for this purpose, a habitat-based, multispecies and species-specific approach is required, whereas models predicting species numbers provide much less information. Therefore, we developed habitat models for every single species. These models take into account the identity of species and functional differences in their relationship to the environment, and include the possibility that species might react to the surrounding landscape at different scales (Holland et al. 2004). The single species models then provide predictions for the assemblage of species most likely to occur under certain environmental conditions (Peppler-Lisbach & Schröder 2004).

Modelling species-environmental relationships usually searches for a single best model for every species, a process with numerous pitfalls and an outcome strongly influenced by the method and data used (Guisan & Zimmermann 2000; Olden & Jackson 2000; Rushton et al. 2004). In contrast to this, Burnham (2002) proposes multi-model inference by averaging over several models. This method has been adopted by ecologists (Rushton et al. 2004), and was successfully incorporated into model building (e. g. Gibson et al. 2004c). In addition, model averaging can be used to assess the relative importance of different factors (Burnham 2002).

In our work, we applied the method of Burnham (2002) to species occurrence data of grasshoppers and leafhoppers (Orthoptera and Hemiptera: Auchenorrhyncha) on brownfields sites. We considered these phytophagous taxa as they are particularly abundant on brownfields (Gilbert 1989; Sanderson 1992b). We aimed to: (1) Assess the relative importance of local factors (site age, vegetation structure, soil) and landscape scale factors (landscape context) for the species community. (2) Gain insight into the shape of the relationship between species and the environment. (3) Describe how species number and composition change during the course of succession. (4) Provide a predictive model. The latter could be used to assess the influence of changing human impact (e. g. faster or slower rates of redevelopment due to changing economic conditions).

4.2 Methods

Study areas and sampling design

The study was carried out in two large cities of Northern Germany, Berlin and Bremen. Berlin (52°30’ N, 13°28’ E, mean temperature 9.7 °C, mean annual precipitation 560 mm) has a more continental climate than Bremen (53°05’ N, 8°44’ E, mean temperature 8.8 °C, mean annual precipitation 694 mm). In each city, we set up study plots of 225 m^2 in a random stratified way (Hirzel & Guisan 2002), covering three gradients: site size, successional age (0 – 40 years) and soil moisture. In Berlin, 89 plots were spread over 370 km^2, in Bremen, 157 plots over 100 km^2. Minimum distance between plots was 80 m. Even though it is known that leafhoppers and grasshoppers can cover such distances, a number of mark-recapture studies indicate that the majority of individuals has an activity radius of less than 40 m (Biedermann 2002b; Cronin 2004; Ingrisch & Köhler 1998; Schuhmacher & Fartmann 2003).

The data were collected in 2003 (Bremen) and 2004 (Berlin). On each plot, we recorded the presence/absence of leafhoppers and grasshoppers. For leafhoppers, sweep-net sampling was carried out four times at monthly intervals between early June and early September. Leafhopper species occur at different times of the year, thus four sampling periods were required to sample all species in the adult stage. Each sampling procedure consisted of 100 sweeps covering the entire plot. The catch was killed with ethyl acetate and frozen. All male adult individuals were determined to species level (female individuals only for species where determination is possible) (Biedermann & Niedringhaus 2004). Grasshoppers were recorded once in late July / early August, when all species are present as adults (Ingrisch & Köhler 1998). To this end, acoustic monitoring (Bellmann 1993a) was used. We recorded all singing grasshoppers for two minutes at six distinct points per plot. In Bremen, a total of 146 leafhopper and 11 grasshopper species was recorded, in Berlin 130 and 15, respectively.

For each plot, we collected a set of environmental factors (see Table 2.2, p. 21). These included local factors (on the plots), namely successional age, vegetation structure and soil parameters, as well as landscape scale factors. The latter describe the landscape context surrounding the plots. Local scale is within the home range, landscape scale between the home range and the regional distribution of a species (Mazerolle & Villard 1999).

Successional age, vegetation structure, soil, and landscape context we refer to as the main driving factors. With the exception of age, each factor was described by several variables. For detailed measures of vegetation structure, we used a white screen (height 150 cm, width 50 cm), divided into rectangles, that was erected perpendicular to the ground (Sundermeier 1999). Using this screen, vertical vegetation cover was estimated for each rectangle looking through a 10 cm wide stand of vegetation at six points per plot. From these estimates, we calculated several height and density parameters (Table 2.2, p. 21). Landscape context parameters (Table 2.2, p. 21) were derived from a map of brownfield types by calculating the proportion of each brownfield type within distances of 25, 50, 75, 100 and 125 m around every plot (Grand & Mello 2004; Holland et al. 2004).

Single species models

Presence/absence models

We used logistic regression, i. e. generalised linear models (GLMs) with a logistic link. This approach by now is well established in ecological modelling, and leads to models which are straightforward to interpret. We aimed to model presence/absence only, since abundance models in practice often provide little or no additional information (Pearce & Ferrier 2001). Moreover, the construction of abundance models in our case would be questionable since species prevalences were overall low. In this respect, we note that Cushman & McGarigal (2004) found infrequently recorded species to be better explained by presence/absence data than by abundance data. We modeled all species with a prevalence (proportion of occupied plots) between 10% and 90%, using the ‘logistf’ package for Splus 6.1 by Heinze & Schemper (2002).

Univariate analyses

Prior to building multiple models, we performed univariate analyses for each environmental variable and each species. This avoided spurious inclusion of variables into multiple models. All univariate models were bootstrapped 300 times (Manly 2001). Each time, we recorded deviance reduction and conducted a likelihood-ratio test. If this test was significant $(p \leq 0.05)$ for at least 95% of the bootstrap iterations, the variable was considered for multiple models (see below).

At this stage, we also determined the shape of the relationship, a process which is crucial for obtaining meaningful models (Austin 2002). Relationships could be either sigmoid or unimodal. In unimodal relationships, we only considered bell-shaped responses, but not bowl-shaped ones. If both sigmoid and unimodal responses were significant, we chose the one with the stronger relationship.

Multiple models

For each species, from all variables passing the univariate performance criteria, we picked a set for building multiple models. Some groups of variables were highly correlated: (i) proportions of the same brownfield type within different radii, (ii) vegetation height parameters derived from ‘screen measurements’ and (iii) vegetation density parameters derived from ‘screen measurements’ (Table 2.2, p. 21). From each of these groups, we chose the variable with the strongest relationship. If different response shapes were found within one group (e. g. positive reaction to vegetation density in the 0-5 cm layer and negative reaction to vegetation density in the 50-100 cm layer), one variable representing each response was picked correspondingly.

This variable set was used to estimate multiple models for all ‘uncorrelated’ (Spearman’s $rho \leq 0.7$) combinations of four, three and two variables. More than four variables would have led to overparameterized models for the sample size of our data (Guisan & Zimmermann 2000). For each model, we (1) performed an LR-test to check if the model was better than any model with one variable less (Ferrier et al. 2002). Additionally we checked (2) whether corrected R^2_N (200 bootstrapping iterations; Harrell 2001) was ≥ 0.3 and (3) coefficients were significantly different from zero ($p \leq 0.15$). The latter, less conservative constraint takes into account that Wald confidence intervals and p-values are not always reliable (Heinze & Schemper 2002). If all three conditions were met, the model was considered to be adequate.

Model averaging

In case several ‘adequate’ models were obtained for a species, averaged coefficients from all models were calculated. To this end, the method of Burnham (2002) was used, which proceeds as follows. For each model in the set, the AIC_c–value was calculated. This small-sample version of the **A**kaike **I**nformation **C**riterion indicates how well a model performs the trade-off between model fit and model complexity. Lower values indicate better models. Models were sorted according to their AIC_c values. For each model m of a species model set M, Akaike weights (w_i) were calculated from the AIC_c differences (Δ_i) between each model and the AIC_c of the best model (see Table 4.1). Akaike weights were calculated as

$$w_i = \frac{\exp(-0.5 \times \Delta_i)}{\sum\limits_{m=1}^{M} \exp(-0.5 \times \Delta_i)}$$

Note that, for each species, the sum of all weights w_i equals 1. Model coefficients were weighted with the corresponding model weight. The sum of all weighted coefficients for a given variable represents the averaged coefficient for this variable (Table 4.1). By this, the sought-after averaged model was obtained for each species.

Performance of single species models

Model performance of single species models describes the agreement between observed and predicted species occurrences, calculated over all plots. To assess this agreement, we used a set of criteria, each describing different aspects of model fit: AUC (**a**rea **u**nder the receiver operator characteristic **c**urve), R^2_N, Cohen’s $Kappa$, sensitivity (correctly predicted species presences), specificity (correctly predicted absences), and CCR (overall **c**orrect **c**lassification **r**ate) (Fielding & Bell 1997; Hosmer & Lemeshow 2000; Manel et al. 2001).

Table 4.1: Demonstration of the model averaging process for the leafhopper *Psammotettix excisus*. In this example, 7 variables are relevant, yielding 7 'adequate' multiple models m_i could be formed. The models were ranked according to their AIC_c (smallest to largest). From AIC_c-differences (Δ_i), Akaike weights (w_i) were calculated. These were then used to calculate weighted coefficients $(\beta \times w_i)$ for each model and furthermore averaged coefficients ('averaged β'), and the variable weights ('relative weight' and '% weight').

m_i	AIC_c	Δ_i	w_i	var.1		var.2		var.2^2		var.3		var.4		var.5		var.6		var.7		Intercept	
				β	$\beta \times w_i$	β	$\beta \times w_i$	β	$\beta \times w_i$	β	$\beta \times w_i$	β	$\beta \times w_i$	β	$\beta \times w_i$	β	$\beta \times w_i$	β	$\beta \times w_i$	β	$\beta \times w_i$
1	55.66	0.00	0.46	0	0	0	0	0	0	-0.03	-0.0133	0	0	0	0	2.5	1.2	0.4	0.163	-3.1	-1.4
2	56.09	0.43	0.37	0	0	0	0	0	0	0	0	0	0	0	0	3.0	1.1	0.3	0.105	-3.8	-1.4
3	58.02	2.37	0.14	0	0	37	5.2	-88	-12.4	0	0	0	0	0	0	0	0	0.3	0.036	-5.2	-0.7
4	63.14	7.48	0.01	0	0	47	0.5	-113	-1.2	0	0	-3.1	-0.003	0	0	0	0	0	0	-4.7	-0.1
5	63.31	7.66	0.01	0	0	0	0	0	0	-0.04	-0.0004	0	0	0	0	0	0	0.4	0.004	-2.1	0.0
6	63.86	8.20	0.01	0	0	36	0.3	-88	-0.7	0	0	0	0	10.2	0.08	0	0	0	0	-14.2	-0.1
7	64.38	8.72	0.01	-0.2	-0.001	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.002	-1.9	0.0
averaged β				-0.001		6.010		-14.302		-0.014		-0.443		0.078		2.263		0.310		-3.730	
relative weight				0.006		0.159		-		0.467		0.011		0.008		0.826		0.982		-	
% weight				0.24		6.5		-		19		0.44		0.31		34		40		-	

var.1	vegetation density, 15-50 cm layer [%]	var.4	soil phosphorus content [t/ha]
var.2	vegetation height [m]	var.5	proportion of brownfields within 25 m
var.2^2	(vegetation height)^2	var.6	proportions of brownfields with scarce, grassy vegetation within 25 m
var.3	litter cover [%]	var.7	cover of *Corynephorus canescens* [%]

Community model

Model building

The community model was composed of all single species models. Simultaneous application of single species models was used to predict the community under a given combination of parameter values. To transform occurrence probabilities of single species models into presences/absences, we used P_{Kappa} as a threshold, defined as the threshold where Cohen's $Kappa$ is maximized (Fielding & Bell 1997).

Performance of the community model

In contrast to single species models, performance of the community prediction is assessed per plot and describes the agreement between observed and predicted species community. To quantify this agreement, four measures were used: Cohen's $Kappa$, sensitivity, specificity and CCR. We performed a randomisation test (Manly 2001; Peppler-Lisbach & Schröder 2004) to verify if model predictions were better than chance. For this test, presences and absences of each species were randomly permuted, resulting in random community compositions for each plot (Olden 2003). This process was repeated 10,000 times, and each time measures of agreement were calculated for each plot. Thus, we created chance distributions for each plot and each measure of agreement. If the actual agreement between the observed and predicted community exceeded the 95%-percentiles of the corresponding chance distributions, we considered the community model for a plot to achieve predictions significantly better than chance.

Relative importance of factors

The relative weight of variables was assessed by summing, for each variable, the Akaike weights w_i of all models that contained the variable (Burnham 2002; Gibson et al. 2004c). The process is demonstrated for one species in Table 4.1. For comparison, the relative weights were converted to percentage values.

4.3 Results

Model performance

48 species (Bremen) and 56 species (Berlin) met the prevalence criterion, i. e. the proportion of occupied plots exceeded 10% but remained below 90%. Of these, 30 species in Bremen (25 leafhopper and 5 grasshopper species), and 28 species in Berlin (24 leafhopper and 4 grasshopper species) were responsive. In other words, the corresponding models exceeded the minimum performance criteria. Prevalence of the responsive species was mostly low, with medians of 26% in Bremen and 37% in Berlin. The species numbers per plot for Bremen ranged between 3-18, with a median of 11. For Berlin, the corresponding range was between 2-21 species, also with a median of 11.

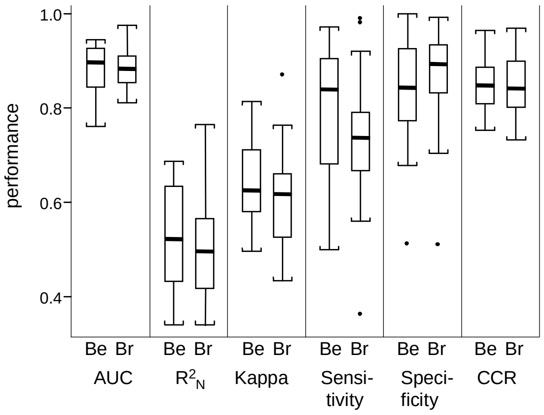

Figure 4.1: Performance of single species models. Shown is, for each performance criterion, the range and distribution of values for all models. For each criterion, the left boxplot represents all Berlin models (Be), the right boxplot all Bremen models (Br). Box: median, 25%- and 75%-percentiles; whiskers: 1.5 × inter-quartile range; outliers drawn as individual points.

The number of variables used in the multiple models was lower in Berlin (2–16, median 5.5) than in Bremen (2–17, median 9). Nevertheless, the performance of the single species models (Figure 4.1) was similar for both study areas, with sensitivity being slightly poorer in Bremen. The community model predicted numbers of species similar to those actually observed on the plots, ranging between 4 and 22 with a median of 12 for Berlin, and between 3 and 17 with a median of 11 for Bremen. The quality of the community predictions, defined as the agreement between observed and predicted species for each plot, was overall better for Berlin than for Bremen (Figure 4.2). For the communities in both cities, median values of sensitivity, specificity and *CCR* were found to be between 0.8 and 0.9, while *Kappa* ranged between 0.6 and 0.7. For the majority of plots, community model predictions were better than chance predictions concerning the sensitivity, *CCR*, and *Kappa*. In contrast, since the prevalence of most species was low, chance values for specificity (i. e. correct absences) were rather high. The community model prediction exceeded these high values for only 56% of the plots in Berlin and 46% in Bremen.

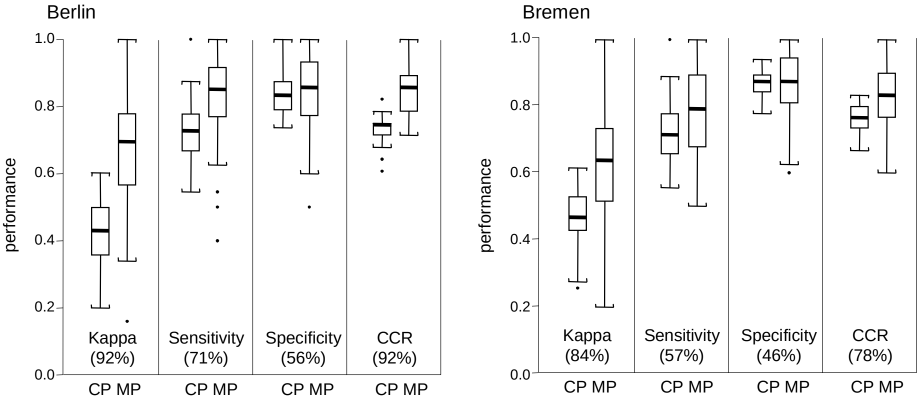

Figure 4.2: Validation of community models. Shown is, for each performance criterion, the range and distribution of values for all plots. For each criterion, two boxplots are drawn. The left boxplot shows the 95%-percentiles of the chance distributions (chance prediction = CP). The right boxplot shows the observed agreements between model predictions and species occurrences (model prediction = MP). Numbers in brackets indicate the proportion of plots where model predictions are better than chance predictions.

Relative importance of factors

The communities in both study areas reacted similarly to the main factors. Vegetation structure was particularly dominant, and accounted for 61% (Berlin) and 46% (Bremen) of the factor weights. Nearly all species were influenced by vegetation structure (Figure 4.3). The median of vegetation structure weight was around 50% (Figure 4.4), with some species almost exclusively controlled by this factor. Landscape context followed in weight, with more influence in Bremen (35%) than in Berlin (19%). Note that, in Bremen, most species presences were influenced by landscape context, in Berlin only half of them (Figure 4.3). Moreover, in Berlin, the magnitude of landscape context influence was considerably lower (Figure 4.4). Soil parameters ranked third in weight (Figure 4.3), with mostly small influence. However, a few species were strongly influenced by soil parameters (Figure 4.4). Site age had little impact in both cities, but did occur in many models (32% of models in Berlin, 50% in Bremen) (Figure 4.3).

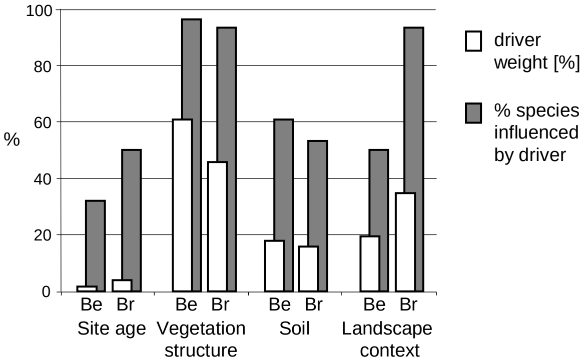

Figure 4.3: Influence of main driving factors. For each factor, the weights within the models are averaged over all species to determine the average weight within the community model (white bars). The proportions of species influenced by each main factor are drawn as grey bars. Be = Berlin models, Br = Bremen models.

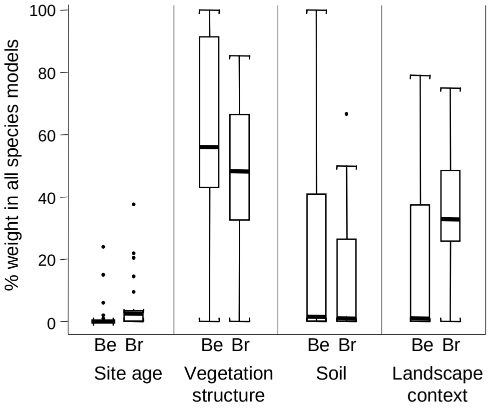

Figure 4.4: Range and distribution of factor weights within species models. For each factor, the left boxplot represents Berlin models (Be), the right boxplot Bremen models (Br).

Shape of species responses to the environment

Most species preferred medium values for site age, vegetation density and height, moss and litter cover, but high values for proportions of grassy brownfields, and low values for proportions of open brownfields, bare soil, soil pH and soil nutrients (Table 4.2).

However, for most factors, all forms of species responses to the environment were encountered. Negative or positive reactions, i. e. decreasing or increasing occurrence probabilities with increasing variable values, could be observed as well as unimodal responses, i. e. highest occurrence probabilities at medium variable values. This implies that, for most driving factors, the entire gradient of values was used by the community of brownfield species. Note that some species showed negative reactions to the proportions of all types of brownfields.

Table 4.2: Summary of species responses to driving factors. We considered negative (–), positive (+) and unimodal (∩) responses. Numbers of variable or response occurrences in averaged models.

	total				Berlin				Bremen			
	sum	-	∩	+	sum	-	∩	+	sum	-	∩	+
site age	24	4	12	8	9	2	4	3	15	2	8	5
vegetation structure												
veg. density	75	13	31	31	38	7	16	15	37	6	15	16
veg. height	59	5	32	22	28	5	15	8	31	0	17	14
moss & litter cover	43	9	8	26	17	4	1	12	26	5	7	14
% bare soil	28	20	7	1	9	7	1	1	19	13	6	0
soil parameters												
ph & soil nutrients	35	23	5	7	16	10	4	2	19	13	1	5
landscape context												
brownfields, all types	11	8	2	1	3	3	0	0	8	5	2	1
open brownfields	22	20	1	1	8	7	0	1	14	13	1	0
brownfields, grassy	31	7	6	18	5	2	0	3	26	5	6	15
brownfields, herbaceous	29	15	3	11	18	8	3	7	11	7	0	4
brownfields, moist to wet	16	6	1	9	NA	NA	NA	NA	16	6	1	9

Some pronounced differences between Berlin and Bremen became apparent when landscape context parameters were considered (Table 4.2). Moist to wet brownfields played an important role in Bremen, where both positive and negative responses were found, but not in Berlin, where this brownfield type did not occur at all. Moreover, the proportions of brownfields with grassy vegetation were important in Bremen, mostly enhancing species occurrences. In Berlin, this brownfield type only played a minor role.

Species assemblage along the successional gradient

Vegetation gradient

The community model, consisting of single species models, can be used to visualize the reaction of the community to a vegetation gradient from scarce and low to dense and high. This gradient essentially represents the successional gradient of vegetation structure. Figure 4.5 illustrates the reactions of species along this gradient, with all other parameters set to fixed values. Both the Berlin and the Bremen gradients are scaled to the actual data distributions of the environmental parameters.

Some species have a wide range under the given parameter combinations, others do not occur at all. About half of the species show clear reactions and occur at distinct sections along the gradient. Pioneer species, like *Macrosteles quadripunctulatus*, are restricted to the left of the gradient (scarce/low vegetation). Other species, such as *Rhopalopyx vitripennis*, prefer medium conditions, whereas some, e. g. *Metrioptera roeseli*, are restricted to the right end of the gradient (dense/high vegetation).

Influence of landscape context

Figure 4.6 (Berlin) and Figure 4.7 (Bremen) illustrate the modifying influence of landscape context. Four constellations of landscape context are shown: (1) no brownfields, vs. high proportions of (2) open brownfields, (3) grassy or herbaceous brownfields and (4, Bremen only) moist to wet brownfields. Occurrence of species along the vegetation gradient is depicted in the same way as in Figure 4.5, but with three (Berlin) or four (Bremen) bars for each species. Each bar represents the occurrence along the gradient in combination with one of the different settings of landscape context (1-4), as outlined above.

As an example, we consider *Athysanus argentarius* for Berlin (Figure 4.6, first species). The upper two bars are the shortest. This means that, without brownfields in the landscape context (upper bar) as well as with high proportions of open brownfields (middle bar), the species is restricted to the right side of the vegetation gradient. However, high proportions of grassy or herbaceous brownfields enhance the occurrence of the species. It then occurs under a wider range of vegetation conditions along the gradient (lower bar).

In Berlin, under the given combination of soil and age parameters, only eleven species (Figure 4.6: first eleven species) exhibit reactions to landscape context: the three bars for each of these species have different lengths. The first six of these species are enhanced by high proportions of grassy or herbaceous brownfields (third bar for each species is the longest). Some species (e. g. *Anaceratagallia ribauti*) are inhibited by open brownfields (second bar is the shortest). Three species (e. g. *Balclutha punctata*) have their widest range with no brownfields in the landscape context (first bar is the longest), indicating that the main habitat of these species may well be outside of brownfield areas.

In Bremen, 24 species react to landscape context under the given parameter combination (Figure 4.7: first 24 species). The first 13 of these have a wider range with high proportions of grassy or herbaceous brownfields. However, five species (e. g. *Macroste-*

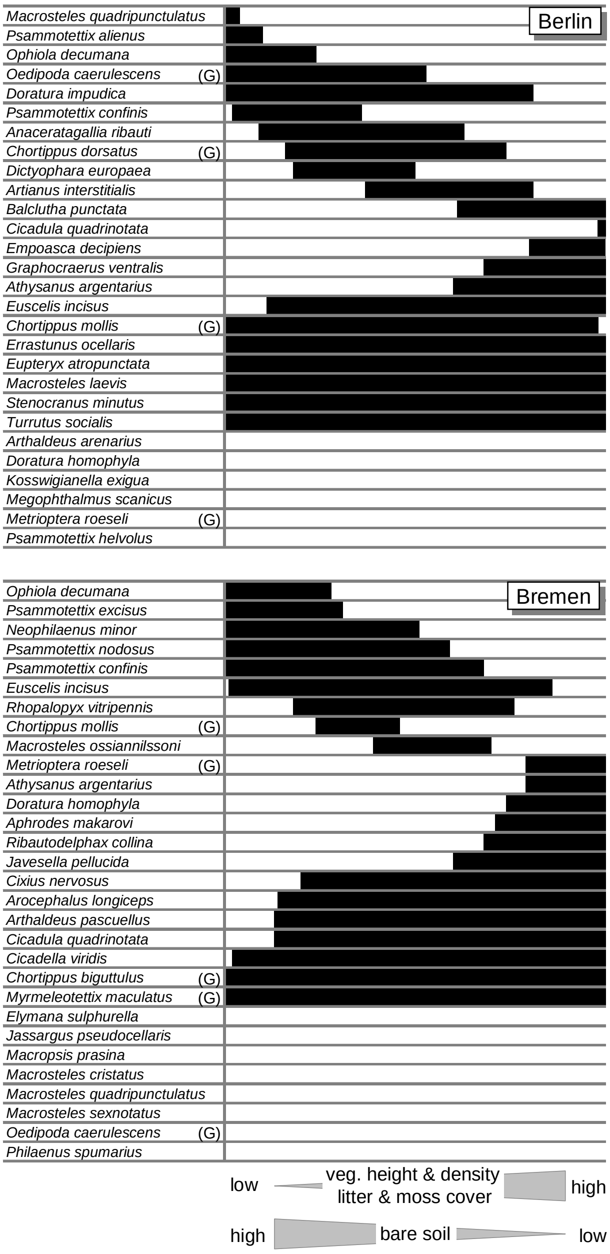

Figure 4.5: Occurrence of species (black bars), based on single species habitat models, on a vegetation gradient. The gradient runs from low to high vegetation height and density, from low to high moss and litter cover, and from high to low proportions of bare soil. ‘Low’ refers to the 5%-percentiles of the data distribution, ‘high’ to the 95%-percentiles. PH, soil nutrients, and proportions of open brownfields are fixed to low values. Proportions of grassy and herbaceous brownfields are fixed to high values. Age is set to 15 years, cover of host plants to high values. All other variables are fixed to their arithmetic mean. (G) = grasshopper species.

