

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

Barbara Strauss and Robert Biedermann

Strauss, B. and Biedermann, R. 2006. Urban brownfields as temporary habitats: driving forces for the diversity of phytophagous insects. – *Ecography* 29: 928–940.

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.

B. Strauss and R. Biedermann (robert.biedermann@uni-oldenburg.de), Landscape Ecology Group, Inst. of Biology and Environmental Sciences, Univ. of Oldenburg, DE-26111 Oldenburg, Germany.

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 (Gibson 1998). 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 biodiver-

sity of a city (Rebele 1994, Gibson 1998, Eyre et al. 2003). Even though created by humans, they represent largely undisturbed, semi-natural habitats (Sanderson 1992), and are home to true urban communities that might not be found elsewhere.

Brownfields are continuously being generated, quickly changed by successional processes (Brown and 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 and Pullin 2002). These two processes generate a spatio-temporal

Accepted 27 September 2006

Copyright © ECOGRAPHY 2006
ISSN 0906-7590

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 and 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 (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, Schwerk 2000, Eyre et al. 2003, Small et al. 2003, 2006) and leafhoppers (Sanderson 1992), 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 and 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 and Zimmermann 2000, Olden and Jackson 2000, Rushton et al. 2004). In contrast to this, Burnham (1998) 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 (Gibson et al. 2004). In addition, model averaging can be used to assess the relative importance of different factors (Burnham 1998).

In our work, we applied the method of Burnham (1998) 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 1992). 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).

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 m² in a random stratified way (Hirzel and Guisan 2002), covering three gradients: site size, successional age (0–40 yr) and soil moisture. In Berlin, 89 plots were spread over 370 km², in Bremen, 157 plots over 100 km². 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 <40 m (Ingrisch and Köhler 1998, Biedermann 2002, Schuhmacher and Fartmann 2003, Cronin 2004).

The data were collected in 2003 (Bremen) and 2004 (Berlin). On each plot, we recorded the presence/absence of leafhoppers and grasshoppers. For leafhoppers, sweepnet 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 and Niedringhaus 2004). Grasshoppers were recorded once in late July/early August, when all species are present as adults (Ingrisch and Köhler 1998). To this end, acoustic monitoring (Bellmann 1993) 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 (Table 1). 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 and 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 1). Landscape context parameters (Table 1) 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 and Mello 2004, Holland et al. 2004).

Table 1. Environmental data recorded for all plots. These were used as explanatory variables within habitat models.

Successional age [yr]

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 and tree layer [%]
- cover of host plants [%] (for mono- and oligophagous leafhoppers), as specified by Nickel (2003)

Soil parameters

- pH (CaCl₂), Ellenberg pH-values (calculated from vegetation data) (Ellenberg 1992)
- P [kg ha⁻¹], K [kg ha⁻¹], ECEC [cmol_c kg⁻¹] (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

Single species models

Presence/absence models

We used logistic regression, i.e. generalized 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 provide little or no additional information (Pearce and 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 and 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 and 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: 1) proportions of the same brownfield type

within different radii, 2) vegetation height parameters derived from “screen measurements” and 3) vegetation density parameters derived from “screen measurements” (Table 1). 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 $r \leq 0.7$) 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 and 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_N^2 (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 and 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 (1998) was used, which proceeds as follows. For each model in the set, the AIC_c -value was calculated. This small-sample version of the Akaike information criterion 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 (Table 2). Akaike weights were calculated as

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

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 2). 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 (area under the receiver operator characteristic curve), R_N^2 , Cohen’s Kappa, sensitivity (correctly predicted species presences), specificity (correctly predicted absences), and CCR (overall correct classification rate) (Fielding and Bell 1997, Hosmer and Lemeshow 2000, Manel et al. 2001).

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 and 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 and 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 1998, Gibson et al. 2004). The process is demonstrated for one species in Table 2. For comparison, the relative weights were converted to percentage values.

Table 2. 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 | | -0.003 | | 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 [$t\ ha^{-1}$]
var.2 vegetation height [m]
var.5 proportion of brownfields within 25 m
var.2² (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* [%]

Results

Model performance

Forty-eight 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 and 18, with a median of 11. For Berlin, the corresponding range was between 2 and 21 species, also with a median of 11.