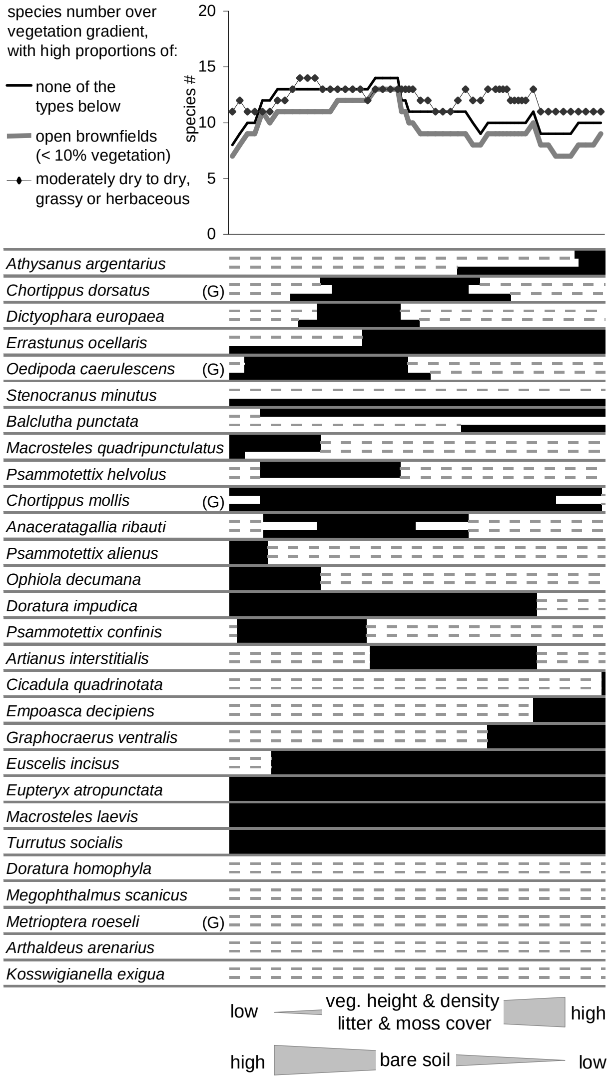

Figure 4.6: Berlin community: influence of landscape context on the occurrence of species on a vegetation gradient (for gradient details see Figure 4.5). For each species, three bars indicate species occurrence with either low (5%-percentile) proportions of open, grassy and herbaceous brownfields (upper bar), high (95%-percentile) proportion of open brownfields (middle bar), or high proportions of grassy and herbaceous brownfields (lower bar). In the top chart, species richness (number of species present) along the vegetation gradient is plotted for each of the three landscape context conditions. (G) = grasshopper species.

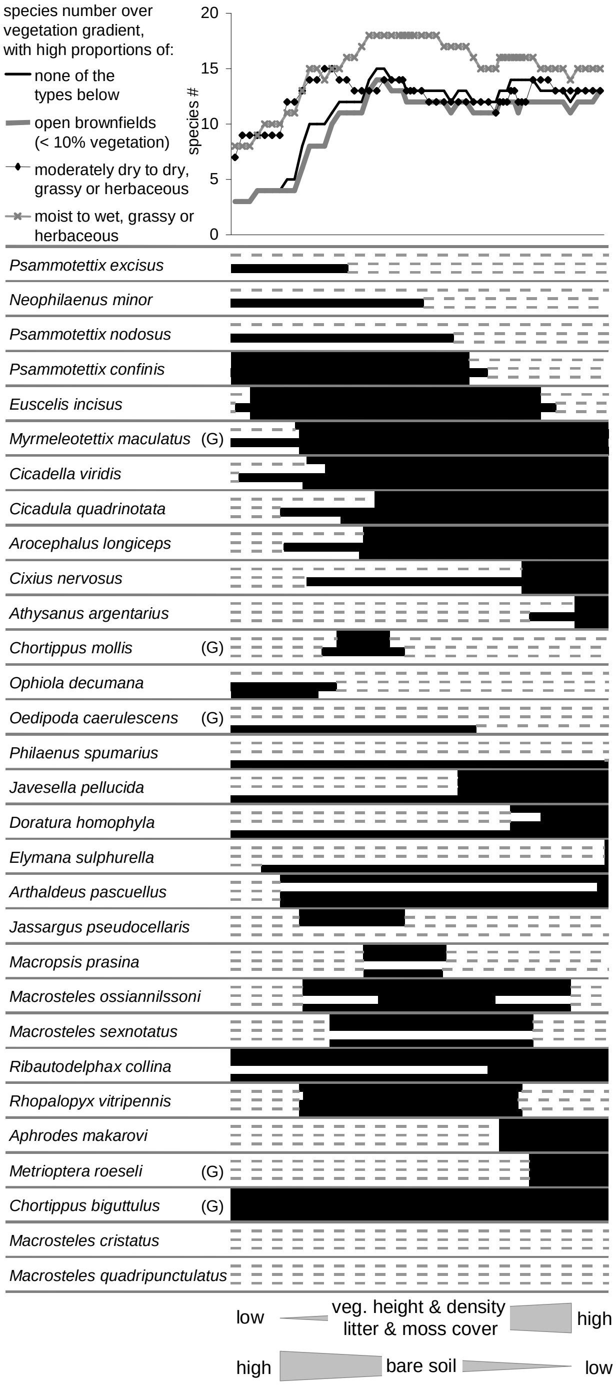

Figure 4.7: Same as Figure 4.6, but for the Bremen community. In addition, a fourth landscape context condition is shown (high proportions of moist to wet brownfields).

les ossiannilssoni) are inhibited by these brownfield types. Some species (e. g. *Doratura homophyla*) are enhanced by moist to wet brownfields (lowest bar is the longest).

Species numbers

The charts on top of Figure 4.6 (Berlin) and Figure 4.7 (Bremen) indicate how species numbers change along the vegetation gradient. Each line represents one condition of landscape context. In Berlin, 23 of 28 modelled species are predicted to occur at some point under the given conditions. In Bremen, this is 28 of 30. Maximum species number at a given point along the gradient is 14 for Berlin, and 18 for Bremen. Overall, species numbers are the lowest without brownfields in the landscape context, as well as with high proportions of open brownfields. In Bremen, species numbers are low at the ‘young’ end of the vegetation gradient. However, numbers raise quickly during the course of succession and then remain constant. In Berlin, changes in species numbers are small, particularly with grassy or herbaceous brownfields.

In both cities, there is no point along the gradient where all species co-occur. Species composition changes considerably over the gradient. For high proportions of grassy and herbaceous brownfields, only 6 out of 12 species in Berlin (and 1 out of 9 in Bremen) that are present at the beginning of the gradient, are also present at the end.

4.4 Discussion

Relative importance and ecological relevance of main driving factors

Vegetation parameters & site age

Our results clearly indicate that vegetation structure was the most influential factor for the communities of grasshoppers and leafhoppers in urban brownfields. A number of previous studies revealed that during succession, insect communities are driven by changes in vegetation structure (Brown et al. 1992; Small et al. 2003). Vegetation structure is known to be of great importance for both leafhoppers (Brown et al. 1992; Morris 2000) and grasshoppers (Brocksieper 1978; Detzel 1998; Ingrisch & Köhler 1998). Vegetation structure influences microclimatic conditions, namely temperature and (soil) moisture, which in both taxa are important factors for development and reproduction.

Vegetation development on urban brownfields goes through a series of successional stages, starting from open, short-lived pioneer vegetation, followed by perennial herbs, perennial grasses, and culminating in scrub woodland (Gilbert 1989; Small et al. 2003). Each successional stage embraces a range of vegetation characteristics (Hollier et al. 1994; Rebele 1994). Since succession is a process acting in time, successional age has the potential to explain the occurrence of species. On the other hand, succession is also driven by soil conditions and the type of succession (primary vs. secondary) (Rebele & Lehmann 2002; Small et al. 2003), and can therefore vary considerably between sites. There is a clear trend towards higher and denser vegetation during succession, but this trend is only loosely related to site age. In our study, this is reflected by the weak influence of site age compared to vegetation parameters.

Landscape context

It has been widely recognized that species reactions cannot be fully understood without considering the influence of the surrounding landscape (Mazerolle & Villard 1999). Most ecological processes depend not only on patch characteristics, but on spatial scales much larger than a habitat patch (Holland et al. 2004). Effects of the landscape context have been demonstrated for a variety of taxa (Mazerolle & Villard 1999).

Since brownfields often form isolated habitats entirely different from their surroundings (Niemelä 1999), we expected the landscape context to have a pronounced influence on brownfield communities. This expectation was met for Bremen, where landscape context had a strong influence. Overall, leafhoppers and grasshoppers in urban brownfields seem to depend more on landscape context than carabid beetles, where only little influence on few species was found (Small et al. 2006). However, in our study, we distinguished different types of brownfields and considered smaller scales than Small et al. (2006).

Many species were reacting positively to high or intermediate proportions of brownfields with grassy vegetation in Bremen. As the majority of leafhoppers feeds on grasses (Morris 2000), this relationship is reasonable. Sanderson (1992b) found higher species diversities on grassy brownfields than on those with ruderal vegetation. In general, the grassland stage is a late stage during brownfield succession. Thus, a high proportion of grassland also goes along with an extended period of colonization.

A number of species reacted negatively to the absence of brownfields, as well as to high proportions of open brownfields. Both might indicate negative reactions to site isolation. In the first case, patches without brownfields in their surroundings may be isolated for those species that have their main habitat on brownfields. In the second case, high proportions of open brownfields may indicate (1) that the site is still young, giving species little time for colonization, and (2) the absence of suitable habitat nearby. With the exception of pioneer species like *Ophiola decumana*, most species seemed to not prefer the most open, scarcely vegetated sites.

Some species showed an unexpected negative reaction to all types of brownfields. We assume that, within an urban environment, these species mainly occur in other habitats, such as gardens or parks. The species which did not show any reaction to landscape context, might either be generalists, which find suitable habitats almost everywhere, or they might be strong dispersers.

Our results confirm that species respond to their environments at different scales, and that the appropriate scale can be estimated by modelling the relationship at a number of scales (Holland et al. 2004). All scales tested within this study were relevant for several species. As larger radii would unavoidably have lead to considerable overlap, causing pseudoreplications (Holland et al. 2004), we cannot test to which extent some species might react at larger scales.

Landscape context seemed to be less influential in Berlin than in Bremen. Our explanation is that moist to wet brownfields, which enhanced or suppressed a number of species in Bremen, were not present in Berlin. In addition, even though the total amount of brownfields around sample plots showed a similar distribution in both cities, brownfield composition was very different. Namely proportions of grassy brownfields were on average much lower in Berlin. The scarce data on these variables might have led to weaker models. This raises the general question to what extent the response to the landscape structure from one area can be extrapolated to another (Fisher et al. 2005).

Overall, our simple measure of landscape context (proportion of brownfield types within circles) worked remarkably well, and did not indicate the need to consider additional measures. According to Gustafson (1998), such proportions can provide almost as much information as more advanced measures of landscape context. Moreover, proportions of brownfield types are easy to calculate and interpret: they indicate patch size and isolation, and are a measure for the 'functional connectivity' of a landscape (Radford & Bennett 2004).

Soil parameters

Even though in some studies soil parameters were found to strongly influence leafhoppers (Cherrill & Rushton 1993) and grasshoppers (Ingrisch & Köhler 1998), they were not of major importance in our study. Soil parameters give direct and indirect information about temperature and moisture. They influence plant growth and therefore vegetation structure. Moreover, they affect the nutritional and physical status of plant tissues, which is important for many phytophagous insects (Morris 2000). In our data, it seems that soil parameters mainly play an indirect role by influencing the vegetation. This influence is directly reflected by our detailed measures of vegetation structure.

Community composition, species numbers and succession

Succession, even though often mainly viewed in vegetational terms, also occurs in insect communities (Morris 2000). Brown et al. (1992), as well as Hollier et al. (1994), found clear successional patterns in leafhopper composition. Along the gradient from scarce and low, to dense and high vegetation, which roughly represents the gradient of vegetation succession on brownfields, we were able to separate pioneer species from species occurring during mid- and late succession. In addition, generalists occurring over the whole gradient could be distinguished.

In contrast to the findings of Brown et al. (1992), some pioneer species did not occur later in succession. Thus we agree with Eversham et al. (1996), who propose that the presence of early successional stages in urban habitats is of great importance. Such habitats are generally absent or difficult to maintain elsewhere.

Studies on changes in insect communities through old-field successional stages (e. g. Brown et al. 1992; Purtauf et al. 2004; Steffan-Dewenter & Tscharntke 1997) found a rapid turnover of species, rather than large changes in species richness. This pattern we observed as well. Only during the early successional stages species numbers were lower, with some species being restricted to these early stages. Thus, maintaining the regional species pool of a city requires a mosaic of all successional stages. This mosaic is currently present in the cities under study, but may change under different economic conditions. In case of economic boom, brownfields are likely to be re-used faster, providing habitat only for a limited number of pioneer species. In case of economic stagnation, site turnover might slow down considerably, and thus young habitat might become scarce.

Model performance and implications

Habitat models, like any statistical approach, do not allow inference for very scarce species. Since many species have been recorded only once or twice, considerable parts of the species pool could not be considered for modelling. On the other hand, the more common species that occurred on at least 10% of the plots, accounted for more than 80% of all species observations. Of those species, more than half could be successfully predicted within the community model. The species that were not responsive within this study might be responding to environmental factors different from those we measured, they might be generalists within brownfields, or our data might not have provided enough observations for sound statistical inference.

Inference from habitat models is of little use if these models do not reflect the species-habitat relationships. Our approach, based on a combination of local and landscape parameters, combined with an advanced model averaging process, yielded models that represented the data well. With two exceptions, all our models reached AUC-values exceeding 0.8, which is considered excellent (Hosmer & Lemeshow 2000); almost half of the models exceeded 0.9, which is regarded as outstanding. On the other hand, these values might be too optimistic, due to possible overfitting to the data. A bootstrapping procedure would enable an unbiased estimate of the model performance (Harrell 2001), but was computationally too extensive to be performed in combination with the model averaging process. Even though single species models performed well, the community predictions resulting from these models did not exceed chance for a number of plots. Olden (2003) and Peppler-Lisbach & Schröder (2004) achieved similar results for modelling communities with species-specific approaches.

Overall, our modelling approach provides a conceptual framework enabling predictions of species composition and richness along the gradient of brownfield succession. The models can be used to predict changes in the community composition if parts of the gradient are cut off (e. g. due to faster redevelopment), or to compare different spatial arrangements of brownfield sites.

However, it is important to note that, at this stage, models are only valid for the study area and data they are based on. generalisations should not be made before transferability of the models has been tested with independent data (Vaughan & Ormerod 2005). Nevertheless, the fact that the main driving factors had similar influence in both data sets, is a positive indication that the observed patterns might, indeed, be general.

4.5 Conclusions

(1) Vegetation structure, influencing microclimate and food resources, was the dominant factor driving the community of leafhoppers and grasshoppers in urban brownfields. Vegetation parameters reflected site conditions more precisely than site age. The latter was found to be only a rough indicator of the successional stage. Landscape context, indicating patch size and isolation, played a considerable role for some species. Soil parameters, as indirect factors, were of minor importance in most cases.

(2) Different species exhibited different functional relationships to the environment. All parts of the successional gradient were used by some species: pioneer species could be identified, as well as mid- and late-successional species and generalists. Species composition changed greatly along the gradient, with not more than approximately half of the species pool present at the same time. Thus, the species community is not static, but changes in composition through space and time as the location and successional stage of brownfields changes.

(3) Combinations of local-scale and species-specific landscape variables were a powerful tool to obtain community predictions. The models generated by our statistical approach appeared to be robust. However, we emphasize that generalisations cannot be made until the models have successfully been transferred to independent data.

Acknowledgements

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Chapter 5

Evaluating temporal and spatial generality: How valid are species-habitat relationship models?

B. Strauss & R. Biedermann. Ecological Modelling (in press).

Abstract

Prior to making general inferences or predictions from habitat models, their generalizability requires thorough assessment. However, systematic testing of model generality is often claimed, but rarely done. We used existing models for phytophagous insects (grasshoppers and leafhoppers) from a study on urban brownfields. Data for model building had been collected in two major cities of Northern Germany, Berlin and Bremen. We transferred these models to test data from another year (Bremen, 30 model transfers), and to test data from different geographic regions (transfer from Berlin to Bremen and vice versa, 30 model transfers). We evaluated discriminatory ability as well as model calibration for the test data. Most transfers (28 in time, 27 in space) were successful, i.e. occupied sites within the test data were assigned higher occurrence probabilities than unoccupied sites, the threshold independent *c*-index for the test data exceeded chance. Our results indicated that models built on the larger dataset (147 plots, Bremen) were more general than the ones basing on the smaller dataset (89 plots, Berlin).

The overall good transferability had three important drawbacks: (1) Models were mostly not well calibrated to the test data, thus predicted occurrence probabilities may not be used as absolute values, but as ordinal ranks. (2) Model fit to the test data often decreased considerably compared to the training data. (3) Dichotomising occurrence probabilities to presence/absence predictions required prior information about species prevalence. Assigning presences to the sites with the highest predicted occurrence probabilities, with the number of presences corresponding to the prevalence, proofed to be a comparatively simple and reliable way of dichotomising predictions. Still, it only allowed predictions exceeding chance for 19 model transfers in time and 23 transfers in space, and required information about species' prevalences.

We qualitatively compared pairs of models for ten species, with one model basing on the Bremen data, one on the Berlin data. Both models had been built with the same modeling technique. Vegetation structure variables were largely comparable between

models. It seemed that they were more directly related to species' occurrences and thus more general than landscape context variables and soil parameters.

5.1 Introduction

Habitat models, also called species distribution models (SDM), which quantify species habitat relationships, see increasing use in ecology and conservation biology (Guisan & Zimmermann 2000; Vaughan & Ormerod 2005). Availability of satellite data and remote sensing techniques enables predictions of species occurrences over large areas. A commonly ignored drawback is that models based on data from one study year or site ('training data') may lose most of their predictive power when applied to data from other years or different geographic regions (Bulluck et al. 2006). Such failure might stem from overfitting of the model to its training data as well as from different conditions experienced in new data (Vaughan & Ormerod 2005). Even though it is often claimed that prior to their application, the validity of models beyond their training data needs to be tested with independent test data (Araujo & Guisan 2006; Pearce & Ferrier 2000b; Vaughan & Ormerod 2005), this is rarely done. Internal validation (e. g. bootstrapping) enables unbiased estimates of model performance for the training data, but it cannot assess a model's generalizability, i. e. its capacity to predict a species' distribution with new data from different regions or different years (Altman & Royston 2000; Randin et al. 2006; Vaughan & Ormerod 2005). Vaughan & Ormerod (2003) propose that independent test data, collected from a geographically discrete region, are the only valid test. Still, few studies systematically investigate the generalizability of models (but see Bulluck et al. 2006; Fleishman et al. 2003; Jensen et al. 2005). It is common to split one data set in training and test data to evaluate a model's performance and generalizability (e. g. Eyre et al. 2005a). However, the significance of such tests may not exceed what could be achieved with internal validation as well. The generalizability of habitat models needs to be evaluated with respect to two aspects: (1) discrimination, and (2) calibration (Pearce & Ferrier 2000b).

Discriminatory power of a model is the capacity to distinguish occupied from unoccupied sites (Pearce & Ferrier 2000b). It can be evaluated by several threshold dependent and threshold independent measures. Threshold dependent measures require dichotomisation of a model's quantitative output (probabilities of occurrence) into presences and absences (Fielding & Bell 1997). The choice of the threshold largely determines the result. Sensitivity (the model's ability to correctly predict presences), specificity (ability to correctly predict absences), and the overall correct classification rate (*CCR*) are easy to interpret. However, they can be highly misleading if chance is not considered. For instance, a model for a rare species can achieve high correct classification if all sites are predicted as absences (Olden et al. 2002). Such a model is of limited use for ecological applications. In general, prevalences different from 0.5 allow high chance predictions. Thus, when using threshold dependent measures, it is necessary to assess if a model's predictions are better than what could be achieved by chance alone (Vaughan & Ormerod 2005).

Despite these threshold related problems, a common goal in ecological applications is to produce presence/absence predictions, making the choice of a threshold unavoidable. During model building, a threshold may be chosen based on the data (Fielding & Bell 1997). If a model is applied to new environmental data, where nothing is known about a species' presence or absence, this way of finding an optimal threshold is not possible. Applying the 'training threshold' to new data might be risky, in particular if prevalences differ between the training data and the area where the model is to be applied.

The selection of one particular threshold tests accuracy under only one scenario and thus limits the capacity to describe generalizability (Pearce & Ferrier 2000b). Threshold independent, non-parametric correlation coefficients like the c-index (equivalent to the AUC and the Wilcoxon statistic) overcome this problem by making direct use of the occurrence probabilities (Vaughan & Ormerod 2005). They compare the mean rank of occurrence probabilities for occupied sites with those of unoccupied sites. The c-index represents the probability that the model assigns a higher probability of occurrence to a randomly chosen occupied site than to a randomly chosen unoccupied one (Hanley & McNeil 1982).

Model calibration addresses the numerical accuracy of predictions, i. e. if each predicted probability is an accurate estimate of the likelihood of detecting a species at a given site (Pearce & Ferrier 2000b). Calibration can be split up into two measurable components: bias and spread. Consistent over- or underestimation (bias) typically results when a species' prevalence differs from the training data (Pearce & Ferrier 2000b). Probabilities that are too extreme (spread), i. e. too low at unoccupied sites and too high at occupied ones, indicate overfitting (Vaughan & Ormerod 2005). Even if a model successfully discriminates new data, calibration might be poor (Vaughan & Ormerod 2005). This becomes a problem if maps with probabilities of occurrence are produced, where, for example, an estimated probability of 0.9 represents an actual probability of only 0.6.

In this paper, we transfer existing habitat models for phytophagous insects in time (data from two years) and space (data from different geographic regions). With these model transfers, we address the following questions:

(1) Can species models from one year and region be used to predict species occurrence in another year and/or different geographic region, namely:

  - Are sites correctly ranked from unsuitable to suitable?
  - Is it possible to apply a threshold that successfully separates occupied from unoccupied sites?
  - Are transferred models well calibrated, allowing quantitative predictions of occurrence probabilities?

(2) Do data from different regions lead to similar models, if the same modeling techniques are applied?

5.2 Methods

Habitat models, training data and test data

For this paper, we used existing SDMs for grasshoppers and leafhoppers (Orthoptera and Hemiptera: Auchenorrhyncha) in urban brownfields (Strauss & Biedermann 2006). Models were available from two study areas in Northern Germany, Berlin (sampled in 2004) and Bremen (sampled in 2003 and 2004). These study areas are located at a distance of 300 km. In Berlin (52°30' N, 13°28'E, mean temperature 9.7 °C, mean annual precipitation 560 mm), 89 plots had been set up in a random stratified way, in Bremen (53°05' N, 8°44' E, mean temperature 8.8 °C, mean annual precipitation 694 mm), 157 plots. For each species with a prevalence $\geq 10\%$, models had been built using logistic regression (i.e. generalized linear models (GLMs) with a logistic link) and model

Table 5.1: Overview of model transfers. Sample size in brackets. Transfer: 'spat.' = spatial, 'temp' = temporal.

training data	test data	# of models	transfer
Bremen 2003 (157)	Bremen 2004 (149)	30	temp.
Bremen 2003 (157)	Berlin 2004 (89)	10	spat., temp.
Berlin 2004 (89)	Bremen 2003 (157)	10	spat., temp.
Berlin 2004 (89)	Bremen 2004 (149)	10	spat.

averaging (Burnham 2002; Gibson et al. 2004c). Only monotonic and univariate relationships were considered. Several 'good' models for a species had been weighted and averaged. This resulted in averaged models for 28 species in Berlin and 30 in Bremen. These models performed well on their training data in terms of discrimination and calibration. Details on the model building process can be found in (Strauss & Biedermann 2006). For ten species, models were available from both study areas.

Environmental variables covered four main driving factors: vegetation structure (e. g. several height and density measures and litter cover), landscape context (proportions of different brownfield types within different radii around the plots), soil parameters (e. g. pH, available water capacity, soil nutrients), and site age (for details, see Strauss & Biedermann 2006). Note that environmental variables approximately covered the same ranges of values in both study areas. However, the distribution of values within the total range differed between Bremen and Berlin.

We applied the SDMs to different test data (Table 5.1). To test transferability in time, the Bremen models were used on test data from the same plots, recorded in the following year. Transferability in space we tested for the ten species that had models for both study areas. Bremen models were applied to Berlin data, and vice versa. The transfers from the Bremen 2003 models to the Berlin 2004 data and from the Berlin 2004 models to the Bremen 2003 data represented transfers in both time and space. Such transfers might be expected to lead to poorer models than transfer in time only. All calculations were performed using Splus 6.1.

Assessing model discrimination

We assessed model discrimination by threshold-dependent (c-index) and threshold-independent measures. A chance model has a c-index of 0.5 (Hanley & McNeil 1982). With small data-sets and/or few observations, confidence limits grow large (McPherson et al. 2004). We therefore performed a randomisation test (Manly 2001) to test if species occurrences were associated with significantly higher predicted probabilities of occurrence. The model's predicted probabilities for the data were randomly distributed over the sites and the c-index was calculated. This procedure was repeated 10.000 times to produce a null (or chance) distribution with a median of 0.5. If a model's c-index exceeded the 95%-percentile of this chance distribution we considered it to be significantly different from chance.

We applied two methods to dichotomise predictions. First, we used P_{Kappa} (threshold that maximizes Cohen's $Kappa$) of the original models (Liu et al. 2005). Second, we assigned presence to the plots with the highest predicted occurrence probabilities. The number of plots that was assigned presence we chose to be the same as the observed number of presences (**p**revalence **b**ased **p**roportion of highest probabilities = pbp). For a species with a prevalence of 30%, the 30% of plots with the highest predicted occurrence probabilities were assigned presence. Since models with high discriminatory power assign the highest occurrence probabilities to occupied sites, we expected this method to correctly classify a substantial proportion of plots. The quality of dichotomised predictions we assessed with four measures of agreement: sensitivity, specificity, *CCR*, and Cohen's *Kappa* (Fielding & Bell 1997). To illustrate 'chance', we generated a chance distribution for each of these measures: for each species, given its prevalence and the number of plots, we randomly distributed the observations over the plots and calculated the measures of agreement. This we repeated 10.000 times. The resulting chance distributions has a median corresponding to the prevalence (for sensitivity), 1−prevalence (for specificity), [prevalence × #of presences] + [(1-prevalence) × #of absences] (for *CCR*) (Fielding & Bell 1997), and approximately 0 (for *Kappa*). The 95%-percentiles depends on prevalence and sample size. We considered the model to perform better than chance with the respective threshold if all measures of agreement exceeded the 95%-percentile of their chance distribution.

Assessing model calibration

For every model transfer, we calculated a calibration curve as described by Pearce & Ferrier (2000b). It relates the logit-transformed model predictions ($\ln[\pi_i/(1-\pi_i)]$) to the observed presences/absences by means of logistic regression. In case of a perfectly calibrated model, the resulting regression line has an intercept of zero and a slope of one (Miller et al. 1991). Transforming logits to probabilities results in curved logistic lines (Figure 5.1). Significant deviations from perfect calibration we tested with likelihood ratio tests (Miller et al. 1991; Pearce & Ferrier 2000b). Deviations of the intercept from 0 indicate bias, with intercepts < 0 resulting in predictions that are too high, and with intercepts > 0 giving too low predictions. Slopes > 1 result in predictions that are too extreme, i. e. too low for probabilities < 0.5 and too high for probabilities > 0.5, indicating overfitting. The reverse occurs for slopes between 0 and 1. If slopes are < 0, the overall trend of predictions is wrong with unoccupied sites having the highest predicted occurrence probabilities. Note that with slopes significantly different from 1, the intercept merely describes the bias for $P = 0.5$ (Vaughan & Ormerod 2005).

Qualitative comparison of models

For the ten species that had models for both study areas, we qualitatively compared these models. Model averaging, which we had used for model building, considers a number of models for each species and does not eliminate significant variables or models like e. g. stepwise procedures. It also allows to assess the weight of each variable within a species' averaged model (Burnham 2002). Thus, via the qualitative model comparison, we could check if the same variables were important in both regions, and compared the functional form of the relationships (Altman & Royston 2000).

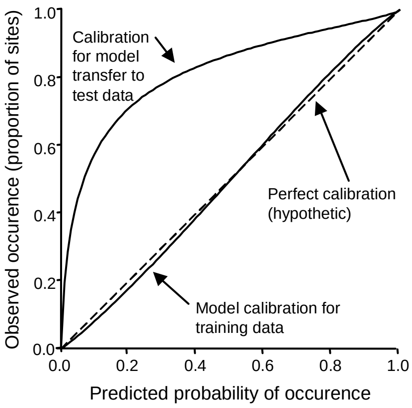


Figure 5.1: Calibration curves, resulting from relating logit-transformed model predictions to observed occurrences by logistic regression. The example shows the Bremen model for *Chortippus mollis* and its transfer to Berlin data. After transfer, significant bias is obvious: consistent underestimate of occurrence probabilities, due to an increase in prevalence from 39% (Bremen) to 81% (Berlin).

5.3 Results

Transfer in time

The detailed results for models transfers in time (transfer of Bremen models 2003 to Bremen data 2004) are shown in Figure 5.2. Numbers below the species name give prevalences: in the case of *Aphrodes makarovi*, 28% in the test data and 15% in the training data. The first black dot gives the c-index of the model transfer: 0.57 for *A. makarovi*. This does not exceed the 95%-percentile of the null distribution generated by a randomisation test. The span between the 50% and the 95%-percentile of this null distribution is indicated by the solid black line. The not successful transfer in terms of c-index is indicated by the minus on top of the species column. For the training data, the c-index was 0.88, shown as an open circle. This far exceeded the 95%-percentile of the null distribution, the distance is shown as a dashed line. The next pair of symbols represents $Kappa$ for test and training data. Again, the open circle represents the training data. In this case of a threshold dependent measure, the black dot represents $Kappa$ for pbp, the 'x' for P_{Kappa} of the original model. The $+$ and $-$ on top indicate that for P_{Kappa}, in *A. makarovi*, $Kappa$ was higher than chance ($+$, upper symbol), for pbp not higher than chance ($-$, lower symbol). The next pairs of symbols represent sensitivity, specificity and CCR in the same way.

Results of all species are summarized in Table 5.2 and Table 5.3. For 28 out of 30 species, the c-index of the model transfer was significantly better than chance. Most models assigned highest occurrence probabilities to occupied test sites, with the exceptions of *Aphrodes makarovi* and *Macrosteles cristatus*. C-index values mostly decreased with model transfer (Table 5.3). Median of this decrease (for the transfers with significant c-index) was -0.11 with a maximum of -0.3 and a minimum of $+0.05$. Applying a threshold caused difficulties. With the models' original P_{Kappa}-threshold, dichotomised predictions exceeded chance for only four models. Pbp performed better, 19 species models exceeded chance (these species' names are printed in bold in Figure 5.2). For the models that could be successfully transferred using pbp, $Kappa$ decreased considerably (median of difference: -0.19).

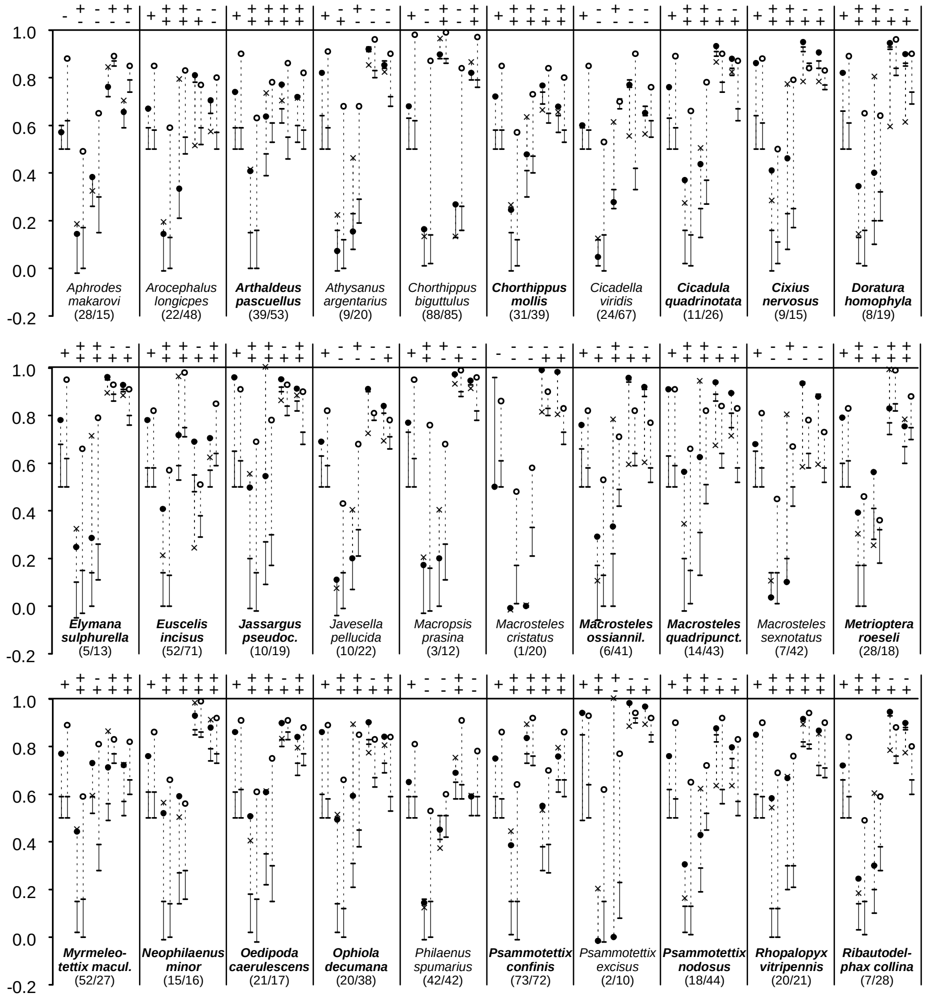


Figure 5.2: Model transfer in time. Discriminatory ability assessed by the threshold independent c-index, and threshold dependent $Kappa$, sensitivity, specificity and CCR. Measures for model transfer (x for P_{Kappa}, black dots for pbp), and for original models (open circles). Chance distributions (50 to 95%-percentiles) for each measure are indicated by black bars. $+/-$ on top of each measure indicate whether the model transfer is better than chance predictions. The upper row represents P_{Kappa}, the lower pbp. Numbers under the species names give prevalences for test / training data. For further explanations see text.

Table 5.2: Results of model transfers: discrimination and calibration with test data. **Discrimination ('discr'):** threshold independent AUC (1^{st} column, non significant values marked grey), threshold dependent measures with P_{Kappa} (2^{nd} column), and with pbp (3^{rd} column). $+$ indicates that all four criteria (sensitivity, specificity, CCR, $Kappa$) exceed chance. **Calibration ('cal')**: intercept (bias, 1^{st} column) and slope (spread, 2^{nd} column), $+$ indicating no significant deviation from 0 (intercept) and 1 (slope).

	Bremen '03 → Bremen '04		Bremen '03 → Berlin '04		Berlin '04 → Bremen '03		Berlin '04 → Bremen '04	
	discr.	cal.	discr.	cal.	discr.	cal.	discr.	cal.
Athysanus argentarius	0.82		0.88 ++	++	0.67 +	+	0.67 +	+
Chorthippus mollis	0.72 +	+	0.86 +	+	0.63 +		0.69 +	
Cicadula quadrinotata	0.76 +		0.85 +	+	0.85 ++	+	0.72	+
Doratura homophyla	0.82 +	+	0.36	+	0.44	+	0.57	+
Euscelis incisus	0.78 +	+	0.73 +	+	0.77 +	+	0.78 ++	++
Macrosteles quadripunctulatus	0.91 +	+	0.90 +		0.76 +	+	0.85 +	+
Metrioptera roeseli	0.79 +	+	0.86 +	+	0.72 +		0.70 ++	+
Oedipoda caerulescens	0.86 +	++	0.72 +		0.70		0.61	
Ophiola decumana	0.86 +	+	0.79 ++	++	0.66 +		0.77 +	+
Psammotettix confinis	0.75 ++	+	0.77 +	+	0.85 +		0.82 +	
Aphrodes makarovi	0.57	+						
Arocephalus longiceps	0.67							
Arthaldeus pascuellus	0.74 ++							
Chorthippus biguttulus	0.68	+						
Cicadella viridis	0.60							
Cixius nervosus	0.86 +	+						
Elymana sulphurella	0.78 +							
Jassargus pseudocellaris	0.96 +							
Javesella pellucida	0.69							
Macropsis prasina	0.77							
Macrosteles cristatus	0.50	+						
Macrosteles ossiannilssoni	0.76 +	+						
Macrosteles sexnotatus	0.68	+						
Myrmeleotettix maculatus	0.77 +							
Neophilaenus minor	0.76 ++	++						
Philaenus spumarius	0.65	+						
Psammotettix excisus	0.94							
Psammotettix nodosus	0.76 +							
Rhopalopyx vitripennis	0.85 ++	++						
Ribautodelphax collina	0.72 +	+						
# of successful transfers	28/4/19		9/2/9		9/1/8		9/3/6	

Table 5.3: Overview of model discrimination for training data ('train.') and test data ('test'), and difference ('diff.') of model performance between training and test data. Median, minimum and maximum values for c-index and $Kappa$ (threshold = pbp). Only successfully transferred models are presented (# = number of models).

Transfer		***c*-index**				**Kappa (p_{crit} = pbp)**			
		#	train.	test	diff.	#	train.	test	diff.
Bremen '03→ Bremen '04	med.	28	0.89	0.76	-0.11	19	0.64	0.41	-0.19
	min.		0.81	0.60	-0.30		0.46	0.25	-0.42
	max.		0.98	0.96	0.05		0.69	0.58	-0.07
Bremen '03→ Berlin	med.	9	0.89	0.85	-0.04	9	0.64	0.41	-0.25
	min.		0.82	0.72	-0.19		0.46	0.24	-0.42
	max.		0.91	0.90	0.03		0.68	0.57	0.08
Berlin→ Bremen '03	med.	9	0.93	0.72	-0.17	8	0.68	0.34	-0.33
	min.		0.83	0.63	-0.31		0.58	0.15	-0.66
	max.		0.94	0.85	-0.06		0.81	0.60	-0.07
Berlin→ Bremen '04	med.	9	0.93	0.72	-0.22	6	0.71	0.34	-0.33
	min.		0.83	0.61	-0.31		0.58	0.18	-0.63
	max.		0.94	0.85	-0.06		0.81	0.46	-0.18

Most models partly lost their calibration when transferred in time (Table 5.2). About half of the models showed significant spread (slope of calibration curve different from 1) with new data. However, for models that could be successfully transferred using pbp, only six out of 19 exhibited significant spread. For the two species where the *c*-index was not significant, the slope of the calibration curve was < 0. This indicates that the overall trend of probabilities was wrong with high predicted occurrence probabilities where observed probabilities were low and vice versa. The other slopes different from 1 were between 0 and 1, indicating overfitting. Most models showed significant bias (intercept different from 0). This could mostly be traced back to differences in prevalence. If prevalence decreased with respect to the training data, the intercept was < 0, resulting in consistent overestimation of occurrence probabilities. Where prevalences were similar, intercepts were not different from 0 (e. g. *Oedipoda caerulescens*, *Neophilaenus minor*). For only three species (*Oedipoda caerulescens, Neophilaenus minor, Rhopalopyx vitripennis*), models were well calibrated to the test data.

Transfer in space

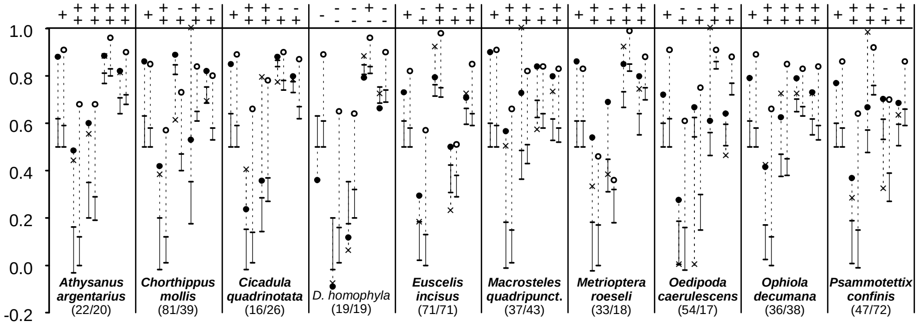
Details of models transfers in space are given in Figure 5.3. Transfers in space worked well for 9 out of 10 species regarding the *c*-index (Table 5.2). Transfer of the model for *Doratura homophyla* failed for all test data and models. Overall, transfer in space worked better from Bremen to Berlin than vice versa: *c*-index decrease was minor for the transfer of Bremen models to Berlin data (median -0.04), but larger for the transfer of Berlin models to Bremen 2003 data (-0.17) and Bremen 2004 data (-0.22) (Table 5.3). For the Bremen 03 → Berlin 04 transfer, all species with significant *c*-index also reached significant dichotomised predictions with pbp as a threshold, even though *Kappa* decrease was considerable (median decrease -0.25). For the Berlin 04 → Bremen 03 transfer, 8 species reached significant 0/1 predictions, for Berlin 04 → Bremen 04, 6 species. P_{Kappa} of the original models performed poorly as a threshold, even though for one species (*Athysanus argentarius*) it performed better than pbp.

Like discrimination, calibration of the Bremen → Berlin transfer was better than vice versa. In the first case, six models showed no significant spread, in the latter one model (2003 data) and three models (2004 data). *Doratura homophyla* calibration curves had slopes < 1 in two cases. This enhances that models for this species could not be transferred in space, which had already been indicated by the lack of discriminatory power. Most models showed bias with the test data, reflecting differences in prevalence. The resulting consistent underestimate of occurrence probabilities in case of prevalence increase showed the example of *Chortippus mollis* (Figure 5.1). Only two models were overall well calibrated to the test data for the Bremen 03 → Berlin 04 transfer (*Athysanus argenarius, Ophiola decumana*), none for Berlin 04 → Bremen 03, and one model for Berlin 04 → Bremen 04 (*Euscelis incisus*).

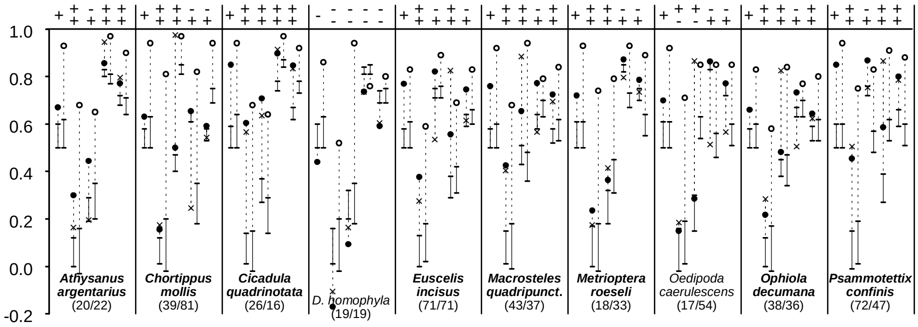
Qualitative comparison of models

The qualitative comparison of Berlin and Bremen models revealed that, regarding the main driving factors, only vegetation structure appeared in all model pairs (Figure 5.4). Age was in both models for three species, landscape context for five and soil parameters for four. Since soil parameters in the models differed between the two study area models for all species, comparison was not possible for these parameters. Investigation of the shape of response curves showed no case of opposite influence of one parameter on a

(1) Transfer of Bremen (2003) models to Berlin (2004) data



(2) Transfer of Berlin (2004) models to Bremen data (2003)



(3) Transfer of Berlin (2004) models to Bremen data (2004)

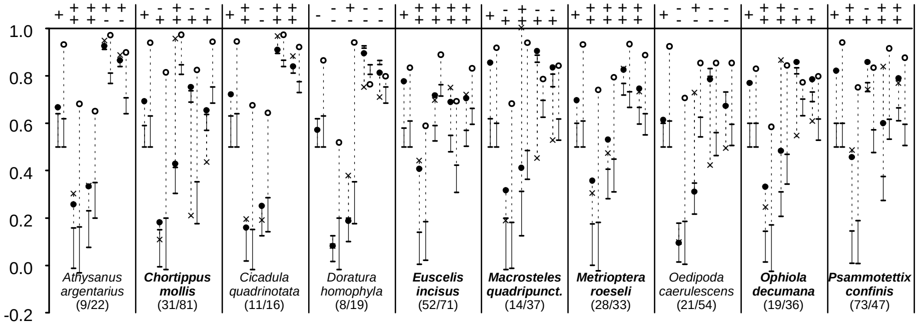
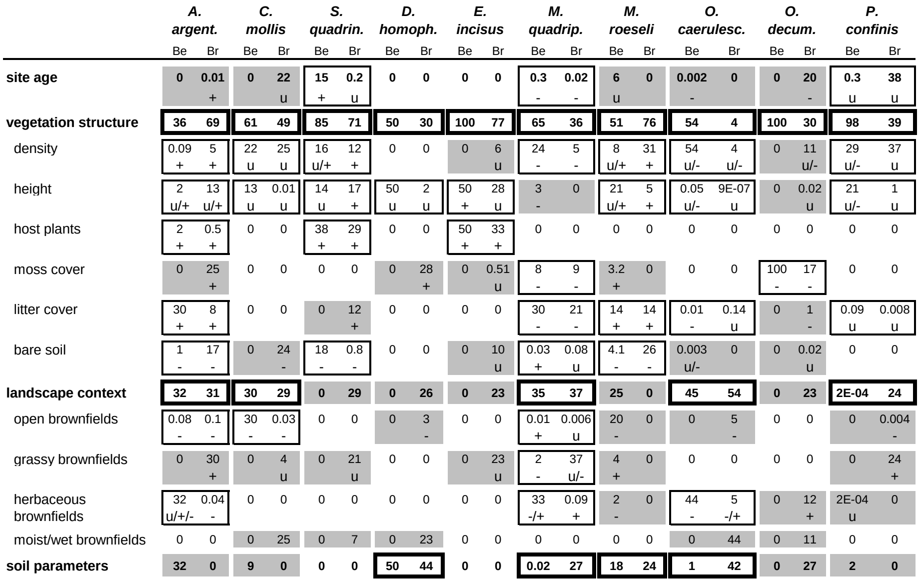


Figure 5.3: Model transfer in space. For details, see Figure 5.2.

species in either study area. In some cases however (e. g. vegetation height for *Cicadula quadrinotata*), one relationship was unimodal and the other monotonic. Overall, vegetation parameters largely agreed between models, even though variable weights usually differed. In contrast to this, for landscape context, mostly different parameters entered into the models.



	A. argent.		***C. mollis***		***S. quadrin.***		***D. homoph.***		***E. incisus***		***M. quadrip.***		***M. roeseli***		***O. caerulesc.***		***O. decum.***		***P. confinis***	
	Be	Br	Be	Br	Be	Br	Be	Br	Be	Br	Be	Br	Be	Br	Be	Br	Be	Br	Be	Br
site age	**0**	**0.01** +	**0**	**22** u	**15** +	**0.2** u	**0**	**0**	**0**	**0**	**0.3** -	**0.02** -	**6** u	**0**	**0.002** -	**0**	**0**	**20** -	**0.3** u	**38** u
vegetation structure	**36**	**69**	**61**	**49**	**85**	**71**	**50**	**30**	**100**	**77**	**65**	**36**	**51**	**76**	**54**	**4**	**100**	**30**	**98**	**39**
density	0.09 +	5 +	22 u	25 u	16 u/+	12 +	0	0	0	6 u	24 -	5 -	8 u/+	31 +	54 u/-	4 u/-	0	11 u/-	29 u/-	37 u
height	2 u/+	13 u/+	13 u	0.01 u	14 u	17 +	50 u	2 u	50 +	28 u	3 -	0	21 u/+	5 +	0.05 u/-	9E-07 u	0	0.02 u	21 u/-	1 u
host plants	2 +	0.5 +	0	0	38 +	29 +	0	0	50 +	33 +	0	0	0	0	0	0	0	0	0	0
moss cover	0	25 +	0	0	0	0	0	28 +	0	0.51 u	8 -	9 -	3.2 +	0	0	0	100 -	17 -	0	0
litter cover	30 +	8 +	0	0	0	12 +	0	0	0	0	30 -	21 -	14 +	14 +	0.01 -	0.14 u	0	1 -	0.09 u	0.008 u
bare soil	1 -	17 -	0	24 -	18 -	0.8 -	0	0	0	10 u	0.03 +	0.08 u	4.1 -	26 -	0.003 u/-	0	0	0.02 u	0	0
landscape context	**32**	**31**	**30**	**29**	**0**	**29**	**0**	**26**	**0**	**23**	**35**	**37**	**25**	**0**	**45**	**54**	**0**	**23**	**2E-04**	**24**
open brownfields	0.08 -	0.1 -	30 -	0.03 -	0	0	0	3 -	0	0	0.01 +	0.006 u	20 -	0	0	5 -	0	0	0	0.004 -
grassy brownfields	0	30 +	0	4 u	0	21 u	0	0	0	23 u	2 -	37 u/-	4 +	0	0	0	0	0	0	24 +
herbaceous brownfields	32 u/+/-	0.04 -	0	0	0	0	0	0	0	0	33 -/+	0.09 +	2 -	0	44 -	5 -/+	0	12 +	2E-04 u	0
moist/wet brownfields	0	0	0	25	0	7	0	23	0	0	0	0	0	0	0	44	0	11	0	0
soil parameters	**32**	**0**	**9**	**0**	**0**	**0**	**50**	**44**	**0**	**0**	**0.02**	**27**	**18**	**24**	**1**	**42**	**0**	**27**	**2**	**0**

Figure 5.4: Qualitative comparison of models based on Berlin (B) vs. Bremen (HB) data. Main driving factors in bold. Numbers indicate variable weight [%], symbols illustrate the functional form of the relationship between species and variable: u = unimodal (bell shaped), $-$ = monotonic, decreasing, $+$ = monotonic, increasing. If a species showed different reactions to one variable complex (e. g. vegetation density: $+$ for density at the 0-5 cm height, u for density at the 25-50 cm height), all are listed. Black frames indicate a variable or variable complex to be present in both models, grey background indicates presence in only one model. No details are given for soil parameters because no species reacted to the same soil parameters in both models.

5.4 Discussion

Model discrimination – *c*-index

It seems that the majority of habitat models tested in this study are general in the sense that they successfully rank test sites from suitable to unsuitable. Models for both taxa (grasshopper and leafhopper) could be transferred equally well. However, the limited number of grasshopper (5 species) does not allow to detect possible differences between the taxa. If the findings in this study hold for other taxa requires further investigation. 57 of 60 transfers achieved a *c*-index exceeding chance. 45 transfers (75%) reached *c*-values $\geq$0.70. This is considered as ‘good’ discrimination by Hosmer & Lemeshow (2000), and Randin et al. (2006) require a *c*-index of 0.7 for successful model transferability . In comparison to our results, Bulluck et al. (2006) found only 56% of their breeding bird models to reach *c*-indexes $\geq$0.70 when transferred to new data in time or space. Randin et al. (2006) achieved sufficient spatial transferability for less than half of their models for alpine plant species. This suggests our models to be robust and general, indicating that model averaging might lead to more stable models than stepwise procedures. The modelling technique used had an influence on model transferability in previous studies (Araujo & Guisan 2006; Randin et al. 2006). However, a clearly superior method has not yet identified.

Still, model transfer mostly went along with a loss of accuracy. This loss was not necessarily larger for transfer in space than for transfer in time, since models could be transferred better from Bremen to Berlin than from Bremen 2003 to Bremen 2004 regarding the *c*-index. Bulluck et al. (2006) found in their study as well that some transfers in space worked better than those in time. Possibly, the Bremen 2004 test data were unusual, being affected by the exceptionally hot and dry summer of 2003. This assumption is supported by the fact that Berlin 2004 models could be transferred more successfully to Bremen 2003 than to Bremen 2004 data. Thus, transfer in space and time did not lead to poorer results than transfer in space or time only. Jensen et al. (2005), who extensively tested model transfer in time for the blue crab *Callinectes sapidus*, found that some years show unique habitat relationships that are not well predicted by models from the other years. The comparison between the years showed that there can be enormous differences in species prevalence, particularly in dynamic habitats like brownfields. However, even though predictive habitat models are generally static (Bulluck et al. 2006; Guisan & Zimmermann 2000), modelling species in disequilibrium using static models is problematic (Gibson et al. 2004b), and theories based on equilibrium might be inadequate for urban communities (Rebele 1994), models from one year were mostly valid in the next and in another region.

A closer look at which species models transferred worse than others reveals that low *c*-values might be associated with eurytopic species. None of the species considered eurytopic (*Aphrodes makarovi, Chortippus biguttulus, Javesella pellucida* and *Philaenus spumarius*) (Detzel 1998; Nickel 2003) reached a *c*-index $\geq$0.7. It seems reasonable that habitat generalists do not exhibit strong species-habitat relationships. If strong relationships are found for such species, they might be an artifact within a particular dataset. In fact, none of these species, though present, had shown significant relationships in the Berlin dataset. Investigations on the relation between species properties (biological traits) and model transferability might be able to reveal more general patterns (Randin et al. 2006).

Model transfer from Bremen to Berlin worked better than vice versa, suggesting that the Bremen models. Randin et al. (2006) suggest such asymmetrical transferability to be caused by differences in the width of environmental ranges or in species abundances. In our case however, environmental ranges had comparable width, and abundance differences did not seem to produce more asymmetric values for the *c*-index. Thus, it seems likely that the Bremen models, based on a larger dataset of 147 plots, were more general than the Berlin ones (based on 89 plots). Harrell et al. (1984) found that smaller training samples had an apparent higher quality, but a large loss in quality when applied to test data. The opposite was true for large training samples. McPherson et al. (2004) obtained best models for very large sample sizes (300-500), Pearce & Ferrier (2000a) recommend sample sizes of >250. In this light, the Berlin dataset in particular might have been too small to build general models. Considering these results it seems desirable to base models on large datasets. On the other hand, test datasets as well require a certain size (Steyerberg et al. 2003), Vaughan & Ormerod (2005) suggest 200. This is particularly important for rare species, since otherwise the *c*-index cannot be calculated reliably (McPherson et al. 2004). Pearce et al. (2001) required sufficient evaluation data to have at least nine species records. Since sample sizes for labor intensive field data are usually restricted by logistic constraints, available money and manpower, it will be difficult to follow these recommendations in practice. Our results indicate that also sample sizes of 150 lead to general models, even though larger samples might allow even better results, and small test data sets might not contain a sufficient amount of observations for rare species.

An interesting finding was that those species that made models in both study areas could be transferred better in time than the others. The fact that they exhibited statistically strong relationships to the measured environmental factors in both regions might indicate that they show stable, general relationships to these factors.

Model calibration

Models applied to new data hardly ever showed good calibration. Considerable bias was fully expected, since prevalences between training and test data differed on a large scale (Pearce & Ferrier 2000b; Vaughan & Ormerod 2005). Bremen models applied to Berlin showed less spread than the other way round. Since spread indicates overfitting, this is another hint that Berlin models might have had a stronger tendency to be overfitted to their small dataset.

The consequence of these findings is that predicted occurrence probabilities cannot be used in a quantitative way since they do not express the true probability of a site as being occupied. Sites are ranked according to their relative probability of being occupied, thus predictions are ordinal rather than quantitative. They should be displayed as ranked categories to avoid quantitative interpretation (Vaughan & Ormerod 2005). If poor calibration of a model is due to a subset of plots for which the model can not be transferred well, such plots can be identified and restrictions placed on the model's use (Miller et al. 1991). In general, intercept and slope of the calibration curve can be used to adjust model predictions (Steyerberg et al. 2003). Such fine-tuning leads to a better model adjustment to the local circumstances of the test data, but not necessarily to a more general model. Thus, this method should be used with caution (Miller et al. 1991).

Dichotomising predictions

Converting occurrence probabilities into presences/absences raises the problem of finding an optimal threshold. When applying models to new environmental data, this problem cannot be overcome without information of the species' prevalence. We clearly showed that using the training data's threshold was doomed to failure since models were mostly poorly calibrated to new data. This resulted in consistent over- or underestimation of occurring probabilities, making the original threshold useless. In some studies, a new optimal threshold was calculated for the test data (e. g. Eyre et al. 2005a; Schröder & Richter 1999/2000). This allows assessment of model transfer to the test data. However, it does not give any hint on what threshold should be used with new data, where true species presence/absence is not known, but to be predicted with the model. If it is possible to gain information on the species prevalences within the area where a model is to be applied, pbp is a promising alternative to defining thresholds, at least for the majority of species. Before relying on it, this should probably be verified with more than one set of test data. If information on prevalence is not accessible, there does not seem to be much point in dichotomising occurrence probabilities since misclassifications are likely.

Qualitative comparison

Comparing the models for Bremen and Berlin allowed a deeper insight into the question why model transfers might succeed or fail. Parameters contained in both models are likely to have a stable relationship to the species' presence and can probably be generalised. Parameters that were in only one of the models might have an indirect influence. The relationship to the underlying direct variable might not be the same in other datasets (Vaughan & Ormerod 2003). This seems to be the case with all soil parameters. Even though they might have had considerable influence in one model, the same parameters never went in the model for the other study area. In the case of *Doratura homophyla*, this led to a model that could be transferred in time (Bremen) but not in space. Landscape context also showed large differences between models. Fisher et al. (2005) note that research has rarely been undertaken to test the assumption that the response to landscape structure from one area can be extrapolated to another. Purtauf et al. (2005) believe that there is a high risk of artificial correlations in hierarchical multi-scale landscape analyses when ecological data are related to the landscape context. Thus it might well be that species – landscape context relationships are region specific. In our study this might stem from the fact that distribution of herbaceous and grassy brownfields differed considerably between the study areas, and moist to wet brownfields were not present in Berlin. Overall, it seems likely that the vegetation structure variables have a more direct relationship to species occurrences than the other variables (Strauss & Biedermann 2006). Thus, their influence was comparable between the study areas. This highlights that for generalizations on the species-environment relationship as well as for model transfer, models basing on direct parameters are more suitable.

The overall trend that there were more variables in the Bremen models was probably caused by the larger dataset. With more data, variables more easily exceeded the significance level. Therefore, differences between models did not necessarily result in poor transferability and might mainly be due to statistical reasons during the model building process. Reactions to vegetation structure were considerably similar in both cities. Since vegetation structure was the most important driving factor, this probably enabled the good overall transferability. Some species exhibited responses that seemed to be relocated (monotonic to unimodal and vice versa) between the study areas. Even though this could be caused by incomplete stratification not covering the whole gradient (Vaughan & Ormerod 2003), it seems more likely that (1) there was a true difference in species reactions between the oceanic Bremen and the more continental Berlin or (2) differences were due to differences in data distributions. The ranges of values (minimum / maximum values) were comparable for all variables between the study areas, but data distribution within the range often differed, in particular for the landscape context variables.

In this context, when applying models in nature conservation practice, one has to keep in mind that models proofed to be transferable are only valid for data ranges present in the test data until the model is tested under different conditions (Vaughan & Ormerod 2003). Therefore, test sites should be carefully selected, representing the full range of environmental conditions present in the training data. This requirement was met within our study, where all plots had been chosen in a random-stratified design, covering the whole gradient of urban brownfield stages.

5.5 Conclusions

The vast majority of models tested in this study turned out to be transferable to new data from different years and different regions. However, some models could not be transferred at all in time or space. This implies that generality always needs to be tested if inference about general relationships is to be drawn or models are to be applied on independent data. Both temporal and spatial transferability should be tested, since single years may exhibit unusual relationships. Certain factors seem to enhance model generality : (1) Large sets of training data. (2) Strong influence of direct variables within models. (3) Species are not eurytopic. (4) Species show significant relationships to environmental variables in more than one study area / dataset.

Model accuracy usually decreases with model transfer. Thus, models that do not fit their training data well should not be transferred. On the other hand, well fitting models do not necessarily transfer well. In most cases, model transfer leads to poor calibration. Predicted occurrence probabilities can therefore not be used quantitatively and should not be presented as such, but as ordinal information on habitat quality.

Dichotomisation of predictions should be avoided without information about species' prevalences. With prevalence information available, the prevalence based proportion of highest probabilities (pbp) allows classification with reasonable accuracy.

Acknowledgements

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Chapter 6

Fit for succession – community structure and life strategies of leafhoppers in urban brownfields

B. Strauss & R. Biedermann. Submitted to Ecological Entomology.

Abstract

1. Urban brownfields offer an excellent opportunity to study successional processes. Changes in the frequencies of biological traits during succession are of particular interest. They shed light on the general reasons for species to emerge and vanish during the course of succession.

2. We studied leafhopper (Hemiptera: Auchenorrhyncha) occurrence data (3763 species observations) of 194 species. Data had been collected on 246 brownfield plots, aged 0 to 40 years, in two cities of Northern Germany.

3. We studied four categorical traits: host plant type, phagy, dormancy, and voltinism. In these traits, we analysed two aspects. (1) Changes in trait category frequencies during succession. (2) Distribution of trait categories (i) within the brownfield species pool vs. the German species pool and (ii) within species observations.

4. Trait categories showed clear successional trends. Young successional stages were related to feeding on herbs, polyphagy, egg overwintering, and 2 generations/year.

5. By analysing combinations of two traits, species could be assigned to four functional groups: species associated with young, intermediate and old sites, and one group indifferent to site age. The pioneer group comprised the least number of species, but the highest number of observations.

6. Categories associated with young site age were overrepresented in the brownfield species pool. Moreover, within this already biased species pool, species with pioneer trait categories occurred with higher frequency. For the slow colonizers among leafhoppers, brownfields seem to be habitats that are hard to exploit.

6.1 Introduction

Species traits

Biological traits are ‘well defined, measurable properties of organisms’ (McGill et al. 2006) that reflect how they live, including growth, feeding, movement, dispersion, and reproduction. More than a century ago, ecologists started to recognize a relationship between the traits of animals and the habitat conditions where they occur (Statzner et al. 2001). Early, ecologists have been aware that trade-offs in biological traits enable animals with different trait combinations to settle equally successful in the same habitat (Statzner et al. 2001). This led to the idea of ’functional groups’, a concept that gained much attention (e.g. Dumay et al. 2004; Ribera et al. 2001). Gitay & Noble (1997) define functional groups as ‘non-phylogenetic groupings of species which perform similarly in an ecosystem, based on a set of common biological attributes’.

Within ecological research, statements about traits give generality and predictability (McGill et al. 2006). One of the objectives of predictive ecology is to know whether species with certain traits will persist under a defined set of environmental conditions (Ribera et al. 2001). In contrast to this, community ecology that focuses on species identities gives valuable and detailed insight, but only into a limited number of species. This species centred ecology may result in a loss of ecological generality and tends towards special cases (McGill et al. 2006). Moreover, it can only study those species that occur with a minimum frequency. In the study of traits, all species may contribute to the picture.

Traits & Succession

During the course of succession, species emerge and vanish. Focusing on the identities of such species might not reveal the biological characteristics that cause populations to increase and decline. Here, the analysis of changes in the frequency of biological traits offers a promising alternative. It sheds light on which traits, or trait categories, are associated with distinct parts of the successional gradient.

There have been a number of studies on insects during secondary succession, e.g. on bees (Steffan-Dewenter & Tscharntke 2001), butterflies (Steffan-Dewenter & Tscharntke 1997), beetles (Brown & Hyman 1986), and leafhoppers (Hollier et al. 1994). From these studies and from general ecological theory, a number of hypotheses concerning traits during succession have been formulated and tested. (1) Niche breadth will decrease, i.e. host plant specialisation will increase from polyphagous to monophagous (e.g. Brown & Southwood 1983; Novotny 1994; Steffan-Dewenter & Tscharntke 1997). (2) The number of generations will decrease (for references, see (1)). (3) Overwintering strategy will shift from nymph to adult (to egg) (e.g. Hollier et al. 1994; Nickel 2003).

Urban brownfields

Urban brownfields (derelict land) are increasingly noticed as habitats of conservation significance (Angold et al. 2006). High habitat diversity and a wide range of environmental conditions (Rebele 1994) provide habitat for species-rich communities (Angold et al. 2006), including rare and endangered species (Eyre et al. 2003). In this respect, it is important to understand if brownfields provide habitat equally suitable for all species of the regional species pool, or if only species exhibiting certain traits are able to colonize these habitats. We hypothesise that certain traits may be more frequent than others, since urban brownfields are strongly influenced by successional processes (e.g. Gilbert 1989), requiring species to constantly track favourable habitats. The existence of brownfields is owed to the creation of habitat, e.g. by demolition of buildings. This new habitat undergoes rapid succession, mostly undirected by man. Typically, young brownfields are dominated by annual herbs, later perennial herbs and grasses dominate, before shrubs and trees establish (Brown & Southwood 1987).

Aim of the study

Leafhoppers (Hemiptera: Auchenorrhyncha) are phytophagous insects fairly abundant on brownfield sites (Sanderson 1992b). We analysed plot-based presence/absence data of leafhoppers. Data were recorded on urban brownfields of different age and successional state. By analysing four categorical traits (host plant type, phagy, dormancy, and voltinism), we aimed to answer the following questions:

(1) Can trait categories be related to site age in agreement with earlier studies on trait frequencies during succession?

(2) Do different combinations of trait categories react in a similar way to site age?

(3) Can combinations be used to classify species into functional groups that show the same occurrence pattern along the successional gradient?

(4) Is the brownfield species pool a representative sample of the potential species pool, with regard to the frequency of trait categories and combinations of trait categories?

(5) Do species with certain trait categories occur particularly rarely or often within species observations?

6.2 Methods

Data

We analysed species occurrence data from urban brownfields in two large cities in Northern Germany (Strauss & Biedermann 2006). The cities under study were Bremen (53° 05' N, 8°44' E, mean temperature 8.8 °C, mean annual precipitation 694 mm), and Berlin (52°30' N, 13°28' E, mean temperature 9.7 °C, mean annual precipitation 560 mm). In both cities, plots of 225 m^2 covered the whole gradient of brownfield successional stages, with 157 plots in Bremen and 89 in Berlin. For each plot, site age was extracted from a time series of aerial photographs. Site age ranged from 0 to 40 years with a median of 6 years.

The data were collected in 2003 (Bremen) and 2004 (Berlin). Sweepnet sampling was carried out four times at monthly intervals between early June and early September. Each sampling procedure consisted of 100 sweeps covering the entire plot. The catch was killed with ethyl acetate and frozen. All male adult individuals were determined to species level (female individuals only for species where determination is possible) (Biedermann & Niedringhaus 2004).

Samples contained a total of 194 species, 146 in Bremen and 130 in Berlin. 82 species occurred in both cities. Species numbers per plot ranged from 0 to 32 with a median of 15. Each species we assigned categories for four traits. Each trait was subdivided into two to four categories: (1) host plant type (herbs, herbs and grasses, grasses, woody plants), (2) phagy = specialisation in host plant species (monophagous, oligophagous, polyphagous), (3) hibernation = overwintering strategy (egg, nymph, adult), and (4) voltinism = number of generations per year (univoltine, bivoltine). Since there were only few species feeding on herbs and grasses, for most analyses, this category was combined with 'herbs'. Trait information was taken from Biedermann & Niedringhaus (2004), Nickel (2003), and Nickel & Remane (2002).

We analysed two kinds of species data. First, we used the species presence/absence data (= observations) on the plots. Each presence of a species on a plot represents one observation. There was a total of 3763 observations, 2179 in Bremen and 1584 in Berlin. Second, we analysed differences between the actual species pool (194 species) and the potential species pool. To this end, we compared to the German species pool, since there was no information available for a more regional species pool of the cities under study. For all German species, we obtained the trait categories named above from the same literature sources. Categories that only occurred within the German, but not within the brownfield species pool, were not analysed.

Relationship between site age and categories of individual traits

The relationship between trait categories and site age, we analysed with the fourth corner method (Legendre et al. 1997). It is based on the inflated data table. This table contains all species observations, their traits, and the corresponding site age. We wanted to test if any of the trait categories reacted differently from the others in its occurrence along the age gradient. Furthermore, we wanted to know which categories differed. Differences we assessed as differences in mean ranks by calculating the Kruskal-Wallis test-statistic (H). This global statistic tests if any group behaves differently. A posteriori testing was done by repeating the test for all pairs of groups. P-values for a posteriori testing were corrected for multiple testing using the Hochberg (1988) procedure (Wright 1992).

For these analyses, the significance of the H-statistic should not be tested in the standard way (Legendre et al. 1997). Since there were usually several species observed at one plot, not all rows of the inflated table were independent, as site age was the same for all species observed on one plot. To overcome this problem, we randomised species observations and the corresponding traits before combining them with site age in the inflated data table. This was done in the way that the observations for each species were randomly distributed over the plots. This way of permuting species' occurrences is based on the environmental control model (Legendre et al. 1997). It assumes that species are found at locations where they encounter appropriate living conditions and that species do that independently of each other.

After each randomisation process, species observations and their traits were combined with site age in the inflated data table. For this data, the H-statistic was calculated. It now represented a chance value that could be expected if there was no association between trait categories and site age. This procedure was repeated 10,000 times, and each time the resulting chance value for the H-statistic was compared to the original value. P-values were derived according to the number of times the chance value was smaller than the original value. If 9,950 (= 95%) of all chance values were smaller than the original value, this corresponded to $p = 0.05$ (Legendre et al. 1997; Manly 2001).

Relationships between site age and category combinations of traits

Combinations of two traits

Next, we addressed interactions between traits. A multiple interaction form of the fourth corner statistic does not yet exist (Legendre et al. 1997). Thus, again the problem of non independent data (see above) arises. However, results for the analyses of one trait at a time did not differ between using the randomisation test as described above and a standard Kruskal-Wallis test. Therefore, we relied on standard statistical testing of the inflated data matrix to assess the significance of interactions between two traits. We calculated the Wald-type test statistic as suggested by Brunner & Puri (2001), using the SAS procedure PROC MIXED. If the interaction was significant ($p \leq 0.05$), we tested which combinations of trait categories were different from each other. For the latter, we used a posteriori testing with the Kruskal Wallis test and the randomisation procedure, as outlined above for individual traits.

Functional groups

Each significant interaction of traits allowed to detect groups of trait combinations that reacted similar to the age gradient. These groups we referred to as 1 (youngest average site age), 2 (intermediate) and 3 (oldest), groups in between as 1.5 or 2.5. These group numbers were used to calculate an 'average group assignment' for each species. By comparing the group assignments for each trait combination and the average group assignments, species with similar patterns could be detected. We then tested if these groups of species indeed showed distinct reactions to the age gradient. Groups emerging from this procedure we considered as 'functional groups' – groups of species, associated with certain combinations of trait categories, that showed similar reactions to the age gradient.

Frequencies of trait categories: brownfield vs. potential species pool

Categories of individual traits

To quantify if the brownfield species pool was a representative sample of the potential species pool, we tested if trait categories within the brownfield species showed the same distribution as within all German leafhoppers. For example, 59% of all German species are monophagous, but only 47% of the brownfield species. The significance of this difference we assessed by a randomisation test with 10,000 iterations (Manly 2001). Tests were conducted in Splus 6.1. We randomly selected the number of brownfield species (194) from the total of 620 German species. Then, for the above example, we calculated the proportion of monophagous species within this random selection of species. This process was repeated 10,000 times. If the actual proportion (47% monophagous species) was smaller than 9,950 (95%) of these chance values, the difference between 47% and 59% was considered to be significant with $p = 0.05$. P-values were corrected for multiple testing using the Hochberg (1988) procedure.

Combinations of trait categories

Next, we combined the categories of all four traits. We analysed the frequencies of the 35 combinations that were found in the brownfield species. Our analyses followed two steps.

First, we tested if any combinations (e.g. of those categories associated with young site age) were more or less frequent than what would be expected from the frequencies of individual trait categories. Since such differences might also occur within the German species pool, we tested both the German and the brownfield species pools. To assess this question, we again conducted randomisation tests as outlined above for the categories of individual traits. To obtain randomised frequencies of category combinations, we used the trait frequencies within the species pools. For each trait, we created a vector that corresponded to the number of species in the pool. Trait frequencies within these vectors were the same as within the original data. We then randomised the vectors and combined them into a table. Each line of this table represented a random combination of trait categories. For each combination, we counted its randomised frequency and compared it to the value within the species pool.

Second, we tested for differences in the frequencies of trait combinations between the German and the brownfield species pools. Again, we used randomisation tests. This time, we randomly selected the appropriate number of species (194) from the German species pool. Within this random species selection, we recorded the frequencies of combinations and compared them to the observed values.

Frequencies of trait categories: species observations vs. species pool

Individual traits

Our analyses of the species pool do not take into account that species occur with different frequencies. We wanted to test if certain trait categories were more or less frequent within observations than within the species pool. For conducting the randomisation test here, we randomly chose species from the brownfield species pool. The number of species corresponded to the number of observations (3763). Each species could be picked several times. We then calculated the random frequencies of trait categories and tested if the observed values significantly differed.

Functional groups

We tested if functional groups (and the combinations comprising them) were more or less abundant within species observations than within the species pool. To this end, we conducted randomisation tests as for individual traits, but compared frequencies of functional groups as well as category combinations.

6.3 Results

Relating trait categories to site age

Individual traits

For all studied traits, the trait categories significantly differed in their reaction to site age ($p < 0.001$). Each trait category showed a distinct distribution concerning site age. For the trait categories associated with the youngest site age (hereafter: young categories), the median of site age was between five and six years for all traits (Figure 6.1, categories I). For those categories associated with the oldest site age (hereafter: old categories), the median of site age was between 9 and 11 years (Figure 6.1, categories III).

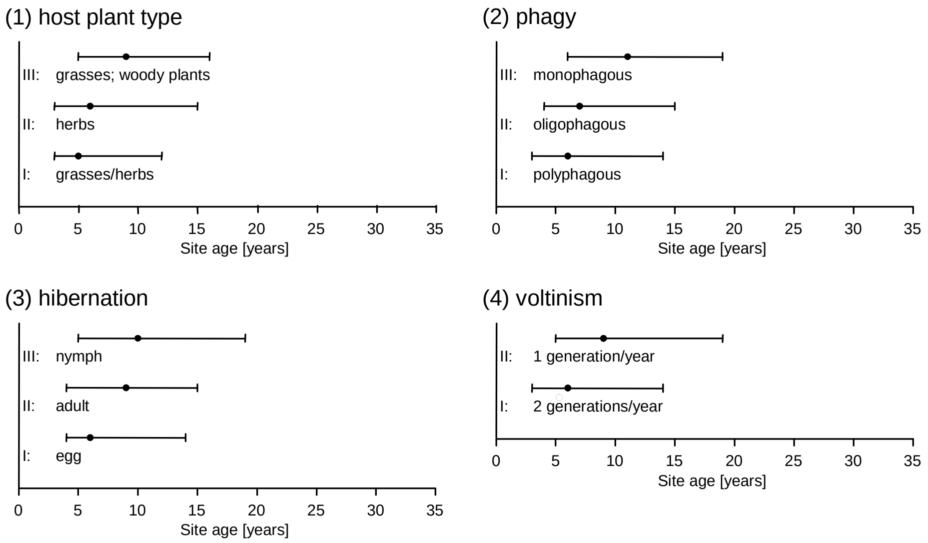


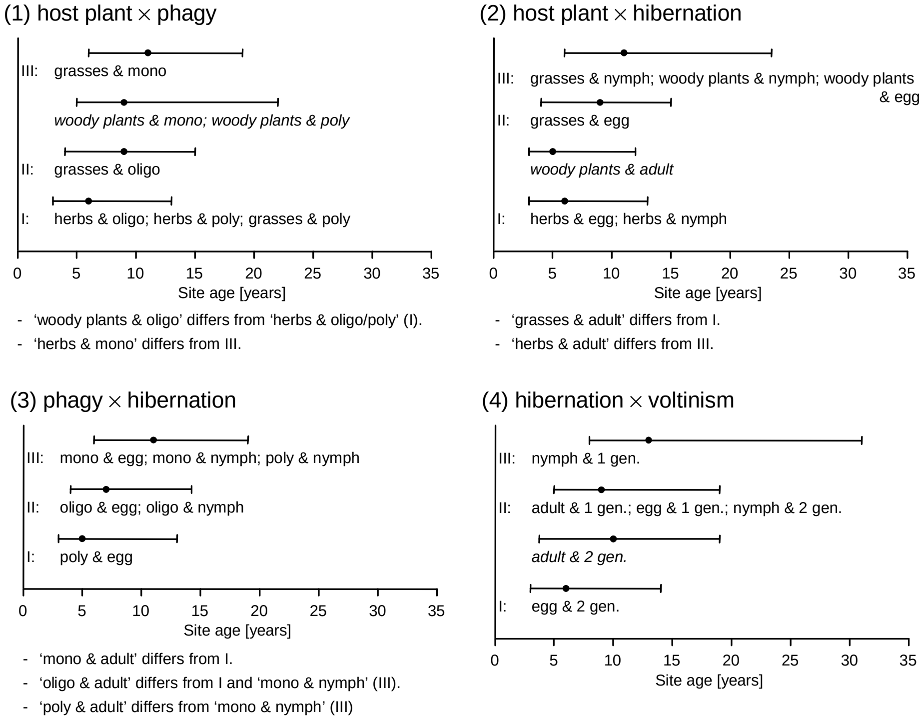
Figure 6.1: Significant differences between trait categories with respect to site age. Bars indicate the inter-quartile range of site age distribution for each trait category, the median is marked with a dot. All numbered groups (I-III) are significantly ($p \leq 0.05$) different from each other.

For host plant type, species feeding on grasses and herbs were associated with the youngest site age, followed by those feeding only on herbs (Figure 6.1). Species feeding only on grasses did not differ from those feeding on woody plants, both forming the group present at the oldest sites. In terms of host plant specialisation, polyphagy represented the young category, monophagy the old category, and oligophagy was in between. For dormancy, overwintering as eggs constituted the young category, followed by adults and nymphs. Bivoltine species were associated with the younger sites, univoltine species with the older ones.

Combinations of two traits

Four of the possible six combinations of two traits showed significant interaction: host plant × phagy ($p < 0.01$), host plant × overwintering ($p = 0.01$), phagy × overwintering ($p < 0.01$), and overwintering × generations ($p = 0.01$). Host plant × generations ($p = 0.22$) and phagy × generations ($p = 0.09$) showed no significant interaction.

Each of the significant combinations exhibited three distinct groups (hereafter: young, intermediate and old group), in three cases there was one additional group between two others (Figure 6.2). However, some combinations did not differ from most others. This was particularly true for many combinations with adult overwinterers. This category exhibited significant differences only in combination with voltinism. Many groups consisted of more than one combination. Apparently, different combinations of young and old categories led to the same reaction to the age gradient. For example, species feeding on grasses (old category) were assigned to the young group if they were polyphagous. Egg overwinterers (young category) were assigned to the old group if they were monophagous, just as polyphagous nymph overwinterers.



- ‘woody plants & oligo’ differs from ‘herbs & oligo/poly’ (I).
- ‘herbs & mono’ differs from III.

- ‘grasses & adult’ differs from I.
- ‘herbs & adult’ differs from III.

- ‘mono & adult’ differs from I.
- ‘oligo & adult’ differs from I and ‘mono & nymph’ (III).
- ‘poly & adult’ differs from ‘mono & nymph’ (III)

Figure 6.2: Significant interactions of two traits. For explanation, see Figure 6.1. Groups without numbers and printed in italics are not different from the groups they stand in between, but from all others. Groups different from only one group or from parts of groups are listed below each plot.

Functional groups

We grouped species with similar patterns of group assignment for trait interactions, and with similar average group assignments. By this, eight groups could be distinguished (Appendix 3, p. 135). After testing for between-group differences, four discrete groups emerged which we will refer to as functional groups.

We divided plots into four age classes (0-2 years; 3-6 years; 7-15 years; 16-40 years) that can be referred to as the ruderal, early-successional, mid-successional and late-successional stage (Brown & Southwood 1987). For each group, we calculated the proportion of observations that it contributed within each age class. Figure 6.3 shows that group I contributed most (approx. 50%) to age class 1, and then decreased. Group II had its highest proportions in age classes 2 and 3, group III in age class 4. Group IV did not show much variation and had low proportions within all age classes. Figure 6.4 depicts another aspect. For each plot, the contribution of each group to the species observations on the plot was calculated. The results are shown as a boxplots for each group within each age class. Even though proportions vary considerably within every age class and group, the same trends as described above are clearly present. Thus, group I is the youngest functional group, group II is intermediate, group III is the oldest group, and group IV is indifferent with respect to site age. The groups differed largely in size, with group I comprising 12% of the species, group II 17%, group III 66% and group IV 5%.

Each group consisted of several combinations (Table 6.1 a), with most combinations (20) assigned to group III. Group I (5 combinations) mostly contained polyphagous

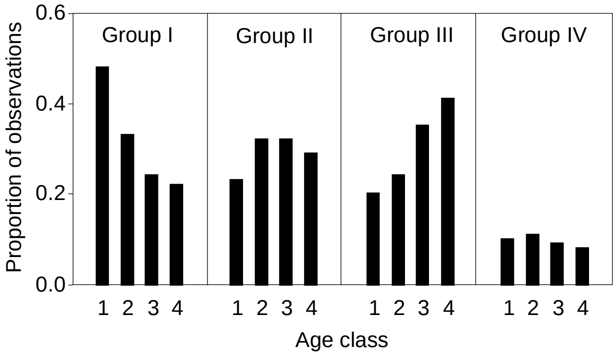


Figure 6.3: Reaction of functional groups (I-IV) to site age. For each functional group, the proportion of observations contributed by each of four age classes is plotted. Age class 1: 0-2 years (62 plots), age class 2: 3-6 years (60 plots), age class 3: 7-15 years (78 plots), age class 4: 16-40 years (46 plots).

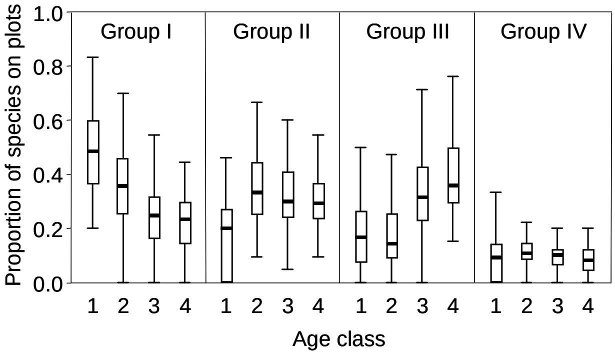


Figure 6.4: Plot-based observations of species belonging to different functional groups (I-IV). For each plot, we calculated the proportion of species belonging to each functional group. These proportions are shown as separate boxplots for each functional group and age class. Boxes show the inter-quartile range, the line inside the boxes represents the median, whiskers are drawn to the nearest value not beyond $1.5\times$ the inter-quartile range. Extreme values are not shown.

and bivoltine species. Species feeding on woody plants, monophagous species and species overwintering as adults never were assigned to that group, no matter with what other categories they were combined. Group II (4 combinations) exclusively contained oligophagous species feeding on grasses or woody plants. Species in group IV (6 combinations) exclusively fed on herbs.

Frequency of trait categories within the species pool

Categories of individual traits

For all four traits, the category frequencies had the same order within the brownfield and the German species pools. However, compared to the German species pool, many categories had significantly higher or lower proportions in the brownfield species (Table 6.2 a). The proportions of species living on herbs (18% vs. 14%) and on grasses/herbs (4% vs. 2%) was slightly, but significantly higher in the brownfield species. There were significantly less monophagous, but more oligophagous and polyphagous species. We found more egg overwinterers, and less adult overwinterers. Fewer species had one

Table 6.1: (a) Brownfield species: assignment of trait category combinations to four functional groups (I-IV). Each group represents different occurrence patterns along the successional gradient of urban brownfields. I = early successional stages, II = intermediate, III = late, IV = indifferent reaction. Blank cells: combinations did not occur in the observed species. **(b)** For each combination, proportion of species pool [%] and proportion of observations [%] are presented. $+$ and $-$ indicate if proportions of observations are significantly more ore less frequent than proportions within the species pool.

			(a) functional groups			**(b) %observations vs. %species**					
gene-rations	over-wintering	host plant type	phagy			phagy					
			mono	oligo	poly	mono		oligo		poly	
		herbs	III	IV	I	0.1	1.5 -	2.1	2.1	6.4	2.6 -
	egg	grasses	III	II	IV	2.2	4.1 -	6.0	5.7	0.2	0.5 -
		woody plants	III	III	III	3.9	14.4 -	0.3	2.1 -	1.2	3.6 -
		herbs			III					0.2	0.5 -
1 gen.	nymph	grasses	III	III		0.1	0.5 -	0.5	2.6 -		
		woody plants			III					1.4	3.1 -
		herbs		IV	IV			1.4	0.5 +	0.5	1.0 -
	adult	grasses	III	II		2.0	2.1	3.6	1.0 +		
		woody plants	III	II	III	0.5	2.6 -	0.1	1.0 -	1.3	0.5 +
		herbs	III	I	I	2.2	4.6 -	5.2	3.6 +	12.3	4.1 +
	egg	grasses	III	II	I	4.0	5.7 -	20.4	9.3 +	5.2	1.0 +
		woody plants	III	III	III	1.4	5.2 -	0.3	3.1 -	0.7	0.5
		herbs		IV				4.7	0.5 +		
2 gen.	nymph	grasses	III	III	III	4.7	6.2 -	1.1	2.1 -	2.0	1.0 +
		woody plants									
		herbs	IV		I	0.8	0.5 +			1.0	0.5 +
	adult	grasses									
		woody plants									

generation, more two generations per year (Table 6.2 a).

Co-occurrence of trait categories

Within the German species pool, there was a number of category combinations that occurred with significantly higher or lower frequency than expected. However, expressed as absolute values, most of these differences were minor (Table 6.3, columns 'Germ.'). The most marked difference was found for the category '2 gen., nymph, grasses, mono.'. It also occurred more frequently within the brownfield species pool (6.3% vs. 1.9%). Mostly, those combinations exhibiting deviations from expected frequencies within the German species showed the same deviations within the brownfield species. However, within the brownfield species, there were additional deviations, with the largest differences for the species with '1 gen., egg, mono.': the species with this combination feeding on herbs, and those feeding on grasses, were less frequent (1.5% vs. 4.1%; 4.1% vs. 7.7%), the ones feeding on woody plant more frequent (14.4% vs. 6.7%). The same was true for '2 gen., egg, grasses, oligo.'.

Frequencies of category combinations differed only little between the brownfield species and all German species (Table 6.3). Most significant differences were small and due to combinations entirely missing within the brownfield species. The largest differences were found for '1 gen., egg, grasses, mono.' (4.1% vs. 13.1% within all German species), '2 gen., egg, grasses, oligo.' (9.3% vs. 3.9%) and '2 gen., egg, herbs, poly.' (4.1% vs. 1.2%).

Table 6.2: **(a)** Distribution [%] of trait categories among the species pool and **(b)** among species observations. $+/-$ indicate significantly ($p \leq 0.05$) higher/lower proportions in the brownfield species pool than in the German species pool (a) or higher/lower proportions within species observations than within the brownfield species pool (b).

	(a) Species pool within			(b) Species observations on brownfield plots	
	Germany	brownfields			
total no. of species / observations	**620**	**194**		**3763**	
host plant type					
• herbaceous plants	14	18	+	20	+
• herbaceous plants and grasses	2	4	+	17	+
• grasses	44	42		52	+
• woody plant (shrubs/trees)	38	36		11	-
phagy (specialization on plant species)					
• monophagous (1 plant species or genus)	59	47	-	22	-
• oligophagous (1 or 2 plant families ***or*** less than 5 species of less than 5 families)	24	34	+	46	+
• polyphagous	14	19	+	32	+
hibernation (overwintering strategy)					
• egg	65	74	+	74	
• nymph	19	16		15	-
• adult	15	10	-	11	+
no. of generations/year					
• univoltine (1 generation/year)	65	52	-	34	-
• bivoltine (2 generations/year)	33	48	+	66	+

Frequency of trait categories within species observations

Categories of individual traits

With one exception (overwintering as egg), all trait categories had different frequencies within observations than within the species pool (Table 6.2 b). In general, those categories that were already more common within the species pool (compared to the German species pool), occurred with significantly higher frequencies. However, this did not apply to the overwintering strategy. 'Adult' was more frequent in the observations, even though it had been less frequent among the species pool. In addition to the trends within the species pool, 'grasses' as host plant were observed more frequently (52% vs. 42%), woody plants less frequently (11% vs. 36%).

With the exception of hibernation, differences were mostly more substantial than those we had found between the species pools (Table 6.2 a & b). For example, monophagous species were by far less frequently observed than found in the species pool (22% vs. 47%). Polyphagous species were much more frequent (32% vs. 19%), as well as bivoltine species (66% vs. 48%).

Functional groups

Group frequencies within observations differed significantly from frequencies within the species pool. Species of group I (30 % of observations vs. 12% in the species pool), group II (31% vs. 17%) and group IV (10% vs. 5%) occurred significantly more often than within the species pool ($p < 0.001$). Species of group III (29% vs. 66%) were observed tremendously less frequently ($p < 0.001$).

With one exception, all combinations of group I were observed more frequently (Table 6.1 b). The largest difference was found for '2 gen., egg, herbs, poly.' (12.3% of

Table 6.3: Combination of trait categories within the German ('Germ.') and the brownfield ('brownf.') species pools. For each combination, expected ('exp.') and observed ('obs.') frequencies [%] are shown. + and – indicate significant deviation of the observed from the expected values. The second column of + and – for the brownfields indicates significant deviations from the German species pool.

gene-rations	over-wintering	host plant type		phagy								
				mono			oligo			poly		
				Germ.	brownf.		Germ.	brownf.		Germ.	brownf.	
1 gen.	egg	herbs	obs.	2.7	1.5 -		1.7	2.1		1.5	2.6	
			exp.	4.4	4.1		1.9	2.6		0.9	1.5	
		grasses	obs.	13.1	4.1 -	-	4.6	5.7		0.2 -	0.5 -	+
			exp.	12.1	7.7		4.9	5.2		2.4	3.1	
		woody plants	obs.	11.9	14.4 +		2.6	2.1 -		2.6	3.6	
			exp.	10.4	6.7		4.3	4.6		2.0	2.6	
	nymph	herbs	obs.	0.2 -	0 -	-	0 -	0 -		0.7	0.5	
			exp.	1.2	1.0		0.5	0.5		0.2	0.5	
		grasses	obs.	2.9	0.5 -	-	2.0	2.6 +		0.2	0 -	-
			exp.	3.4	1.5		1.4	1.0		0.7	0.5	
		woody plants	obs.	0.9 -	0.0 -	-	0.7	0.0 -	-	3.1 +	3.1 +	
			exp.	2.9	1.5		1.2	1.0		0.5	0.5	
	adult	herbs	obs.	0.9	0 -	-	0.7	0.5		0.9	1.0 +	
			exp.	0.9	0.5		0.3	0.5		0.2	0	
		grasses	obs.	3.1	2.1 +		1.4	1.0		0 -	0 -	
			exp.	2.6	1.0		1.0	0.5		0.5	0.5	
		woody plants	obs.	4.3 +	2.6 +		2.2 +	1.0		0.2	0.5	+
			exp.	2.2	1.0		0.9	0.5		0.5	0.5	
2 gen.	egg	herbs	obs.	3.4	4.6		2.0	3.6		1.2	4.1	+
			exp.	2.4	3.6		1.0	2.6		0.5	1.5	
		grasses	obs.	5.3	5.7		3.9	9.3 +	+	0.7	1.0	
			exp.	6.5	6.7		2.7	5.2		1.4	2.6	
		woody plants	obs.	6.3	5.2		2.6	3.1		0.9	0.5	
			exp.	5.6	6.2		2.4	4.1		1.2	2.6	
	nymph	herbs	obs.	0.0 -	0 -		0.2	0.5	+	0 -	-	
			exp.	0.7	0.5		0.2	0.5		0.2		
		grasses	obs.	6.3 +	6.2 +		0.9	2.1		0.3	1.0	+
			exp.	1.9	1.5		0.7	1.0		0.3	0.5	
		woody plants	obs.	0.2 -	0 -	-	0 -	0.0 -		0.3	0 -	-
			exp.	1.5	1.0		0.7	1.0		0.3	0.5	
	adult	herbs	obs.	0.3	0.5		0 -	0 -		0.2	0.5	+
			exp.	0.5	0.5		0.2	0.1		0	0	
		grasses	obs.	0 -	0 -		0.2	0 -	-	0 -	0 -	
			exp.	1.4	1.0		0.5	0.5		0.3	0.5	
		woody plants	obs.	0.2 -	0 -	-	0 -	0 -		0 -	0	
			exp.	1.2	0.5		0.5	0.5		0.2	0	

observations vs. 4.1% of species). Group III contained many species with low prevalences, in particular the combination ‘1 gen., egg, woody plants, mono.’. This combination accounted for 14.4% of species vs. 3.9% of observations. The most abundant combination was ‘2 gen., egg, grasses, oligo.’ from group II. It accounted for 20.4% of all observations vs. 9.3% of species.

6.4 Discussion

Traits and successional age

We could clearly identify trait categories that enable species to colonize brownfield sites faster than others. Polyphagous species of several phytophagous insect taxa are considered and have been shown to be typical pioneers (e.g. Brown & Southwood 1983; Hollier et al. 1994; Nickel & Hildebrandt 2003; Novotny 1995; Statzner et al. 2001). Polyphagous species do not rely on the occurrence of particular food plants, thus they can live and reproduce as soon as any vegetation starts to grow. Vegetation succession on brownfield sites typically starts with annual herbs (Brown & Southwood 1987), thus species feeding on these plants may be quick colonizers. This is even enhanced in leafhopper species that can feed both on herbs and grasses, enabling species to make use of most plants possibly growing during early succession. Perennial grasses only occur later during succession (Brown & Southwood 1987), and so do the species feeding on them. Woody plants establish even later in the successional series, thus a time-lag between the occurrence of species feeding on grasses and those feeding on woody plants might be excepted, but could not be seen in our data. This might be caused by large differences in the pace of tree settlement, depending on soil fertility (Rebele 1992). The trait ŚphagyŠ clearly revealed that the persistence of the host plant influences life histories of phytophagous insects (Denno & Roderick 1991).

Concerning overwintering strategy, our results differed from what others suggested for leafhoppers. Hollier et al. (1994) found that adult and nymph overwinterers were favoured during early succession. Brown (1991) suggests adult overwintering to be favourable during early succession, when food resources are limited and individuals have to disperse in order to locate food. Nymph overwintering Brown (1991) associates with early and mid successional stages, egg overwintering with late succession. Nickel (2003) considered the correlation between overwintering stage and successional stage to be uncertain with a weak evidence for a shift from nymph to adult stage. In our data, however, there was strong evidence for a shift from egg to nymph. Species overwintering as nymphs start feeding early in the season, in February or March. Nymphs of egg overwinterers occur in April or May and thus start feeding much later. Hibernation is therefore correlated with the onset of feeding in spring. As young brownfields are dominated by annual plants (Brown & Southwood 1987), they start to provide food much later than older brownfields dominated by perennials. Thus, egg overwintering is a preferable strategy for young brownfields. The trait category ‘adult’ overall seemed to have less influence than ‘egg’ and ‘nymph’. This might be due to the fact that adults are capable of migrating to suitable habitats for overwintering (Nickel 2003).

In pioneer insect species, life-cycles are shorter (Brown 1991; Brown & Southwood 1983; Frouz et al. 2003). Novotny (1994) found more bivoltine leafhopper species in ephemeral habitats, which is in agreement with our results. Even though some bivoltine leafhopper species show different levels of flight activity between generations (Nickel

2003), two generations per year offer twice the chance to spread. Consequently, the second generation might colonize newly emerged habitat that had been free of vegetation only months earlier. Brown (1991) suggests that the rapid turnover of plant individuals during early succession provides suitable nutrition throughout the growing season, whereas later during succession, host plants may only provide food in a suitable form for a limited period each year.

Functional groups

Many leafhopper species that have been described as pioneers before were indeed assigned to group I, e.g. *Cicadella viridis* or the *Macrosteles* species (Nickel 2003; Novotny 1994). Others, like *Javesella pellucida* or *Laodelphax striatella*, in other studies considered pioneers (Nickel 2003), in our study were placed in group III. These are species known for their flight activity (della Giustina & Balasse 1999; Waloff 1973). Thus, information on flight activity might allow finer grouping. It is obvious that traits influencing dispersal should play an important role during succession, since species need to colonize the newly emerged habitat. Flight capability could be expressed e.g. as the relation of wing and abdomen length or of wing surface area and body weight (Nickel 2003). However, only for few species these data are available. Therefore, wing-dimorphism, i.e. the occurrence of brachypterous individuals, was used as an alternative measure of leafhopper flight capacity by Novotny (1995). In general, brachypterous insect species are expected to increase during succession (Brown & Southwood 1987; Nickel 2003; Novotny 1995). However, the proportions of macropterous and brachypterous individuals within leafhopper species are often variable within and between populations (Nickel 2003). In addition, flight capability is not necessarily a measure of flight activity, a trait widely unknown for most leafhoppers (but see della Giustina & Balasse 1999; Waloff 1973). For this reason, traits concerning dispersal capability were not considered in this study.

Our results made obvious that the pioneer group does not only comprise the 'super-pioneer' (2 gen., egg, herbs, poly.). Other combinations are apparently also suitable for fast colonization. For instance, '1 gen.' is a late category. However, along with the young categories 'egg, herbs, poly.', it allows fast colonization. Trade-offs in traits enable species with different trait combinations to settle successful in the same habitat (Statzner et al. 2001). Still, in our data there were less combinations that allowed fast colonization than combinations that were typical for later successional stages. This might be due to the fact that structural diversity increases during succession (Brown & Southwood 1987), allowing more strategies.

Even though group I comprised only few species, these were overly abundant. This indicates that the studied brownfields overall represented habitats that were particularly suitable for pioneer species. It this context, we note that the combination of all pioneer categories (2 gen., egg, herbs, poly.) was particularly abundant.

Group III contained many species with low prevalences. Even though brownfields obviously offer habitat for many of these species, only a small portion of brownfields is suitable for each particular species. This effect was most pronounced with the combination '1 gen., egg, woody plant, mono.'. This is remarkable, since this combination was so particularly frequent within the species pool. Overall, the low occurrence rates of group I members might indicate that these species are more specialised and thus find suitable habitat only at few locations. Since it was mainly the mono- and oligophagous members of this group that were observed particularly rarely, food plant limitation to a few sites might indeed be an important reason. In general, species of late successional stages (as group III) have smaller niche breadths (Brown & Southwood 1983; Steffan-Dewenter & Tscharntke 2001). Moreover, the species in this group might also be weak dispersers. In this case, they could only reach sites close to a source habitat, but not spread over all suitable brownfield habitats within the limited period of time that these habitats persist.

The most successful combination in brownfields was one of group II: '2 gen., egg, grasses, oligo.'. This combination not only contained more species than expected. It was also particularly frequently observed. This combination seems to be adapted best to the environmental conditions that the sampled brownfield sites provide.

Trait frequencies within the species pool and within species observations

Within the brownfield species pool, the categories associated with the youngest successional age ('young categories') were consistently more frequent than within the German species pool. In both species pools, the young categories for phagy and voltinism were the least frequent, however. It seems that there are only few species adapted to early successional stages, but these occur in large numbers.

One might assume a co-occurrence of certain categories, e.g. that young categories combine more often than young with old ones. For the German species pool, however, this was largely not true, at least not to a great extent. Why '2 gen., nymph, grasses, mono.' was particularly frequent, remains unclear. Grasses might provide particularly suitable habitat for nymph overwintering. In the brownfield species, co-occurrence of categories was slightly more common. Brownfields obviously favour some pioneer combinations (group II: '2 gen., egg, grasses, oligo.', group I: '2 gen., egg, herb, poly.'). Particularly 'slow' combinations were found less frequently (group III: '1 gen., egg, grasses, mono.', '1 gen., nymph, grasses, mono.'). Frequencies within species observations even enhanced this trend. Species exhibiting young traits or assigned to the functional groups I and II were tremendously more frequent.

6.5 Conclusions

(1) For all traits, there were clear successional trends. Pioneer categories were: feeding on herbs, polyphagy, bivoltinism and egg overwintering. The shift from categories associated with young sites to those associated with old ones occurred during the first 10 years of succession.
(2) The occurring 35 combinations of trait categories could be assigned to four functional groups. Groups favoured either early, intermediate or late successional age, one group was indifferent. Grouping might be refined with information on flight capacity and/or activity. This would require extensive data collection.
(3) The brownfield species pool was not a representative sample of the total species pool. Even though we considered sites up to 40 years old, species with pioneer trait categories were overrepresented. This trend was enhanced by species observations. Most observations were due to a few species and category combinations. Thus, even though brownfields offer habitat for many species, most of them only occur on a few, mostly older sites. The variety of trait combinations and thus species living on older brownfields is larger than on young ones, where the same traits and species sets are found on most sites.
(4) There was no large-scale co-occurrence of trait categories. Remarkable exceptions

were high proportion of ‘2 gen., egg, grasses, oligo’ and of ‘1 gen., egg, woody plants, mono’. The former seems to be the most successful strategy on brownfields, comprising 20% of observations. The latter seems to stem from high habitat diversity in brownfields, offering a limited amount of habitat for many different, highly specialised species.
(5) Species with traits that do not allow for fast colonization seem to be less well suited to occupy the potential habitat that brownfields offer.

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Chapter 7

Synthesis & perspective

7.1 Urban brownfields as habitats for phytophagous insects

The results presented in the chapters 3 – 6 clearly revealed that the collective of urban brownfields within a city offers habitat to a wide range of leafhopper and grasshopper species. Roughly one third of the German species pool, both for leafhoppers and grasshoppers (not counting *Tetrix* species and night active species), was present on the study plots. Thus, brownfields are a hotspot of biodiversity. The species pool does not only comprise generalists, but also specialists as well as rare and endangered species (Gemmell & Connell 1984; Gibson 1998). *Oedipoda caerulescens* provides an excellent example. This species suffers from a large-scale loss of its original habitats (Detzel 1998). However, *Oedipoda caerulescens* found a new home in urban brownfields (Ritzau 1985), where it was common in the cities under study.

Habitat conditions on brownfields are diverse (Eversham et al. 1996; Rebele 1992; Schwerk 2000). In the study areas, they range from very open, barely vegetated sites to pre-forest stages dominated by birches, willows or false acacia. This coexistence of different habitat conditions offers suitable habitat for species with very different habitat requirements. Indeed, different species make use of different parts of the vegetational gradient. The community models revealed species that are only present when the vegetation is scarce and low (Chapter 4). Other species prefer medium conditions, whereas some only occur with dense and high vegetation. A number of species occurs over a wide range of conditions, these species can considered to be generalists. Differences in species occurrence along the age gradient can be traced back to biological traits (Chapter 6).

7.2 Driving forces for the species community

It turned out that **vegetation structure** was of outstanding importance in influencing species occurrences. Most species were predominantly influenced by this factor. This is not surprising, since many studies have shown the strong influence of vegetation structure on phytophagous insects before (Fröhlich 1994; Hollier et al. 1994; Kruess & Tscharntke 2002; Morris 2000; Sanderson 1992b). However, the high importance of vegetation structure implies that an individual brownfield, as its vegetation structure changes quickly during succession, offers suitable habitat for a particular species only for a limited period of time. Hence, a species encounters good habitat quality at locations that quickly change, and it has to reach these locations during the limited time, where they offer favourable habitat conditions.

Therefore, the accessibility of a site could be expected to be considerably influenced by the spatial arrangement of brownfield sites. Hence, **landscape context** should be an important factor. However, even though landscape context did play a considerable role, this was not true to the extent that could be assumed. Only few species exhibited strong negative reactions to low proportions of suitable habitat in the surroundings, i. e. to site isolation. This coincides with the results of Wood & Pullin (2002) and Small et al. (2006), who found that butterflies and carabids in urban habitats were limited more by the availability of suitable habitat than by their ability to move among habitat patches.

This comparatively small influence of landscape context might be due to two factors. First, most leafhopper and grasshopper species seem to not depend on large sites to build up viable populations (Biedermann 2002a, 2004; Cronin 2004; Detzel 1998). Thus, they are probably not restricted by site size. Second, it is likely that most brownfield sites are not truly isolated. Tiny patches of potential habitat connecting the larger sites are found in abundance along roads and sidewalks, at the edge of parking lots, on sparsely used outdoor storages, or along tracks.

In this context, it is important to note that the results based on the community model only apply to responsive species. It might well be that species who are more affected by site isolation are so scarce on brownfield sites that they did not pass the prevalence criterion of 10%. Hence, the relationship between such species and landscape context was not analysed within the habitat modelling context. Indeed, results from the trait analyses suggest that species with certain trait categories are less well adapted to fast colonization. For these species, older, nutrient poor sites, that show retarded succession, and sites in the direct vicinity of already existing sites, might be important for maintaining populations (Small et al. 2006).

It seems tempting to equate successional stage with **successional age**, since successional age is so much easier to measure. Indeed, successional age is in this study as well as in others (Rebele & Lehmann 2002; Steffan-Dewenter & Tscharntke 1997) strongly correlated with higher and denser vegetation, increasing litter cover, increasing moss cover, and decreasing proportions of bare soil. However, succession is not as linear as one might expect (Steffan-Dewenter & Tscharntke 2001). 60% of variance explained by site age, as in a study by Hollier et al. (1994), seem to be an exception. Small et al. (2003) and Sanderson (1993) found that the influence of site age was relatively small. Nevertheless, site age is correlated to the occurrence of most species in Berlin and Bremen, even though the influence of site age within the community model is rather week. Overall, age is only a course indicator of the successional stage. Factors like nutrients, parent material and seed bank have a much larger influence on the course of succession (Gibson 1998; Rebele 1992; Rebele & Lehmann 2002). Thus, directly measured vegetation structure is a far better indicator for species occurrence than the indirect measure 'site age'.

7.3 Species diversity & species turnover during succession

In general, since many species are monophagous or oligophagous, the diversity of phytophagous insects depends to some extent on the diversity of plant species. Rebele (1992) proposes a plant species increase on poor soils and during primary succession, but a decrease on rich soils and during secondary succession. However, in an experimental study, Rebele & Lehmann (2002) did not find much change in plant species numbers during five years of succession. On the brownfield sites in Berlin and Bremen that were sampled for my study, there was an overall tendency of highest plant species numbers during mid succession (Schadek 2006). This might imply that the number of phytophagous insects should also be the highest at that time.

In contrast to this, Brown & Southwood (1987) propose highest species numbers of phytophagous insects during mid succession, but suggest that an increase in structural diversity will keep spcies numbers high during late succession. This largely resembles the findings in this work. Considering model predictions, numbers of leafhoppers and grasshoppers do not change much after a quick raise at the beginning of succession (Chapter 4). Correlating total species numbers (not only responsive species) to site age gives a similar picture. Spearman's *rho* indicates a species increase for leafhoppers in time ($rho = 0.58, p < 0.001$). The scatter plot of site age vs. species numbers (Figure 7.1) reveals that this increase largely occurs during the first five years of succession.

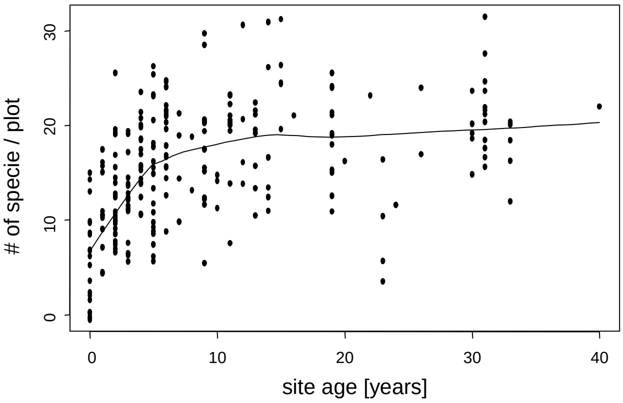

Figure 7.1: Scatter plot of number of leafhopper species per plot vs. site age. The trend line was fitted with a local regression ('loess') using the Splus function 'scatter.smooth'.

However, this pattern might not be the same for other taxa. Steffan-Dewenter & Tscharntke (1997) did not find any change in butterfly species numbers during the first four years of old field succession.

Results of the trait analyses (Chapter 6) suggest that a different view on species numbers might be necessary. The vast majority of species belongs to the functional group III which is associated with high successional age. Most of these group III species occur with very low prevalences. Thus, when taking into account not the per plot species diversity, but rather the diversity over all plots of one successional age class, results might be different. However, these numbers largely resemble the 'quick rise at the beginning' scheme: For leafhoppers, total number of species present on the pioneer sites (0-2 years) is 94, on young sites (3-6 years) 112, on medium sites (7-15 years) 150, and on old sites (>15 years) 148. For details, see Appendix 5, p. 140. Thus, numbers are low at the pioneer and young sites, but then remain constant. Nevertheless, it seems that high total numbers of species might be reached slightly later than high per plot numbers, where changes occur mostly within the first five years.

30 of the 94 species present at the pioneer sites were not present at any of the old sites. Most of these were present at the first three age stages. Only 8 species were confined to the youngest sites (Appendix 5, p. 140). These might be considered pioneer species that disappear during succession. On the other hand, 63 species were only present on the medium and/or old sites, 24 of these were restricted to the old sites. This enhances the findings of the trait analyses that there are by far more late successional specialists than early successional specialists (Chapter 6). This result most likely reflects the wider habitat diversity that can be found on older sites. These sites are often characterized by a small scale mosaic of open grassland and groups of trees and shrubs. Whether this habitat diversity levels out after very long periods of time, cannot be answered here.

Overall, results indicate that changes in species richness are less important than species turnover, i. e. changes in species composition. This is true both for an individual site and for all sites of the same successional age. This has been shown for old field successions before, particularly during early succession (Brown et al. 1992; Purtauf et al. 2004; Steffan-Dewenter & Tscharntke 1997). Hence, species turnover seems to be the key to the high species diversity found on brownfields. There is no particular successional stage which is by far more species rich than the others. It is rather the coexistence of different successional stages and brownfields of different origin that enables the high habitat diversity which in return leads to high biodiversity. The youngest sites are home to the relatively fewest species, and few species are restricted to these sites. However, as young successional stages are generally absent or difficult to maintain within traditional nature reserves (Eversham et al. 1996), brownfields play an important role in providing such habitats.

7.4 Why are many species so rare?

Despite the fact that the brownfield species pool is remarkably rich, most species are not common within brownfields. Certainly, most species survey data exhibit some species with very low occurrence frequencies. For leafhoppers, this is an ubiquitous phenomenon in the field. Nickel (2003) recorded up to 25% of immigrant species occurring as single specimens. In the brownfield data, such species are likely present as well. Species recorded with one specimen on one site in one year, but not in the next, can be regarded as such ‘tourists’ (Appendix 1, p. 131).

However, there are many species present in both years with very low frequencies. Why is that? On one hand, there might be species that indeed find suitable habitats in brownfields and build up populations there. But due to weak dispersing abilities, they are not colonizing all suitable habitats. On the other hand, some species might have special habitat requirements that are met on a few brownfields only. The latter is the case for many species living on certain tree species, which are restricted to a few, mostly old sites. Examples are *Viridicerus ustulatus*, living on *Populus alba*, or *Tremulicerus tremulae*, living on *Populus tremula*.

In this context, it is important to note that most of the occurring red list species are very rare. This might pose a serious threat to the idea that brownfields could offer a save harbour for species loosing habitat elsewhere. If a species occurs on only one or two out of 250 plots, this seems somewhat random. If this particular brownfield site is lost, then the species is lost. For these rare species, it would be important to collect more data to find out if they are regular colonizers of brownfields and what kind of brownfields they settle on.

7.5 Habitat models

Implications from habitat models

Habitat models based on logistic regression and presence/absence data were suitable to describe species occurrences and to reveal the driving forces shaping the brownfield communities. The main purpose in this work was to provide a predictive model that can be used to assess (1) species assemblage under given environmental conditions, (2) the influence of main environmental driving factors, and (3) the generality of the species-environment relationships. Such an explanatory approach needs to simultaneously consider all possible models (Mac Nally 2000). This was achieved in an elegant way by model averaging. The approach allowed an individual set of environmental factors for each species. In order to obtain the best possible models, this is crucial. This is particularly important for landscape context. Different species use landscapes differently and at different scales, making it difficult to abstract landscape properties in a way that makes sense for all species (Burgman et al. 2005).

However, if species are to be predicted in areas where their presence is not known, these models are less suitable. They are complex and make use of all the data that were available in this study. It is unlikely that such a variety of environmental data is available for other areas. On the other hand, the model averaging approach can easily be modified in the way that only models with certain subsets of variables – ones that are available – are considered. In Chapter 3 (Strauss & Biedermann 2005), I demonstrated how a single, simple model can be used to predict presence/absence over a whole area. However, such models might be weaker, and models might pass the minimum performance criteria for less species.

A promising approach to obtain environmental variables for large areas are satellite data (Rushton et al. 2004). From these, both local and landscape scale factors can be derived (e. g. Eyre et al. 2005b; Gibson et al. 2004c; Osborne et al. 2001). Applying such an approach to brownfields might allow easier predictions without expensive data collection on the ground. However, this matter needs some investigation to clarify if the small scale vegetation structure that the studied insects react to could be extracted from satellite data. In any case, it is likely that satellite derived data are less direct variables, and that species reactions are therefore harder to interpret, and that the resulting models might be less general.

Model performance

Overall, the models had satisfying quality. They were well in the performance range that other studies achieved (e. g. Olden 2003; Peppler-Lisbach & Schröder 2004). This good performance might be considered to be in contrast to the central ecological assumption that static statistical models only work well for species that are in equilibrium with the environment (Austin 2002; Guisan & Zimmermann 2000), and that modelling species in disequilibrium using static models is problematic (Gibson et al. 2004c). For urban communities, which are mostly in a state of disequilibrium, theories based on equilibrium could be assumed to be inadequate (Rebele 1994). However, obviously the models successfully predicted species presences.

In this context, I suggest that the responsive species are species that response quickly to environmental changes. They are able to reach a large portion of suitable sites, but are hardly present before or after conditions are favourable for them. Thus, these species might be in equilibrium despite their changing environment. Species with slower reactions exhibit a time lag between emergence of suitable habitat and colonization. I propose that these species were either to rare to be modelled, or their species-habitat relationships were masked by their absence from suitable habitat. In the latter case, they appeared to be not responsive. Some of these species might reveal their environmental needs only when dynamic models are used, that include information on population processes (Wilson et al. 2005). Such models, however, require data that are manifold more tedious, costly and time consuming to collect (Elith & Burgman 2003).

Model generality

Transferability of models between the study areas as well as in time was mostly good (5). On the other hand, it also became obvious that it is important to always test transferability before drawing general conclusions from a model or before applying it to a different area. Even good models might only be good for the data they base on. Models for eurytopic species need to be handled with particular care. Relationships found for such species may well be confined to a particular data set. Since such species usually have high prevalences, many of them are candidates for model building, and some will indeed be responsive to the data. Within a region, the resulting models might be valid, but general inference should not be drawn from them.

There is some indication that reactions to landscape context and soil parameters are more region specific than those to vegetation structure. In other words, direct variables exhibit more general relationships than indirect ones (Vaughan & Ormerod 2003). Research on testing the transferability of responses to landscape structure has rarely been undertaken (Fisher et al. 2005). It turned out to be a major problem to dichotomise predictions when models are applied to new data. There does not seem to be an easy way to find an appropriate threshold, unless information on species prevalences is available. In general, it seems best to not dichotomise such predictions, and to treat them as ranked occurrence probabilities or habitat suitability rather than as absolute numbers.

In the context of model transferability and generality, Graf et al. (2006) point out another promising approach for obtaining general models that might also be successful for the brownfield species. In their study, they used models for capercailzie built on data pooled from several regions. These models classified data in each single region almost as well as models that were based exclusively on data from each region. Furthermore, they were a lot more valid for the other regions than the single region models. This approach is restricted to species that occur in different study regions, but so is the testing of model transferability used in Chapter 5. This is a general problem for testing model transferability. Only a very small proportion of species were responsive in both study areas, allowing the testing of transferability in space (see Table 7.1 and Appendix 4, p. 139).

7.6 Species traits

A serious drawback for the use of habitat models is that they are restricted to the more common species, and within those, to the ones that are responsive to the measured environmental factors. This resulted in that only about 20% of the species, both in Bremen and in Berlin, could be modelled. These represented about 50% of the observations (58% in Bremen, 49% in Berlin). Only 10 of the species models could be checked for their transferability in space. Obviously, the faunas of the two study areas are considerably different. This makes it hard to detect general patterns by the use of habitat models.

At this point, trait analyses provided a powerful tool. The biological characteristics of species that are associated with different parts of the age gradient could be revealed (Chapter 6). This also moved away from the question ‘which species are found at which parts of the gradient’, to ‘why are these species found at certain parts of the gradient’. For this purpose, habitat models are far less suited, since it is not easy to infer the underlying processes from the patterns detected by statistical models (Tyre et al. 2001). However, it is hard to compare between different taxa, and a large number of species is necessary to obtain meaningful results. Therefore, grasshopper occurrences could not be assessed within this framework.

For leafhoppers, I could identify trait categories (1 generation/year, egg overwintering, polyphagy, feeding on herbs) that were associated with young successional age. By using combinations of trait categories, I was able to assign species to one of four distinct functional groups. These groups exhibited different reactions with respect to the age gradient and comprised a pioneer group, an intermediate group, a late successional

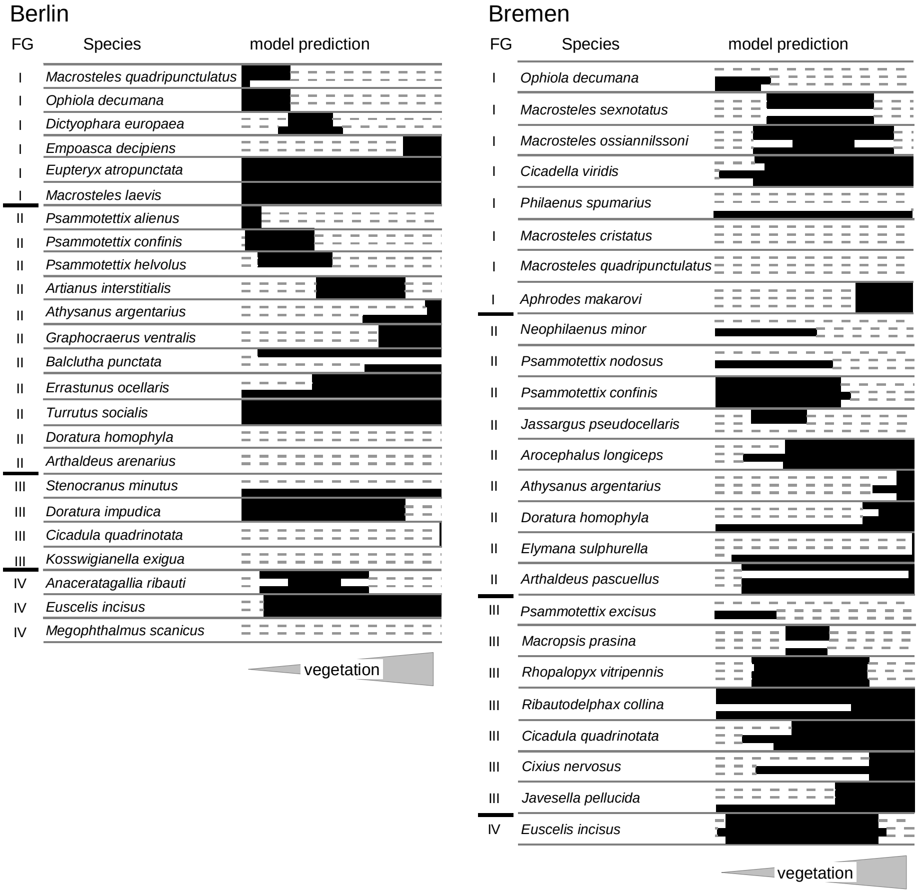

Figure 7.2: Assignment of responsive species to functional groups ('FG') according to their traits, in comparison to their predicted reaction to the vegetation gradient ('model prediction'). For details of the vegetation gradient, see Chapter 4, Figures 4.5 & 4.6, pp. 52 & 53.

group, and an indifferent group.

Model predictions vs. functional group assignment

However, the assignment to functional groups only gives a simplified picture. On the species level, it is inferior to a species-based modelling approach. This becomes obvious when inspecting Figure 7.2, where functional group assignment is compared to species occurrence along the vegetational gradient, as predicted by the habitat models. It would be expected that model predictions for group I species, for instance, are restricted to the left part of the vegetation gradient (scarce and low vegetation).

For some species, group assignment and model prediction agree well, e. g. *Macrosteles quadripunctulatus* (group I), *Psammotettix helvolus* (group II) in Berlin, *Cixius nervosus* (group III) in Bremen, *Euscelis incisus* (group IV) in Berlin and Bremen. Still, most species occur at other sections of the vegetational gradient than the group assignment implies. One possible reason for this deviation is that the vegetational gradient is not equal to the age gradient. However, more important is probably that the functional group approach is only a course framework that compares how species with certain trait categories occur *on average* on the age gradient. Deviations of individual species from this average can be considerable. Thus, additional traits would be required in order to allow a finer group assignment. This would require extensive data collection, since key traits that describe e. g. the dispersal ability are not known for most species. In addition, approaches considering several traits and several environmental factors at the same time, would certainly lead to more precise results. Statistical methods for this purpose are not well developed. RLQ, a three-table ordination technique (Choler 2005; Ribera et al. 2001), considers several traits and environmental factors, but does not lead to a clear grouping of species.

It is important to note that the average site age for the ‘oldest’ trait category is mostly around 10 years (Chapter 6). It is likely that there is a group of species that occurs later. However, there was no statistically significant evidence for this, a finding that might be due to the scare occurrence data on these species. Thus, group III comprises species with a wide span of site age preferences, ranging from mid to late successional.

Modelling success vs. functional group assignment

The highest proportion of responsive species was found within groups I and II, the pioneer and the intermediate group (Table 7.1). These groups contained far less species than group III, but a much higher proportion passed the prevalence criterion of 10% for habitat modelling (14 of 23 species in group I, 20 of 33 in group II, but only 27 of 128 in group III). From these species, the majority was responsive in groups I (10 species) and II (16 species), whereas only about one third (10 species) in group III. I assume that the trait categories of groups I and II, which allow the fast colonization of new habitat, result in an occupancy of most suitable habitat patches. This leads to presence/absence data that can be successfully grasped by regression methods. On the other hand, species with combinations of trait categories that are associated with old site age, are largely determined not only by the quality of the habitat, but by their ability to reach it. Exceptions are group III species with high dispersal abilities. The occurrence of these group III species can be modelled. However, most group III species are either too rare to be modelled, or their species-environment relationships are weak. The overall lower prevalence of the group III species, also of those that could be modelled, gives some support for the former. Also note that the modelling success for the group III species is particularly poor for the Berlin data. Apparently, low prevalence in combination with a small data set provides a difficult base for detecting significant relationships. Therefore, larger datasets might be able to support significant models for more of these species. Details for the modelling success for each species are given in Appendix 4, p. 139.

7.7 Preserving the diversity of urban brownfields

Not all species find habitat on brownfields. It has been proposed that three responses to urbanization can be found: species not present (or at significantly lower abundance) in urban environments, species present only (or at higher abundance) in urban environments, and species present in both rural and urban sittings with no particular affinity for either (Kirby 1984; McIntyre 2000; McKinney 2002). Thus, brownfield species are not a random sample of the regional species pool, not all species have the same chance to find suitable habitat on brownfields. Chapter 6 provided strong evidence that species with pioneer trait categories are more abundant within the brownfield species pool and occur with higher frequencies.

Table 7.1: Overview of number of species in total, number passing the modelling prevalence criterion (10%), and number of responsive species. Numbers are given for the total of Bremen and Berlin species ('total'), species present only in Bremen (Br), species present only in Berlin (Be), and species present both in Bremen and Berlin (Br & Be).

		# of species		
		total	prevalence > 10%	responsive
FG I	total	23	14	10
	Br / Be / Br&Be	17 / 19 / 13	10 / 12 / 7	7 / 6 / 1
FG II	total	33	20	16
	Br / Be / Br&Be	27 / 21 / 15	14 / 14 / 9	10 / 11 / 4
FG III	total	128	27	10
	Br / Be / Br&Be	95 / 84 / 51	13 / 18 / 7	7 / 4 / 1
FG IV	total	10	7	3
	Br / Be / Br&Be	7 / 6 / 3	4 / 6 / 3	1 / 3 / 1

Apparently, some species do not deal well with the characteristics of urban brownfields. In contrast to semi-natural habitats, brownfields are continually being generated and destroyed in the normal course of urban renewal and redevelopment, and as fashions and the needs of industry change. However, those species that *do* live on brownfields largely depend on this repeated renewal, since they use only part of the successional gradient. Brownfields are species rich not despite their high spatial and temporal variability, but because of it. Local extinction of species, unavoidably going along with this variability, is typical for urban habitats (Rebele 1994).

It is obvious that biodiversity in urban brownfields cannot be maintained by traditional ways of nature conservation, i. e. by permanently protecting some particularly species rich sites from economic use. This would not allow the full variety of species, at least not without heavy management. However, for a number of species, it might be favourable to allow some sites a longer than usual development. In general, late successional stages are very rare (Rebele 1994). More old stages would offer additional habitat for species depending on late stages. Of particular value might be very nutrient poor sites that exhibit a retarded development. These can be colonised by species that are slow colonizers, but depend on early- or mid-successional stages (Small et al. 2006).

Preserving, or even enlarging the biodiversity in urban brownfields requires 'imaginative solutions to encourage derelict land to be allowed to develop good habitats while maintaining the cycle and spatial relations of its production and renewal' (Gibson 1998). This thesis aimed to provide insight into the mechanisms of species survival in these habitats. The work provides an empirical and scientific base for new approaches in city development, approaches that encourage the creation as well as the re-use of brownfields, namely in a pattern that creates species rich temporary habitats.

Summary

Summary

Urban brownfields (derelict sites) offer a wide range of habitat conditions and are home to a variety of species. Brownfield habitats change quickly in time (due to succession), and in space (due to deconstruction and redevelopment). Species colonizing brownfields have to constantly track suitable habitat. This thesis aimed to provide insight into the mechanisms of species survival in these habitats. The results provide an empirical and scientific base for approaches in city development that help in preserving, or even enlarging, the biodiversity in urban brownfields.

I investigated two taxa of **phytophagous insects**, leafhoppers and grasshoppers. Species presence/absence was recorded on a total of 250 plots in the cities of Bremen and Berlin, Germany. Bremen was covered in 2003 and 2004, Berlin in 2004 only. I detected a total of 17 grasshopper species and 214 leafhopper species. For each plot, I recorded **environmental variables**: local factors (site age, vegetation structure, soil parameters), and landscape context.

A large focus of this thesis was **habitat modelling**. Within this framework, I could study several aspects. First, I demonstrated the use and application of habitat models for the conservation of **rare and endangered species**. Models can be used to provide habitat suitability maps. With such maps, suitable habitat for a species can be identified. This requires environmental data to be available on the landscape scale.

Next, I built habitat models for **all species** in the community that had a prevalence of at least 10%. This was the case for 74 species, 6 of which were grasshoppers. I used a model averaging approach instead of searching for a single best model. For each species, I averaged several good models. 45 species (39 leafhoppers, 6 grasshoppers) were responsive, i. e. their habitat models exceeded the minimum performance criteria in one or both cities. Different species showed different reactions on an environmental gradient from scarce and low to dense and high vegetation. Along this gradient, species composition changed largely, whereas species numbers remained rather constant after a first quick raise. Moreover, the model averaging enabled me to assess the **influence of each environmental factor** on the species community. The results revealed that most species were predominantly determined by vegetation structure, followed by landscape context, soil parameters and site age. For most species, local factors were the most important. Only few species were strongly influenced by landscape context, even though some showed clear negative reactions to low proportions of brownfields in the surroundings. Site age turned out to be only a course indicator of the successional stage. Qualitative comparison of the Bremen and Berlin models indicated that vegetation structure variables were more directly related to species occurrences and thus more general than landscape context variables and soil parameters.

Prior to making general inferences or predictions from habitat models, their **generalizability** requires thorough assessment. For this purpose, I transferred models in time and space. The 30 Bremen models, built basing on the 2003 data, I applied to the 2004 data. For the 10 species that were responsive in both cities, I tested model transferability in space: I applied the Bremen models to the Berlin data, and the Berlin models to the Bremen 2003 and the Bremen 2004 data. Most transfers (28 of 30 in time, 27 of 30 in space) were successful. This means that occupied sites within the test data were assigned significantly higher occurrence probabilities than unoccupied sites. The good transferability had three important drawbacks: (1) Models were mostly not well calibrated to the test data, thus predicted occurrence probabilities may not be used as absolute values, but as ordinal ranks. (2) Model fit to the test data often decreased considerably compared to the training data. (3) dichotomising occurrence probabilities to presence/absence mostly results in considerable misclassification. A meaningful threshold to separate predicted presences from absences cannot be achieved without information on the prevalence of a species.

The modeling approach cannot reveal the biological reasons for species using different parts of the successional gradient. In order to achieve insight here, I analyzed four **biological traits** of all 194 leafhopper species that were present in the Bremen 2003 and Berlin 2004 data. I studied four categorical traits: host plant type, phagy, dormancy and voltinism. First, I considered the total of 3763 species observations. Using the 'fourth corner' method, I analysed changes in trait category frequencies with **increasing successional age**. Trait categories showed clear successional trends. Young successional stages were related to feeding on herbs, polyphagy, egg overwintering and 2 generations/year. Analysing combinations of two traits allowed the assignment of species to four functional groups: species associated with young, intermediate and old sites, and one group indifferent to site age. The pioneer group contained the least number of species, but the highest number of observations. These findings only reflected trends, and they only considered site age. Hence, agreement between functional group assignment of species and model predictions of single species models was mostly poor. Still, it became obvious that mostly species of the young and intermediate group could be modelled. Therefore, the influence of the environmental factors, as assessed by the habitat models, is mostly valid for these groups.

I analysed the distribution of trait categories within (1) the brownfield **species pool** vs. the German species pool and (2) species observations. I could show that trait categories associated with young site age were overrepresented in the brownfield species pool. Moreover, within this already biased species pool, species with pioneer trait categories occurred with higher frequency.

In conclusion, the major findings were that the insect community is not static along the successional gradient. Many species show clear preferences for certain successional stages. Thus, maintaining the regional species pool of a city requires a mosaic of all successional stages. The typical brownfield species profit from and depend on the continuous generation and destruction. On the other hand, results also suggest that many species are less suited to the dynamics of their habitat. Those might profit from some older and well connected sites.

Zusammenfassung

Stadtbrachen bieten eine Vielfalt unterschiedlicher Lebensräume und werden von einer Vielzahl von Arten bewohnt. Brachehabitate sind von schnellen Veränderungen geprägt, und zwar sowohl von zeitlichen Veränderungen (durch Sukzession), als auch von räumlichen Veränderungen (durch Neuentstehung bzw. Zerstörung von Freiflächen durch Abriss bzw. Wiederbebauung). Arten, die Brachen besiedeln, müssen ständig aufs Neue für sie günstige Habitatbedingungen aufspüren. Das Ziel der vorliegenden Arbeit war es, ein besseres Verständnis dafür zu gewinnen, wie Arten in solchen Habitaten überleben. Die Ergebnisse bieten eine empirische und wissenschaftliche Grundlage für Ansätze in der Stadtentwicklungsplanung, welche die Biodiversdiät auf Brachflächen erhalten oder sogar vergrößern.

Ich untersuchte Zikaden und Heuschrecken, zwei Gruppen **phytophager Insekten**. Die Präsenz/Absenz der Arten erfasste ich auf 250 Untersuchungsflächen in Bremen und Berlin. Bremen wurde 2003 und 2004 bearbeitet, Berlin nur 2004. Insgesamt konnte ich 17 Heuschrecken- und 214 Zikadenarten nachweisen. Außerdem erfasste ich an jeder Probefläche verschiedene **Umweltvariablen**: lokale Variablen (Flächenalter, Vegetationsstruktur, Boden) sowie den Landschaftskontext.

Ein Schwerpunkt dieser Arbeit lag auf der **Habitatmodellierung**. In diesem Rahmen konnte ich verschieden Aspekte untersuchen. Zuerst zeigte ich Nutzen und Anwendung von Habitatmodellen für den Schutz seltener und **gefährdeter Arten**. Die Modelle können zur Erstellung von Habitateignungskarten benutzt werden, mit deren Hilfe die für eine Art geeigneten Habitate abgegrenzt werden können. Dies setzt ein flächiges Vorliegen der entsprechenden Umweltvariablen voraus.

Als nächstes erstellte ich Habitatmodelle für **alle Arten**, die eine Prävalenz von mindestens 10% aufwiesen. Dies traf für 74 Arten zu, von denen 6 Heuschrecken waren. Im Zuge der Modellierung verwendete ich das ‚Model Averaging', anstatt nach einem einzigen besten Modell zu suchen. Dabei bildete ich für jede Art den Durchschnitt aus mehreren guten Modellen. Die Vorkommen von 45 Arten (39 Zikaden, 6 Heuschrecken) zeigten einen signifikanten Zusammenhang zu den Umweltparametern, d.h. die Qualität der Habitatmodelle für diese Arten erfüllte bestimmte Mindestanforderungen in einer oder in beiden Städten. Die verschiedenen Arten zeigten unterschiedliche Reaktionen auf dem Gradienten von schütterer und niedriger zu dichter und hoher Vegetation. Dabei änderte sich die Artzusammensetzung entlang des Gradienten stark, während die Artenzahl nach einem schnellen Anstieg ziemlich konstant blieb.

Darüber hinaus ermöglichte das Model Averaging, den **Einfluss jeder Umweltvariable** auf die Artengemeinschaft abzuschätzen. Die Ergebnisse zeigten, dass die meisten Arten hauptsächlich von der Vegetationsstruktur beeinflusst wurden, gefolgt von Landschaftskontext, Boden und Flächenalter. Für die meisten Arten waren lokale Parameter wichtiger. Nur wenige Arten wurden sehr stark vom Landschaftskontext beeinflusst. Einige Arten zeigten jedoch deutlich negative Reaktionen auf geringe Flächenanteile von Brachflächen in der Umgebung. Es stellte sich heraus, dass das Flächenalter nur ungefähre Rückschlüsse auf das Sukzessionsstadium ermöglicht. Ein qualitativer Vergleich der Bremer und Berliner Modelle deutete darauf hin, dass Vegetationssturkurparameter direkter mit dem Artvorkommen verknüpft sind und deswegen allgemeingültiger sind als Landschaftskontext und Boden.

Bevor auf Grundlage von Habitatmodellen Rückschlüssen gezogen oder Vorhersagen getroffen werden, ist es nötig, deren **Allgemeingültigkeit** zu überprüfen. Zu diesem

Zweck habe ich die Modelle in Raum und Zeit übertragen. Die 30 Bremer Modelle, die auf den Daten von 2003 basierten, wendete ich auf die Daten von 2004 an. Für die 10 Arten, für die in beiden Städten Modelle vorlagen, überprüfte ich außerdem die räumliche Übertragbarkeit. Hierfür wendete ich die Bremer Modelle auf die Berliner Daten an, und die Berliner Modelle auf die Bremer Daten sowohl von 2003 als auch von 2004. Die meisten Modellübertragungen (28 von 30 in der Zeit, 27 von 30 im Raum) waren erfolgreich. Das bedeutet, dass den besiedelten Flächen signifikant höhere Vorkommenswahrscheinlichkeiten zugewiesen wurde als den unbesiedelten. Diese gute Übertragbarkeit hatte drei wichtige Einschränkungen: (1) Die Modelle waren nicht gut an die Testdaten angepasst. Das bedeutet, dass die vorhergesagten Vorkommenswahrscheinlichkeiten nicht als absolute Werte verwendet werden dürfen, sondern nur als Rangwerte. (2) Die Vorhersage für die Testdaten war oft deutlich schlechter als für die Trainingsdaten. (3) Eine Trennung der Vorkommenswahrscheinlichkeiten in Vorkommen und Nichtvorkommen führt oft zu beträchtlichen Fehlklassifizierungen. Ein guter Schwellenwert zur Trennung zwischen Vorkommen und Nichtvorkommen kann nur gefunden werden, wenn Informationen zur Prävalenz einer Art zur Verfügung stehen.

Der Modellierungsansatz ist nicht im Stande, die biologischen Gründe offen zu legen, aufgrund derer die Arten unterschiedliche Bereiche des Sukzessionsgradienten nutzen. Um diese Frage zu beantworten, analysierte ich vier **biologische Merkmale (Traits)** aller 194 Zikadenarten, die in den Bremer Daten von 2003 und in den Berliner Daten vorkamen. Ich untersuchte vier kategoriale Merkmale: Art der Nährpflanze, Nährpflanzenspezialisierung, Überwinterung und Generationenzahl. Zuerst betrachtete ich die 3763 Beobachtungen von Arten auf den Probeflächen. Mit Hilfe der ‚Fourth Corner' Methode analysierte ich Veränderungen in den Häufigkeiten der Merkmalskategorien bei zunehmendem **Sukzessionsalter**. Die Merkmalskategorien zeigten deutliche Tendenzen. Junge Sukzessionsstadien standen im Zusammenhang mit Kräutern als Nährpflanze, Polyphagie, Ei-Überwinterung und zwei Generationen pro Jahr. Die Analyse von Kombinationen aus zwei Traits erlaubte es, die Arten in vier funktionelle Gruppen einzuteilen: (1) Arten junger Flächen, (2) Arten mittelalter Flächen, (3) Arten älterer Flächen, sowie (4) eine Gruppe von Arten, die nicht auf das Flächenalter reagierte. Diese Ergebnisse spiegelten jedoch nur Trends wieder, und sie berücksichtigen auch nur das Flächenalter. Deswegen stimmten die Gruppenzuordnung und die Modellvorhersagen der Einzelartmodelle oft nicht gut überein. Es wurde jedoch deutlich, dass es hauptsächlich die Arten der jungen und der mittleren Gruppe waren, für die Modelle gebildet werden konnten. Dies bedeutet, dass der Einfluss der verschiedenen Umweltfaktoren hauptsächlich für diese Arten Gültigkeit besitzt.

Zudem untersuchte ich die Verteilung von Merkmalsausprägungen (1) innerhalb des Brachflächen-**Artenpools** im Vergleich zum deutschen Artenpool, und (2) innerhalb der Beobachtungen. Ich konnte zeigen, dass Merkmalsausprägungen, die mit jungem Flächenalter korreliert waren, innerhalb der Brachearten überdurchschnittlich häufig vertreten waren. Außerdem kamen von den Arten dieses somit ohnehin schon verzerrten Artenpools die Arten besonders häufig vor, die Pioniermerkmale aufwiesen.

Zusammenfassend lässt sich sagen, dass die Artengemeinschaft sich entlang des Sukzessionsgradienten nicht statisch verhält. Viele Arten zeigen eine deutliche Präferenz für bestimmte Sukzessionsstadien. Deswegen ist für die Erhaltung des regionalen Artenpools einer Stadt ein Nebeneinander aller Sukzessionsstadien nötig. Die typischen Brachearten profitieren und sind abhängig vom ständigen Entstehen und Verschwinden von Flächen. Andererseits geben die Ergebnisse auch Hinweise darauf, dass viele Arten weniger gut mit der Dynamik ihres Lebensraums zurechtkommen. Diese Arten könnten von einigen älteren und gut verbundenen Flächen profitieren.

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Appendix

Appendix 1: Leafhoppers: Red list status (RL), prevalence (plots # = no. of occupied plots), and number of specimens per plot (Σ = total, minimum, median, maximum) for all species. Red list categories: 1 = critically endangered, 2 = endangered, 3 = vulnerable, V = near threatened, R = rare, G = status unknown, possibly threatened, D = data deficient.

Species	RL	Berlin					Bremen 2003					Bremen 2004				
		plots	specimens				plots	specimens				plots	specimens			
		#	Σ	min	med	max	#	Σ	min	med	max	#	Σ	min	med	max
Acanthodelphax denticauda (Boh.)	3											2	2	1	1	1
Acanthodelphax spinosa (Fieb.)		5	8	1	1	4	5	39	2	3	26	4	6	1	1	3
Agallia brachyptera (Boh.)							1	1	1	1	1					
Aguriahana stellulata (Burm.)							2	2	1	1	1					
Alebra albostriella (Fall.)		2	7	2	4	5	8	29	1	2	8	2	2	1	1	1
Allygidius atomarius (F.)	3	1	1	1	1	1										
Allygidius commutatus (Fieb.)							1	1	1	1	1					
Allygus mixtus (F.)		2	3	1	2	2	3	4	1	1	2	1	1	1	1	1
Allygus modestus (Scott)		1	1	1	1	1										
Alnetoidia alneti (Dhlb.)												5	7	1	1	2
Anaceratagallia ribauti (Oss.)		54	174	1	1	26						1	1	1	1	1
Anaceratagallia venosa (Geoffr.)	V						7	17	1	2	6	4	9	1	1	6
Anoscopus albifrons (L.)							1	1	1	1	1	1	2	2	2	2
Anoscopus flavostriatus (Don.)							1	1	1	1	1					
Anoscopus serratulae (F.)							3	4	1	1	2	11	39	1	1	17
Aphrodes bicincta (Schrk.)							29	76	1	1	21	24	93	1	2	18
Aphrodes diminuta (Rib.)	3											1	1	1	1	1
Aphrodes makarovi (Zachv.)		66	464	1	4	53	23	44	1	1	8	37	99	1	1	21
Aphrophora alni (Fall.)		15	28	1	1	4	1	1	1	1	1					
Aphrophora pectoralis (Mats.)							1	1	1	1	1					
Aphrophora salicina (Goeze)							1	1	1	1	1					
Arocephalus languidus (Fl.)	3	1	1	1	1	1										
Arocephalus longiceps (Kbm.)							75	653	1	2	181	33	103	1	1	17
Arocephalus punctum (Fl.)							6	9	1	2	2	4	5	1	1	2
Arthaldeus arenarius (Rem.)		10	12	1	1	3	5	9	1	1	3	1	1	1	1	1
Arthaldeus pascuellus (Fall.)		8	39	1	1	27	73	809	1	4	89	46	349	1	2	212
Artianus interstitialis (Germ.)		30	166	1	2	31	1	1	1	1	1	2	2	1	1	1
Asiraca clavicornis (F.)	3	9	12	1	1	2										
Athysanus argentarius (Metc.)		20	28	1	1	5	31	78	1	1	9	13	16	1	1	2
Balclutha punctata (F.)		51	216	1	3	20	17	28	1	1	4	23	35	1	1	8
Cercopis vulnerata (Rossi)		1	1	1	1	1	8	25	1	2	10	5	5	1	1	1
Chloriona glaucescens (Fieb.)	3						2	3	1	2	2					
Chlorita paolii (Oss.)		86	2894	1	12	421	7	9	1	1	2	37	140	1	2	23
Cicadella viridis (L.)		24	33	1	1	5	105	1136	1	3	259	36	66	1	1	7
Cicadula flori (J.Shlb.)	V						7	34	1	6	11	1	2	2	2	2
Cicadula frontalis (H.-S.)	V											1	1	1	1	1
Cicadula persimilis (Edw.)							7	73	1	3	35	3	3	1	1	1
Cicadula quadrinotata (F.)		14	64	1	1	26	41	648	1	3	145	16	94	1	3	19
Cicadula saturata (Edw.)	3						1	1	1	1	1					
Circulifer haematoceps (M. & R.)	R	11	21	1	1	7										
Cixius cambricus (China)	2	3	15	0	4	8										
Cixius nervosus (L.)		5	7	1	1	2	24	38	1	1	9	13	13	1	1	1
Conomelus anceps (Germ.)							12	75	1	1	31	3	12	1	2	9
Conosanus obsoletus (Kbm.)		1	2	2	2	2	5	7	1	1	2					
Criomorphus albomarginatus (Curt.)		1	2	2	2	2	8	12	1	1	3	1	1	1	1	1
Deltocephalus pulicaris (Fall.)		2	11	1	6	10	1	2	2	2	2	3	3	1	1	1
Dicranotropis hamata (Boh.)		28	90	1	2	19										
Dictyophara europaea (L.)	3	41	723	1	3	164										
Dikraneura variata (Hardy)		5	5	1	1	1	15	68	1	1	18	4	16	1	4	8
Doratura homophyla (Fl.)		17	30	1	1	4	35	157	1	3	20	17	25	1	1	7
Doratura impudica (Horv.)	2	21	52	1	3	8	16	86	1	4	19	1	1	1	1	1
Doratura stylata (Boh.)												8	11	1	1	3
Edwardsiana avellanae (Edw.)	D											1	2	2	2	2
Edwardsiana crataegi (Dgl.)							1	1	1	1	1					
Edwardsiana flavescens (F.)							1	1	1	1	1					
Edwardsiana prunicola (Edw.)		1	1	1	1	1										
Edwardsiana rosae (L.)		1	2	2	2	2										
Edwardsiana salicicola (Edw.)							4	5	1	1	2	3	3	1	1	1
Edwardsiana sociabilis (Oss.)	D	2	6	1	3	5										
Edwardsiana tersa (Edw.)							1	1	1	1	1					
Elymana sulphurella (Zett.)		3	4	1	1	2	20	44	1	1	18	7	12	1	1	4
Emelyanoviana mollicula (Boh.)		1	1	1	1	1						3	3	1	1	1
Empoasca decipiens (Paoli)		30	597	1	5	226	8	41	1	2	28	11	41	1	1	20
Empoasca pteridis (Dhlb.)		64	923	1	7	171	3	5	1	1	3	5	6	1	1	2
Empoasca vitis (Göthe)		29	288	1	5	47	19	58	1	2	22	7	12	1	1	3
Errastunus ocellaris (Fall.)		56	599	1	6	49	37	497	1	5	80	35	152	1	1	55
Erzaleus metrius (Fl.)		1	1	1	1	1	1	1	1	1	1					
Euides basilinea (Germ.)	V	1	1	1	1	1	1	1	1	1	1					
Eupelix cuspidata (F.)		3	5	1	2	2	5	27	1	3	10	7	7	1	1	1

Appendix 1 (continued).

Species	RL	Berlin					Bremen 2003					Bremen 2004				
		plots	specimens				plots	specimens				plots	specimens			
		#	Σ	min	med	max	#	Σ	min	med	max	#	Σ	min	med	max
Eupteryx adspersa (H.-S.)	R	1	1	1	1	1										
Eupteryx atropunctata (Goeze)		30	282	1	3	126	2	2	1	1	1	2	2	1	1	1
Eupteryx aurata (L.)		2	7	3	4	4	11	24	1	1	12	2	4	1	2	3
Eupteryx calcarata (Oss.)		15	983	1	1	787										
Eupteryx curtisii (Fl.)		1	1	1	1	1										
Eupteryx decemnotata (R.)	2	4	13	1	1	10										
Eupteryx florida (Rib.)		5	8	1	1	4										
Eupteryx notata (Curt.)							2	4	1	2	3					
Eupteryx stachydearum (Hardy)												1	1	1	1	1
Eupteryx tenella (Fall.)	3	5	17	1	1	12										
Eupteryx urticae (F.)							1	1	1	1	1					
Eupteryx vittata (L.)							2	4	1	2	3					
Eurhadina pulchella (Fall.)		1	3	3	3	3	6	18	1	2	8	4	5	1	1	2
Eurybregma nigrolineata (Scott)		2	10	1	5	9	1	1	1	1	1	1	1	1	1	1
Eurysa lineata (Perr.)		2	7	3	4	4						1	1	1	1	1
Eurysula lurida (Fieb.)							4	5	1	1	2					
Euscelidius schenckii (Kbm.)		18	51	1	1	21										
Euscelidius variegatus (Kbm.)	V	2	12	1	6	11	11	19	1	1	3	4	5	1	1	2
Euscelis incisus (Kbm.)		63	638	1	6	50	112	736	1	3	128	78	335	1	3	20
Fagocyba carri (Edw.)		1	1	1	1	1										
Fagocyba cruenta (H.-S.)		9	23	1	1	9	16	67	1	2	22	23	84	1	1	37
Fieberiella septentrionalis (W.Wg.)		6	7	1	1	2	4	4	1	1	1	1	1	1	1	1
Florodelphax leptosoma (Fl.)	V						1	1	1	1	1	1	1	1	1	1
Gargara genistae (F.)		1	1	1	1	1										
Graphocephala fennahi (Young)							1	1	1	1	1					
Graphocraerus ventralis (Fall.)		36	134	1	3	16	21	103	1	1	42	10	24	1	2	8
Haematoloma dorsatum (Ahr.)												1	1	1	1	1
Hesium domino (Reut.)		9	9	1	1	1										
Hyledelphax elegantula (Boh.)							4	24	1	4	15	1	2	2	2	2
Iassus lanio (L.)		1	1	1	1	1	1	1	1	1	1					
Idiocerus herrichii (Kbm.)	3	2	4	1	2	3						2	2	1	1	1
Idiocerus lituratus (Fall.)							1	2	2	2	2	2	2	1	1	1
Idiocerus similis (Kbm.)												1	1	1	1	1
Idiocerus stigmaticalis (Lew.)							4	4	1	1	1	2	2	1	1	1
Idiocerus vicinus (Mel.)							2	4	1	2	3					
Issus coleoptratus (F.)	V	1	1	1	1	1										
Jassargus pseudocellaris (Fl.)							25	907	1	4	155	12	109	1	8	38
Javesella dubia (Kbm.)							6	46	1	4	21	1	1	1	1	1
Javesella forcipata (Boh.)	3	3	4	1	1	2										
Javesella obscurella (Boh.)							4	4	1	1	1					
Javesella pellucida (F.)		13	25	1	2	4	34	110	1	2	15	15	25	1	1	7
Kelisia monoceros (Rib.)	2	3	13	1	4	8										
Kelisia sabulicola (W.Wg.)	3	1	1	1	1	1	30	332	1	1	112	14	48	1	2	11
Kosswigianella exigua (Boh.)		10	40	1	1	19	37	8027	1	3	2919	22	795	1	3	329
Kyboasca bipunctata (Osh.)	1						1	1	1	1	1					
Kybos butleri (Edw.)							1	1	1	1	1	1	1	1	1	1
Kybos lindbergi (Lnv.)		1	1	1	1	1										
Kybos populi (Edw.)												1	1	1	1	1
Kybos rufescens (Mel.)							10	208	1	5	94	7	88	1	1	72
Kybos smaragdula (Fall.)		7	17	1	1	7	7	31	1	2	16	6	13	1	2	5
Kybos strigilifer (Oss.)		1	3	3	3	3	7	57	1	2	37	1	1	1	1	1
Kybos virgator (Rib.)		2	39	8	20	31	9	41	1	5	8					
Laburrus impictifrons (Boh.)	2	1	6	6	6	6										
Laodelphax striatella (Fall.)		14	37	1	1	10	14	15	1	1	2	1	3	3	3	3
Liguropia juniperi (Leth.)							1	1	1	1	1					
Limotettix striola (Fall.)							3	5	1	1	3	2	2	1	1	1
Linnavuoriana decempunctata (Fall.)	3											2	3	1	2	2
Linnavuoriana sexmaculata (Hardy)		3	10	1	1	8	1	2	2	2	2	1	2	2	2	2
Macropsis cerea (Germ.)							9	20	1	1	7	5	12	1	1	6
Macropsis fuscinervis (Boh.)												1	5	5	5	5
Macropsis fuscula (Zett.)		2	2	1	1	1	2	2	1	1	1	1	1	1	1	1
Macropsis graminea (F.)		1	2	2	2	2	1	2	2	2	2					
Macropsis gravesteini (W.Wg.)	R						4	10	1	2	6					
Macropsis infuscata (J.Shlb.)							2	3	1	2	2	1	2	2	2	2
Macropsis notata (Proh.)	3	4	5	1	1	2	1	3	3	3	3					
Macropsis ocellata (Prov.)							6	24	1	3	9					
Macropsis prasina (Boh.)							19	186	1	3	89	5	6	1	1	2
Macropsis scutellata (Boh.)		1	5	5	5	5										
Macropsis viridinervis (W.Wg.)	2											4	16	1	5	6

Appendix 1 (continued).

Species	RL	Berlin					Bremen 2003					Bremen 2004				
		plots	specimens				plots	specimens				plots	specimens			
		#	Σ	min	med	max	#	Σ	min	med	max	#	Σ	min	med	max
Macrosteles cristatus (Rib.)							26	123	1	1	26	8	23	1	2	9
Macrosteles frontalis (Scott)	3						4	13	2	3	6					
Macrosteles horvathi (W.Wg.)							6	23	1	2	12					
Macrosteles laevis (Rib.)		59	1188	1	7	190	94	867	1	3	81	23	85	1	2	13
Macrosteles lividus (Edw.)	2	1	1	1	1	1										
Macrosteles maculosus (Then)	3	18	77	1	3	11										
Macrosteles ossiannilssoni (Ldb.)	3						65	373	1	2	41	9	28	1	3	6
Macrosteles quadripunctulatus (Kbm.)	3	33	229	1	2	47	58	680	1	7	53	22	205	1	6	55
Macrosteles septemnotatus (Fall.)												2	9	3	5	6
Macrosteles sexnotatus (Fall.)		13	21	1	1	4	66	399	1	1	122	10	18	1	1	6
Macrosteles variatus (Fall.)		3	91	1	12	78										
Megadelphax sordidula (Stål)		5	12	1	1	8	14	184	1	4	109	8	12	1	1	4
Megophthalmus scanicus (Fall.)		13	18	1	1	3	30	88	1	2	24	22	43	1	1	6
Metidiocerus elegans (Fl.)		1	1	1	1	1										
Metidiocerus rutilans (Kbm.)		3	4	1	1	2	2	2	1	1	1					
Micantulina stigmatipennis (M. & R.)	3	1	12	12	12	12										
Mirabella albifrons (Fieb.)	3	5	6	1	1	2										
Mocuellus collinus (Boh.)		22	115	1	2	47	16	52	1	1	17	8	17	1	1	6
Mocydiopsis parvicauda (Rib.)		1	1	1	1	1	8	31	1	1	22					
Muellerianella fairmairei (Perr.)	D						1	1	1	1	1					
Muirodelphax aubei (Perr.)	D	11	45	1	1	21	1	1	1	1	1					
Neoaliturus fenestratus (H.-S.)	3	12	16	1	1	3	18	53	1	1	11	10	12	1	1	3
Neophilaenus campestris (Fall.)		4	5	1	1	2										
Neophilaenus lineatus (L.)							6	6	1	1	1	1	1	1	1	1
Neophilaenus minor (Kbm.)	V						25	358	1	8	54	24	381	1	8	75
Oncopsis alni (Schrk.)												1	1	1	1	1
Oncopsis appendiculata (W.Wg.)	3	1	1	1	1	1	2	5	1	3	4					
Oncopsis avellanae (Edw.)	R											1	3	3	3	3
Oncopsis carpini (J.Shlb.)												2	2	1	1	1
Oncopsis flavicollis (L.)		6	52	1	3	31	7	54	1	6	31	7	22	1	2	7
Oncopsis subangulata (J.Shlb.)		2	4	1	2	3	5	14	1	2	7	6	9	1	1	3
Ophiola decumana (Kontk.)		32	81	1	1	10	56	236	1	3	16	29	70	1	2	8
Ophiola transversa (Fall.)	3	1	2	2	2	2										
Orientus ishidae (Mats.)		11	13	1	1	3										
Paluda flaveola (Boh.)		19	30	1	1	6	3	11	1	1	9	3	4	1	1	2
Paralimnus phragmitis (Boh.)	V											1	1	1	1	1
Philaenus spumarius (L.)		18	28	1	1	6	63	262	1	1	20	59	141	1	1	14
Populicerus confusus (Fl.)		1	1	1	1	1	4	4	1	1	1					
Populicerus nitidissimus (H.-S.)		1	5	5	5	5										
Populicerus populi (L.)		3	7	2	2	3	14	32	1	1	8	2	2	1	1	1
Psammotettix alienus (Dhlb.)		50	253	1	4	26	11	12	1	1	2	1	1	1	1	1
Psammotettix confinis (Dhlb.)		42	272	1	4	49	113	1716	1	11	82	109	1156	1	6	78
Psammotettix excisus (Mats.)	3						16	244	1	9	50	11	66	1	3	18
Psammotettix helvolus (Kbm.)		44	489	1	4	55						18	37	1	1	7
Psammotettix kolosvarensis (Mats.)	3	10	20	1	1	8										
Psammotettix nodosus (Rib.)							72	668	1	4	68	25	48	1	1	6
Psammotettix poecilus (Fl.)	2	5	20	1	2	11										
Rhopalopyx adumbrata (C.Shlb.)							5	12	1	1	7	2	2	1	1	1
Rhopalopyx preyssleri (H.-S.)		3	3	1	1	1	3	3	1	1	1	1	1	1	1	1
Rhopalopyx vitripennis (Fl.)	3	12	27	1	2	5	33	660	1	9	121	30	269	1	4	104
Rhytidodus decimusquartus (Schrk.)		1	1	1	1	1	3	3	1	1	1					
Rhytistylus proceps (Kbm.)	3						3	3	1	1	1	4	9	1	2	5
Ribautiana tenerrima (H.-S.)		1	5	5	5	5	5	6	1	1	2	1	1	1	1	1
Ribautodelphax albostriata (Fieb.)		6	24	1	1	18	2	3	1	2	2	2	2	1	1	1
Ribautodelphax collina (Boh.)		1	2	2	2	2	42	470	1	2	167	12	34	1	2	8
Ribautodelphax pungens (Rib.)												2	2	1	1	1
Speudotettix subfusculus (Fall.)		1	1	1	1	1	13	29	1	1	6	4	11	1	3	4
Stenocranus major (Kbm.)							5	16	1	4	5	2	2	1	1	1
Stenocranus minutus (F.)		23	180	1	2	100	8	133	1	1	122					
Streptanus aemulans (Kbm.)							3	3	1	1	1					
Streptanus marginatus (Kbm.)		1	11	11	11	11	2	8	4	4	4					
Streptanus sordidus (Zett.)							2	2	1	1	1					
Tachycixius pilosus (Ol.)							6	34	2	6	8	4	7	1	1	4
Thamnotettix dilutior (Kbm.)		1	1	1	1	1										
Tremulicerus distinguendus (Kbm.)		4	11	2	3	4	4	5	1	1	2					
Tremulicerus tremulae (Estl.)							2	8	1	4	7	3	3	1	1	1
Tremulicerus vitreus (F.)		3	5	1	2	2						1	2	2	2	2
Turrutus socialis (Fl.)		29	362	1	3	65										
Typhlocyba quercus (F.)							2	2	1	1	1	3	4	1	1	2
Verdanus abdominalis (F.)												1	1	1	1	1
Viridicerus ustulatus (M. & R.)		5	11	1	2	3	3	4	1	1	2	2	6	2	3	4
Xanthodelphax straminea (Stål)	3						21	47	1	2	8	6	7	1	1	2
Zygina angusta (Leth.)							2	6	2	3	4	1	2	2	2	2
Zygina hyperici (H.-S.)		30	178	1	1	67	6	7	1	1	2	22	140	1	2	58
Zygina schneideri (Günth.)		1	1	1	1	1										
Zyginidia scutellaris (H.-S.)							67	249	1	2	21	65	204	1	1	17

Appendix 2: Grasshoppers: Red list status (RL), prevalence (no. of occupied plots, Br = Bremen, Be = Berlin) and success of habitat modelling (‘m. Br’ = model Bremen, ‘m. Be’ = model Berlin). Red list categories: 1 = critically endangered, 2 = endangered, 3 = vulnerable, V = near threatened. Modelling results: x = species was responsive, – = species was not responsive. Species with prevalence <10% (no modelling attempt) are marked grey.

Species	RL	Br03	Br04	Be	m. Br03	m. Be
Chortippus albomarginatus (De Geer)		41	34	20	-	-
Chortippus apricarius (Linné)	V	2	1	34	▨	-
Chortippus biguttulus (Linneé)		130	124	12	x	-
Chortippus brunneus (Thunberg)		105	125	80	-	-
Chortippus dorsatus (Zetterstedt)		2	1	43	▨	x
Chortippus mollis (Charpentier)	V	62	46	72	x	x
Chortippus parallelus (Zetterstedt)		1	5	5	▨	▨
Chrysochraon dispar (Germar)				8	▨	-
Metrioptera roeseli (Hagenbach)		22	34	29	x	-
Metrioptera bicolor (Philippi)				59	▨	x
Myrmelotettix maculatus (Thunberg)		44	79		x	▨
Oedipoda caerulescens (Linné)	3	34	37	48	x	x
Omocestus haemorrhoidalis (Charpentier)	V			3	▨	▨
Omocestus viridulus (Linneé)				2	▨	▨
Pholidoptera griseoaptera (De Geer)		3			▨	▨
Platycleis albopunctata (Goeze)	V			29	▨	-
Sphingonotus caerulans (Linné)	2			1	▨	▨

Appendix 3: Leafhopper species and their occurrence frequencies, traits, group classifications for combinations of 2 traits (1=ťyoung’, 2=ťintermediate’, 3=ťold’ successional stages), and overall allocation into four functional groups (I-IV), representing different occurrence patterns along the successional gradient of urban brownfields. RL = red list status (see Appendix 1).

RL	Species name	frequency [no. of plots] Bremen	frequency [no. of plots] Berlin	no. of generations	overwintering strategy	host plant type	phagy	phagy x overwintering	host plant x phagy	generations x overwintering	host plant x overwintering	average trait combination group
	Group I: Species of early successional stages. Mostly 'young' trait combinations. 23 species, 1131 observations											
	Aphrodes makarovi	23	66	1	egg	herbs	polyphagous	1	1	2	1	1.3
	Chlorita paolii	7	86	2	egg	herbs	oligophagous	2	1	1	1	1.3
	Cicadella viridis	105	24	2	egg	grasses	polyphagous	1	1	1	2	1.3
3	*Dictyophara europaea*		41	1	egg	herbs & grasses	polyphagous	1	1	2	1	1.3
	Emelyanoviana mollicula		1	2	egg	herbs	polyphagous	1	1	1	1	1.0
	Empoasca decipiens	8	30	2	adult	herbs	polyphagous	NA	1	1.5	NA	1.3
	Empoasca pteridis	3	64	2	egg	herbs	polyphagous	1	1	1	1	1.0
	Eupteryx atropunctata	2	30	2	egg	herbs	polyphagous	1	1	1	1	1.0
	Eupteryx aurata	11	2	2	egg	herbs	polyphagous	1	1	1	1	1.0
	Eupteryx curtisii		1	2	egg	herbs	oligophagous	2	1	1	1	1.3
2	*Eupteryx decemnotata*		4	2	egg	herbs	oligophagous	2	1	1	1	1.3
	Eupteryx florida		5	2	egg	herbs	oligophagous	2	1	1	1	1.3
	Eupteryx notata	2		2	egg	herbs	oligophagous	2	1	1	1	1.3
	Eupteryx vittata	2		2	egg	herbs	oligophagous	2	1	1	1	1.3
	Euscelidius schenckii		18	1	egg	herbs	polyphagous	1	1	2	1	1.3
V	*Euscelidius variegatus*	11	2	1	egg	herbs	polyphagous	1	1	2	1	1.3
	Macrosteles cristatus	26		2	egg	herbs & grasses	polyphagous	1	1	1	1	1.0
	Macrosteles laevis	94	59	2	egg	herbs & grasses	polyphagous	1	1	1	1	1.0
3	*Macrosteles ossiannilssoni*	65		2	egg	grasses	polyphagous	1	1	1	2	1.3
3	*Macrosteles quadripunctulatus*	58	33	2	egg	herbs & grasses	polyphagous	1	1	1	1	1.0
	Macrosteles sexnotatus	66	13	2	egg	herbs & grasses	polyphagous	1	1	1	1	1.0
	Ophiola decumana	56	32	2	egg	herbs	oligophagous	2	1	1	1	1.3
	Philaenus spumarius	63	18	1	egg	herbs & grasses	polyphagous	1	1	2	1	1.3
	Group II: Species of intermediate successional stages. Mostly in 'intermediate' group. 33 species, 1177 observations											
	Anoscopus albifrons	1		1	egg	grasses	oligophagous	2	2	2	2	2.0
	Anoscopus flavostriatus	1		1	egg	grasses	oligophagous	2	2	2	2	2.0
	Anoscopus serratulae	3		1	egg	grasses	oligophagous	2	2	2	2	2.0
3	*Arocephalus languidus*		1	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Arocephalus longiceps	75		2	egg	grasses	oligophagous	2	2	1	2	1.8
	Arthaldeus pascuellus	73	8	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Artianus interstitialis	1	30	1	egg	grasses	oligophagous	2	2	2	2	2.0
	Athysanus argentarius	31	20	1	egg	grasses	oligophagous	2	2	2	2	2.0
	Balclutha punctata	17	51	1	adult	grasses	oligophagous	NA	2	2	NA	2.0
	Conosanus obsoletus	5	1	1	egg	grasses	oligophagous	2	2	2	2	2.0
	Deltocephalus pulicaris	1	2	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Dikraneura variata	15	5	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Doratura homophyla	35	17	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Elymana sulphurella	20	3	1	egg	grasses	oligophagous	2	2	2	2	2.0
	Errastunus ocellaris	37	56	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Graphocraerus ventralis	21	36	1	egg	grasses	oligophagous	2	2	2	2	2.0
	Jassargus pseudocellaris	25		2	egg	grasses	oligophagous	2	2	1	2	1.8
	Limotettix striola	3		2	egg	grasses	oligophagous	2	2	1	2	1.8
	Mocuellus collinus	16	22	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Neophilaenus campestris		4	1	egg	grasses	oligophagous	2	2	2	2	2.0
V	*Neophilaenus minor*	25		1	egg	grasses	oligophagous	2	2	2	2	2.0
	Paluda flaveola	3	19	1	egg	grasses	oligophagous	2	2	2	2	2.0
	Psammotettix alienus	11	50	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Psammotettix confinis	113	42	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Psammotettix helvolus		44	2	egg	grasses	oligophagous	2	2	1	2	1.8
3	*Psammotettix kolosvarensis*		10	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Psammotettix nodosus	72		2	egg	grasses	oligophagous	2	2	1	2	1.8
	Streptanus aemulans	3		2	egg	grasses	oligophagous	2	2	1	2	1.8
	Streptanus sordidus	2		2	egg	grasses	oligophagous	2	2	1	2	1.8
	Turrutus socialis		29	2	egg	grasses	oligophagous	2	2	1	2	1.8
	Zygina angusta	2		1	adult	woody plants	oligophagous	NA	NA	2	1.5	1.8
	Zygina schneideri		1	1	adult	woody plants	oligophagous	NA	NA	2	1.5	1.8
	Zyginidia scutellaris	67		1	adult	grasses	oligophagous	NA	2	2	NA	2.0

Appendix 3 (continued).

RL	Species name	frequency [no. of plots] Bremen	frequency [no. of plots] Berlin	no. of generations	overwintering strategy	host plant type	phagy	phagy x overwintering	host plant x phagy	generations x overwintering	host plant x overwintering	average trait combination group
	Group III: Species of old successional stages. At least one combination is '3'. 128 species, 1090 observations.											
	IIIa: "young" and "old" categories											
	Cercopis vulnerata	8	1	1	nymph	herbs & grasses	polyphagous	3	1	3	1	2.0
	Eupteryx adspersa		1	2	egg	herbs	monophagous	3	NA	1	1	1.7
	Eupteryx calcarata		15	2	egg	herbs	monophagous	3	NA	1	1	1.7
3	*Eupteryx tenella*		5	2	egg	herbs	monophagous	3	NA	1	1	1.7
	Eupteryx urticae	1		2	egg	herbs	monophagous	3	NA	1	1	1.7
3	*Macrosteles frontalis*	4		2	egg	herbs	monophagous	3	NA	1	1	1.7
3	*Macrosteles maculosus*		18	2	egg	herbs	monophagous	3	NA	1	1	1.7
	Macrosteles variatus		3	2	egg	herbs	monophagous	3	NA	1	1	1.7
3	*Micantulina stigmatipennis*		1	2	egg	herbs	monophagous	3	NA	1	1	1.7
	Zygina hyperici	6	30	2	egg	herbs	monophagous	3	NA	1	1	1.7
	IIIb: 'young', 'intermediate' and 'old' categories											
	Aguriahana stellulata	2		1	egg	woody plants	polyphagous	1	2.5	2	3	2.1
	Allygidius commutatus	1		1	egg	woody plants	polyphagous	1	2.5	2	3	2.1
	Allygus mixtus	3	2	1	egg	woody plants	polyphagous	1	2.5	2	3	2.1
	Allygus modestus		1	1	egg	woody plants	polyphagous	1	2.5	2	3	2.1
	Aphrophora alni	1	15	1	egg	woody plants	polyphagous	1	2.5	2	3	2.1
	Arocephalus punctum	6		2	egg	grasses	monophagous	3	3	1	2	2.3
V	*Cicadula flori*	7		2	egg	grasses	monophagous	3	3	1	2	2.3
	Cicadula persimilis	7		2	egg	grasses	monophagous	3	3	1	2	2.3
	Cicadula quadrinotata	41	14	2	egg	grasses	monophagous	3	3	1	2	2.3
	Edwardsiana crataegi	1		2	egg	woody plants	oligophagous	2	NA	1	3	2.0
	Edwardsiana flavescens	1		2	egg	woody plants	oligophagous	2	NA	1	3	2.0
	Edwardsiana prunicola		1	2	egg	woody plants	oligophagous	2	NA	1	3	2.0
	Edwardsiana rosae		1	2	egg	woody plants	oligophagous	2	NA	1	3	2.0
	Edwardsiana salicicola	4		2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Edwardsiana sociabilis		2	2	egg	woody plants	oligophagous	2	NA	1	3	2.0
	Edwardsiana tersa	1		2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Empoasca vitis	19	29	1	adult	woody plants	polyphagous	NA	2.5	2	1.5	2.0
	Erzaleus metrius	1	1	2	egg	grasses	monophagous	3	3	1	2	2.3
	Fagocyba carri		1	2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Fagocyba cruenta	16	9	2	egg	woody plants	polyphagous	1	2.5	1	3	1.9
	Fieberiella septentrionalis	4	6	1	egg	woody plants	polyphagous	1	2.5	2	3	2.1
3	*Idiocerus herrichii*		2	1	adult	woody plants	monophagous	NA	2.5	2	1.5	2.0
	Idiocerus vicinus	2		1	adult	woody plants	monophagous	NA	2.5	2	1.5	2.0
	Javesella pellucida	34	13	2	nymph	grasses	polyphagous	3	1	2	3	2.3
1	*Kyboasca bipunctata*	1		2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Kybos butleri	1		2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Kybos lindbergi		1	2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Kybos rufescens	10		2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Kybos smaragdula	7	7	2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Kybos strigilifer	7	1	2	egg	woody plants	monophagous	3	2.5	1	3	2.4
	Kybos virgator	9	2	2	egg	woody plants	monophagous	3	2.5	1	3	2.4
2	*Laburrus impictifrons*		1	1	egg	herbs	monophagous	3	NA	2	1	2.0
	Laodelphax striatella	14	14	2	nymph	grasses	polyphagous	3	1	2	3	2.3
	Liguropia juniperi	1		1	adult	woody plants	monophagous	NA	2.5	2	1.5	2.0
	Macropsis scutellata		1	1	egg	herbs	monophagous	3	NA	2	1	2.0
	Macrosteles horvathi	6		2	egg	grasses	monophagous	3	3	1	2	2.3
2	*Macrosteles lividus*		1	2	egg	grasses	monophagous	3	3	1	2	2.3
	Metidiocerus rutilans	2	3	1	adult	woody plants	monophagous	NA	2.5	2	1.5	2.0
	Muellerianella fairmairei	1		2	egg	grasses	monophagous	3	3	1	2	2.3
3	*Ophiola transversa*		1	1	egg	herbs	monophagous	3	NA	2	1	2.0
	Orientus ishidae		11	1	egg	woody plants	polyphagous	1	2.5	2	3	2.1
3	*Psammotettix excisus*	16		2	egg	grasses	monophagous	3	3	1	2	2.3
2	*Psammotettix poecilus*		5	2	egg	grasses	monophagous	3	3	1	2	2.3
3	*Rhopalopyx vitripennis*	33	12	2	egg	grasses	monophagous	3	3	1	2	2.3
	Ribautiana tenerrima	5	1	2	egg	woody plants	oligophagous	2	NA	1	3	2.0
	Viridicerus ustulatus	3	5	1	adult	woody plants	monophagous	NA	2.5	2	1.5	2.0

Appendix 3 (continued).

RL	Species name	frequency [no. of plots] Bremen	frequency [no. of plots] Berlin	no. of generations	overwintering strategy	host plant type	phagy	phagy x overwintering	host plant x phagy	generations x overwintering	host plant x overwintering	average trait combination group
	Alebra albostriella	8	2	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
3	*Allygidius atomarius*		1	1	egg	woody plants	oligophagous	2	NA	2	3	2.3
	Aphrophora pectoralis	1		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Aphrophora salicina	1		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Arthaldeus arenarius	5	10	1	egg	grasses	monophagous	3	3	2	2	2.5
3	*Cicadula saturata*	1		1	egg	grasses	monophagous	3	3	2	2	2.5
	Conomelus anceps	12		1	egg	grasses	monophagous	3	3	2	2	2.5
	Criomorphus albomarginatus	8	1	1	nymph	grasses	oligophagous	2	2	3	3	2.5
	Dicranotropis hamata		28	2	nymph	grasses	oligophagous	2	2	2	3	2.3
2	*Doratura impudica*	16	21	1	egg	grasses	monophagous	3	3	2	2	2.5
	Eurhadina pulchella	6	1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Eurybregma nigrolineata	1	2	1	nymph	grasses	oligophagous	2	2	3	3	2.5
	Eurysa lineata		2	1	nymph	grasses	oligophagous	2	2	3	3	2.5
	Gargara genistae		1	1	egg	woody plants	oligophagous	2	NA	2	3	2.3
	Graphocephala fennahi	1		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Hesium domino		9	1	egg	woody plants	oligophagous	2	NA	2	3	2.3
	Hyledelphax elegantula	4		2	nymph	grasses	oligophagous	2	2	2	3	2.3
	Iassus lanio	1	1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Idiocerus lituratus	1		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Idiocerus stigmaticalis	4		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Javesella dubia	6		2	nymph	grasses	oligophagous	2	2	2	3	2.3
3	*Javesella forcipata*		3	1	nymph	grasses	oligophagous	2	2	3	3	2.5
	Javesella obscurella	4		2	nymph	grasses	oligophagous	2	2	2	3	2.3
2	*Kelisia monoceros*		3	1	egg	grasses	monophagous	3	3	2	2	2.5
3	*Kelisia sabulicola*	30	1	1	adult	grasses	monophagous	NA	3	2	NA	2.5
	Linnavuoriana sexmaculata	1	3	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Macropsis cerea	9		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Macropsis fuscula	2	2	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Macropsis graminea	1	1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Macropsis gravesteini	4		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Macropsis infuscata	2		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
3	*Macropsis notata*	1	4	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Macropsis ocellata	6		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Macropsis prasina	19		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Metidiocerus elegans		1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Mocydiopsis parvicauda	8	1	1	adult	grasses	monophagous	NA	3	2	NA	2.5
3	*Oncopsis appendiculata*	2	1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Oncopsis flavicollis	7	6	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Oncopsis subangulata	5	2	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Populicerus confusus	4	1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Populicerus nitidissimus		1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Populicerus populi	14	3	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Rhopalopyx adumbrata	5		1	egg	grasses	monophagous	3	3	2	2	2.5
	Rhopalopyx preyssleri	3	3	1	egg	grasses	monophagous	3	3	2	2	2.5
	Rhytidodus decimusquartus	3	1	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
3	*Rhytistylus proceps*	3		1	egg	grasses	monophagous	3	3	2	2	2.5
	Stenocranus major	5		1	adult	grasses	monophagous	NA	3	2	NA	2.5
	Stenocranus minutus	8	23	1	adult	grasses	monophagous	NA	3	2	NA	2.5
	Streptanus marginatus	2	1	1	nymph	grasses	oligophagous	2	2	3	3	2.5
	Tremulicerus distinguendus	4	4	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Tremulicerus tremulae	2		1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Tremulicerus vitreus		3	1	egg	woody plants	monophagous	3	2.5	2	3	2.6
	Typhlocyba quercus	2		1	egg	woody plants	oligophagous	2	NA	2	3	2.3

Appendix 3 (continued).

RL	Species name	frequency [no. of plots] Bremen	frequency [no. of plots] Berlin	no. of generations	overwintering strategy	host plant type	phagy	phagy x overwintering	host plant x phagy	generations x overwintering	host plant x overwintering	average trait combination group
	IIId: mainly 'old' category combiantions											
	Acanthodelphax spinosa	5	5	2	nymph	grasses	monophagous	3	3	2	3	2.8
3	*Chloriona glaucescens*	2		2	nymph	grasses	monophagous	3	3	2	3	2.8
2	*Cixius cambricus*		3	1	nymph	woody plants	polyphagous	3	2.5	3	3	2.9
	Cixius nervosus	24	5	1	nymph	woody plants	polyphagous	3	2.5	3	3	2.9
V	*Euides basilinea*	1	1	2	nymph	grasses	monophagous	3	3	2	3	2.8
	Eupelix cuspidata	5	3	2	nymph	grasses	monophagous	3	3	2	3	2.8
	Eurysula lurida	4		1	nymph	grasses	monophagous	3	3	3	3	3.0
V	*Florodelphax leptosoma*	1		2	nymph	grasses	monophagous	3	3	2	3	2.8
V	*Issus coleoptratus*		1	1	nymph	woody plants	polyphagous	3	2.5	3	3	2.9
	Kosswigianella exigua	37	10	2	nymph	grasses	monophagous	3	3	2	3	2.8
	Megadelphax sordidula	14	5	2	nymph	grasses	monophagous	3	3	2	3	2.8
3	*Mirabella albifrons*		5	2	nymph	grasses	monophagous	3	3	2	3	2.8
	Muirodelphax aubei	1	11	2	nymph	grasses	monophagous	3	3	2	3	2.8
	Ribautodelphax albostriata	2	6	2	nymph	grasses	monophagous	3	3	2	3	2.8
	Ribautodelphax collina	42	1	2	nymph	grasses	monophagous	3	3	2	3	2.8
	Speudotettix subfusculus	13	1	1	nymph	woody plants	polyphagous	3	2.5	3	3	2.9
	Tachycixius pilosus	6		1	nymph	woody plants	polyphagous	3	2.5	3	3	2.9
	Thamnotettix dilutior		1	1	nymph	woody plants	polyphagous	3	2.5	3	3	2.9
3	*Xanthodelphax straminea*	21		2	nymph	grasses	monophagous	3	3	2	3	2.8
	Group IV: Species don't react to site age. 'Young' and 'intermediate' trait combinations. 10 species, 365 observations.											
	Agallia brachyptera	1		1	egg	herbs	oligophagous	2	1	2	1	1.5
	Anaceratagallia ribauti		54	1	adult	herbs	oligophagous	NA	1	2	NA	1.5
V	*Anaceratagallia venosa*	7		1	egg	herbs	oligophagous	2	1	2	1	1.5
	Aphrodes bicincta	29		1	egg	herbs	oligophagous	2	1	2	1	1.5
3	*Asiraca clavicornis*		9	1	adult	herbs	polyphagous	NA	1	2	NA	1.5
	Circulifer haematoceps		11	1	adult	herbs	polyphagous	NA	1	2	NA	1.5
	Euscelis incisus	112	63	2	nymph	herbs & grasses	oligophagous	2	1	2	1	1.5
	Megophthalmus scanicus	30	13	1	egg	herbs	oligophagous	2	1	2	1	1.5
3	*Neoaliturus fenestratus*	18	12	2	adult	herbs	monophagous	NA	NA	1.5	NA	1.5
	Neophilaenus lineatus	6		1	egg	grasses	polyphagous	1	1	2	2	1.5

Appendix 4: Leafhoppers: Habitat modelling success. For each species, the number of occupied plots is given ('# Br' for Bremen, '# Be' for Berlin). Modelling results ('model Br' for Bremen, 'model Be' for Berlin): x = species was responsive, – = species was not responsive. Species with prevalence <10% (no modelling attempt) are marked grey.

	# Br	# Be	model Br	model Be
Group I				
Aphrodes makarovi	23	66	-	x
Chlorita paolii	7	86		-
Cicadella viridis	105	24	x	-
Dictyophara europaea		41		x
Empoasca decipiens	8	30		x
Empoasca pteridis	3	64		-
Eupteryx atropunctata	2	30		x
Euscelidius schenckii		18		-
Macrosteles cristatus	26		x	
Macrosteles laevis	94	59	-	x
Macrosteles ossiannilssoni	65		x	
Macrosteles quadripunctulatus	58	33	x	x
Macrosteles sexnotatus	66	13	x	-
Ophiola decumana	56	32	x	x
Philaenus spumarius	63	18	x	-
Emelyanoviana mollicula		1		
Eupteryx aurata	11	2		
Eupteryx curtisii		1		
Eupteryx decemnotata		4		
Eupteryx florida		5		
Eupteryx notata	2			
Eupteryx vittata	2			
Euscelidius variegatus	11	2		
Group II				
Arocephalus longiceps	75		x	
Arthaldeus pascuellus	73	8	x	x
Artianus interstitialis	1	30		x
Athysanus argentarius	31	20	x	x
Balclutha punctata	17	51	-	x
Doratura homophyla	35	17	x	x
Elymana sulphurella	20	3	x	
Errastunus ocellaris	37	56	-	x
Graphocraerus ventralis	21	36	-	x
Jassargus pseudocellaris	25		x	
Mocuellus collinus	16	22	-	-
Neophilaenus minor	25		x	
Paluda flaveola	3	19		-
Psammotettix alienus	11	50		x
Psammotettix confinis	113	42	x	x
Psammotettix helvolus		44		x
Psammotettix kolosvarensis		10		-
Psammotettix nodosus	72		x	
Turrutus socialis		29		x
Zyginidia scutellaris	67		-	
Anoscopus albifrons	1			
Anoscopus flavostriatus	1			
Anoscopus serratulae	3			
Arocephalus languidus		1		
Conosanus obsoletus	5	1		
Deltocephalus pulicaris	1	2		
Dikraneura variata	15	5		
Limotettix striola	3			
Neophilaenus campestris		4		
Streptanus aemulans	3			
Streptanus sordidus	2			
Zygina angusta	2			
Zygina schneideri		1		
Group III				
Aphrophora alni	1	15		-
Arthaldeus arenarius	5	10		-
Cicadula quadrinotata	41	14	x	x
Cixius nervosus	24	5	x	
Dicranotropis hamata		28		-
Doratura impudica	16	21	-	x
Empoasca vitis	19	29	-	-
Eupteryx calcarata		15		-
Fagocyba cruenta	16	9	-	-
Hesium domino		9		-
Javesella pellucida	34	13	x	-
Kelisia sabulicola	30	1	-	
Kosswigianella exigua	37	10	-	x
Laodelphax striatella	14	14	-	-
Macropsis prasina	19		x	-
Macrosteles maculosus		18		-
Muirodelphax aubei	1	11		-
Orientus ishidae		11		-
Psammotettix excisus	16		x	
Rhopalopyx vitripennis	33	12	x	-
Ribautodelphax collina	42	1	x	
Stenocranus minutus	8	23		x
Xanthodelphax straminea	21		-	-
Zygina hyperici	6	30		-
Acanthodelphax spinosa	5	5		
Aguriahana stellulata	2			
Alebra albostriella	8	2		
Allygidius atomarius		1		
Allygidius commutatus	1			
Allygus mixtus	3	2		
Allygus modestus		1		
Aphrophora pectoralis	1			
Aphrophora salicina	1			
Arocephalus punctum	6			
Cercopis vulnerata	8	1		
Chloriona glaucescens	2			
Cicadula flori	7			
Cicadula persimilis	7			
Cicadula saturata	1			
Cixius cambricus		3		
Conomelus anceps	12			
Criomorphus albomarginatus	8	1		
Edwardsiana crataegi	1			
Edwardsiana flavescens	1			
Edwardsiana prunicola		1		
Edwardsiana rosae		1		
Edwardsiana salicicola	4			
Edwardsiana sociabilis		2		
Edwardsiana tersa	1			
Erzaleus metrius	1	1		
Euides basilinea	1	1		
Eupelix cuspidata	5	3		
Eupteryx adspersa		1		
Eupteryx tenella		5		
Eupteryx urticae	1			
Eurhadina pulchella	6	1		
Eurybregma nigrolineata	1	2		
Eurysa lineata		2		
Eurysula lurida	4			
Fagocyba carri		1		
Fieberiella septentrionalis	4	6		
Florodelphax leptosoma	1			
Gargara genistae		1		
Graphocephala fennahi	1			
Hyledelphax elegantula	4			
Iassus lanio	1	1		
Idiocerus herrichii		2		
Idiocerus lituratus	1			
Idiocerus stigmaticalis	4			
Idiocerus vicinus	2			
Issus coleoptratus		1		
Javesella dubia	6			
Javesella forcipata		3		
Javesella obscurella	4			
Kelisia monoceros		3		
Kyboasca bipunctata	1			
Kybos butleri	1			
Kybos lindbergi		1		
Kybos rufescens	10			
Kybos smaragdula	7	7		
Kybos strigilifer	7	1		
Kybos virgator	9	2		
Laburrus impictifrons		1		
Liguropia juniperi	1			
Linnavuoriana sexmaculata	1	3		
Macropsis cerea	9			
Macropsis fuscula	2	2		
Macropsis graminea	1	1		
Macropsis gravesteini	4			
Macropsis infuscata	2			
Macropsis notata	1	4		
Macropsis ocellata	6			
Macropsis scutellata		1		
Macrosteles frontalis	4			
Macrosteles horvathi	6			
Macrosteles lividus		1		
Macrosteles variatus		3		
Megadelphax sordidula	14	5		
Metidiocerus elegans		1		
Metidiocerus rutilans	2	3		
Micantulina stigmatipennis		1		
Mirabella albifrons		5		
Mocydiopsis parvicauda	8	1		
Muellerianella fairmairei	1			
Oncopsis appendiculata	2	1		
Oncopsis flavicollis	7	6		
Oncopsis subangulata	5	2		
Ophiola transversa		1		
Populicerus confusus	4	1		
Populicerus nitidissimus		1		
Populicerus populi	14	3		
Psammotettix poecilus		5		
Rhopalopyx adumbrata	5			
Rhopalopyx preyssleri	3	3		
Rhytidodus decimusquartus	3	1		
Rhytistylus proceps	3			
Ribautiana tenerrima	5	1		
Ribautodelphax albostriata	2	6		
Speudotettix subfusculus	13	1		
Stenocranus major	5			
Streptanus marginatus	2	1		
Tachycixius pilosus	6			
Thamnotettix dilutior		1		
Tremulicerus distinguendus	4	4		
Tremulicerus tremulae	2			
Tremulicerus vitreus		3		
Typhlocyba quercus	2			
Viridicerus ustulatus	3	5		
Group IV				
Anaceratagallia ribauti		54		x
Aphrodes bicincta	29		-	
Asiraca clavicornis		9		-
Circulifer haematoceps		11		-
Euscelis incisus	112	63	x	x
Megophthalmus scanicus	30	13	-	x
Neoaliturus fenestratus	18	12	-	-
Agallia brachyptera	1			
Anaceratagallia venosa	7			
Neophilaenus lineatus	6			

Appendix 5: Leafhoppers: Number of occupied plots per age class. Total of Bremen 2003 and Berlin 2004 (246 plots).

Species	0-2 years	3-6 years	7-15 years	>15 years
Acanthodelphax spinosa	0	0	4	6
Agallia brachyptera	0	0	1	0
Aguriahana stellulata	0	0	0	2
Alebra albostriella	0	1	1	8
Allygidius atomarius	1	0	0	0
Allygidius commutatus	0	0	0	1
Allygus mixtus	0	1	0	4
Allygus modestus	0	0	0	1
Anaceratagallia ribauti	8	13	23	10
Anaceratagallia venosa	0	0	2	5
Anoscopus albifrons	0	0	0	1
Anoscopus flavostriatus	0	0	0	1
Anoscopus serratulae	1	0	1	1
Aphrodes bicincta	1	10	13	5
Aphrodes makarovi	7	33	32	17
Aphrophora alni	0	3	8	5
Aphrophora pectoralis	0	0	0	1
Aphrophora salicina	0	0	0	1
Arocephalus languidus	0	0	0	1
Arocephalus longiceps	6	22	32	15
Arocephalus punctum	0	0	2	4
Arthaldeus arenarius	0	0	11	4
Arthaldeus pascuellus	5	19	32	25
Artianus interstitialis	0	5	19	7
Asiraca clavicornis	0	2	4	3
Athysanus argentarius	0	10	22	19
Balclutha punctata	4	19	31	14
Cercopis vulnerata	0	0	4	5
Chloriona glaucescens	1	1	0	0
Chlorita paolii	17	24	34	18
Cicadella viridis	20	34	47	28
Cicadula flori	0	0	5	2
Cicadula persimilis	0	1	3	3
Cicadula quadrinotata	5	6	26	18
Cicadula saturata	0	0	1	0
Circulifer haematoceps	5	2	4	0
Cixius cambricus	0	1	2	0
Cixius nervosus	0	2	16	11
Conomelus anceps	0	0	8	4
Conosanus obsoletus	3	0	2	1
Criomorphus albomarginatus	0	2	3	4
Deltocephalus pulicaris	0	1	2	0
Dicranotropis hamata	2	7	11	8
Dictyophara europaea	4	10	23	4
Dikraneura variata	1	2	12	5
Doratura homophyla	7	25	14	6
Doratura impudica	3	7	19	8
Edwardsiana crataegi	0	0	0	1
Edwardsiana flavescens	1	0	0	0
Edwardsiana prunicola	0	1	0	0
Edwardsiana rosae	0	0	1	0
Edwardsiana salicicola	0	0	3	1
Edwardsiana sociabilis	0	0	1	1
Edwardsiana tersa	0	0	1	0
Elymana sulphurella	2	8	8	5
Emelyanoviana mollicula	0	1	0	0
Empoasca decipiens	4	5	14	15
Empoasca pteridis	11	18	23	15
Empoasca vitis	12	14	14	8
Errastunus ocellaris	11	21	39	22
Erzaleus metrius	0	0	1	1
Euides basilinea	0	0	1	1
Eupelix cuspidata	0	2	5	1
Eupteryx adspersa	0	0	1	0
Eupteryx atropunctata	7	6	11	8
Eupteryx aurata	4	3	2	4
Eupteryx calcarata	0	3	5	7
Eupteryx curtisii	0	0	0	1
Eupteryx decemnotata	2	1	1	0
Eupteryx florida	1	0	2	2
Eupteryx notata	0	0	0	2
Eupteryx tenella	0	0	3	2
Eupteryx urticae	0	0	0	1
Eupteryx vittata	0	0	1	1
Eurhadina pulchella	0	0	0	7
Eurybregma nigrolineata	0	0	2	1
Eurysa lineata	0	0	2	0
Eurysula lurida	0	0	3	1
Euscelidius schenckii	2	6	4	6
Euscelidius variegatus	5	4	3	1
Euscelis incisus	32	51	63	29
Fagocyba carri	0	0	0	1
Fagocyba cruenta	1	6	8	10
Fieberiella septentrionalis	2	0	4	4
Florodelphax leptosoma	0	0	0	1
Gargara genistae	0	0	1	0
Graphocephala fennahi	1	0	0	0
Graphocraerus ventralis	4	9	28	16
Hesium domino	0	3	2	4
Hyledelphax elegantula	0	1	1	2
Iassus lanio	0	0	0	2
Idiocerus herrichii	0	0	0	2
Idiocerus lituratus	0	0	0	1
Idiocerus stigmaticalis	1	0	3	0
Idiocerus vicinus	0	1	1	0
Issus coleoptratus	1	0	0	0
Jassargus pseudocellaris	2	4	5	14
Javesella dubia	1	0	1	4
Javesella forcipata	0	0	1	2
Javesella obscurella	2	1	0	1
Javesella pellucida	3	9	24	11
Kelisia monoceros	0	1	2	0
Kelisia sabulicola	3	4	17	7
Kosswigianella exigua	7	3	22	15
Kyboasca bipunctata	0	0	1	0
Kybos butleri	1	0	0	0
Kybos lindbergi	0	0	1	0
Kybos rufescens	4	1	5	0
Kybos smaragdula	2	4	6	2
Kybos strigilifer	0	0	8	0
Kybos virgator	1	4	6	0
Laburrus impictifrons	0	0	1	0
Laodelphax striatella	8	5	9	6
Liguropia juniperi	1	0	0	0
Limotettix striola	3	0	0	0
Linnavuoriana sexmaculata	0	0	3	1
Macropsis cerea	0	1	5	3
Macropsis fuscula	0	1	2	1
Macropsis graminea	1	0	1	0
Macropsis gravesteini	0	0	3	1
Macropsis infuscata	0	1	0	1
Macropsis notata	0	1	3	1
Macropsis ocellata	1	1	3	1
Macropsis prasina	2	3	12	2
Macropsis scutellata	0	0	1	0
Macrosteles cristatus	12	7	2	5
Macrosteles frontalis	2	0	1	1
Macrosteles horvathi	5	1	0	0
Macrosteles laevis	44	41	47	21
Macrosteles lividus	0	1	0	0
Macrosteles maculosus	7	7	2	2
Macrosteles ossiannilssoni	25	19	15	6
Macrosteles quadripunctulatus	44	24	18	5
Macrosteles sexnotatus	18	25	24	12
Macrosteles variatus	0	1	0	2
Megadelphax sordidula	2	0	6	11
Megophthalmus scanicus	2	10	15	16
Metidiocerus elegans	1	0	0	0
Metidiocerus rutilans	0	2	2	1
Micantulina stigmatipennis	0	0	1	0
Mirabella albifrons	0	1	2	2
Mocuellus collinus	5	8	17	8
Mocydiopsis parvicauda	0	0	5	4
Muellerianella fairmairei	0	0	1	0
Muirodelphax aubei	2	2	7	1
Neoaliturus fenestratus	10	6	10	4
Neophilaenus campestris	1	2	0	1
Neophilaenus lineatus	1	3	2	0
Neophilaenus minor	2	2	15	6
Oncopsis appendiculata	0	0	2	1
Oncopsis flavicollis	0	1	8	4
Oncopsis subangulata	0	1	4	2
Ophiola decumana	39	22	20	7
Ophiola transversa	0	0	1	0
Orientus ishidae	1	2	5	3
Paluda flaveola	1	4	8	9
Philaenus spumarius	9	26	33	13
Populicerus confusus	1	2	2	0
Populicerus nitidissimus	0	0	1	0
Populicerus populi	2	3	3	9
Psammotettix alienus	11	21	20	9
Psammotettix confinis	36	48	56	15
Psammotettix excisus	2	1	11	2
Psammotettix helvolus	4	11	24	5
Psammotettix kolosvarensis	0	3	6	1
Psammotettix nodosus	10	25	29	8
Psammotettix poecilus	1	2	2	0
Rhopalopyx adumbrata	1	0	2	2
Rhopalopyx preyssleri	1	0	3	2
Rhopalopyx vitripennis	2	5	21	17
Rhytidodus decimusquartus	0	0	1	3
Rhytistylus proceps	0	0	2	1
Ribautiana tenerrima	0	0	5	1
Ribautodelphax albostriata	0	0	6	2
Ribautodelphax collina	4	4	20	15
Speudotettix subfusculus	1	3	3	7
Stenocranus major	0	0	5	0
Stenocranus minutus	0	6	14	11
Streptanus aemulans	0	1	0	2
Streptanus marginatus	0	0	0	3
Streptanus sordidus	0	1	0	1
Tachycixius pilosus	0	1	0	5
Thamnotettix dilutior	0	1	0	0
Tremulicerus distinguendus	1	3	1	3
Tremulicerus tremulae	0	1	0	1
Tremulicerus vitreus	1	1	1	0
Turrutus socialis	3	2	16	8
Typhlocyba quercus	0	0	0	2
Viridicerus ustulatus	2	3	2	1
Xanthodelphax straminea	0	7	9	5
Zygina angusta	0	0	0	2
Zygina hyperici	6	9	14	7
Zygina schneideri	0	0	1	0
Zyginidia scutellaris	9	12	28	18

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Lebenslauf

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Erklärung

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

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

Des Weiteren 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 3, Chapter 4 und Chapter 5 dieser Arbeit wurden bereits veröffentlicht:

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Strauss B. & Biedermann R. (2006): Urban brownfields as temporary habitats: Driving forces for the diversity of phytophagous insects. Ecography 29: 928-940. doi:10.1111/j.2006.0906-7590.04765.x.

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