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 (Fig. 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 (Fig. 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 con-

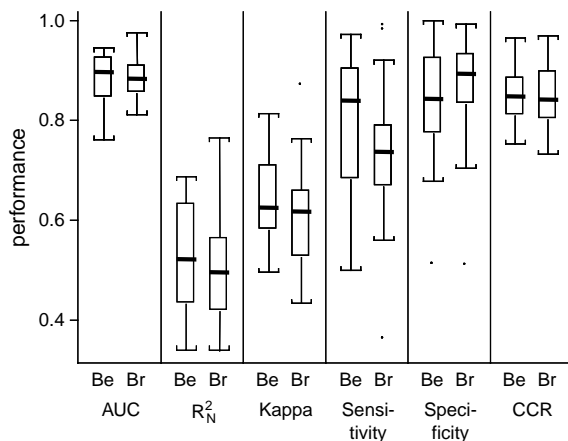


Fig. 1. Performance of single species models. Shown is, for each performance criterion, the range and distribution of values for all models. For each criterion, the left boxplot represents all Berlin models (Be), the right boxplot all Bremen models (Br). Box: median, 25%- and 75%-percentiles; whiskers: $1.5 \times$ interquartile range; outliers drawn as individual points.

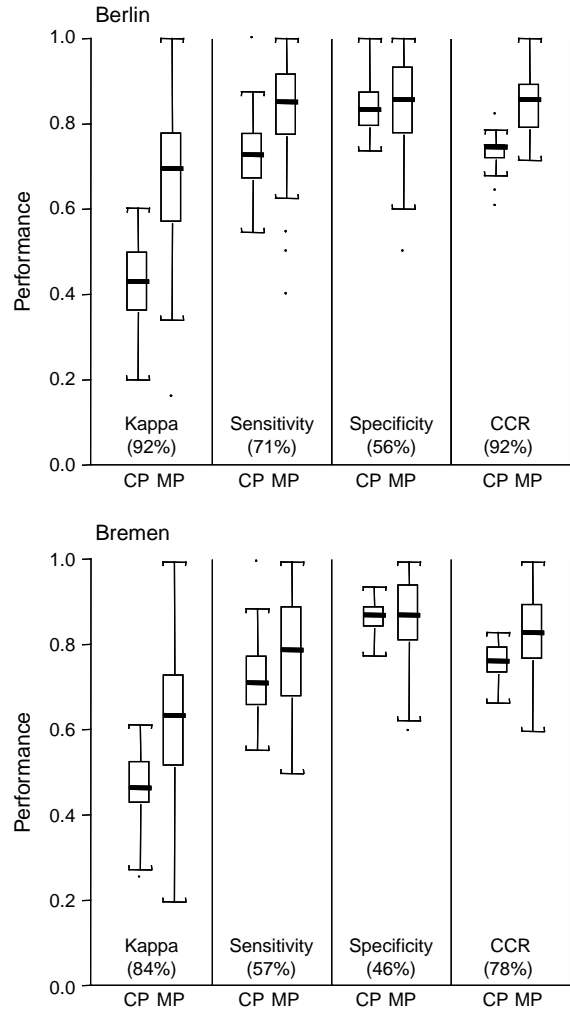


Fig. 2. Validation of community models. Shown is, for each performance criterion, the range and distribution of values for all plots. For each criterion, two boxplots are drawn. The left boxplot shows the 95%-percentiles of the chance distributions (chance prediction = CP). The right boxplot shows the 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.

trast, 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.

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

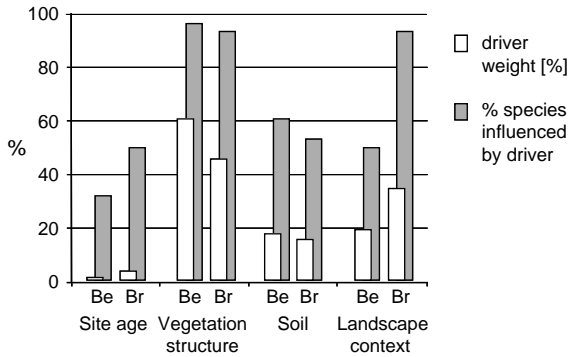


Fig. 3. Influence of main driving factors. For each factor, the weights within the models are averaged over all species to determine the average weight within the community model (white bars). The proportions of species influenced by each main factor are drawn as grey bars. Be = Berlin models, Br = Bremen models.

influenced by vegetation structure (Fig. 3). The median of vegetation structure weight was around 50% (Fig. 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 (Fig. 3). Moreover, in Berlin, the magnitude of landscape context influence was considerably lower (Fig. 4). Soil parameters ranked third in weight (Fig. 3), with mostly small influence. However, a few species were strongly influenced by soil parameters (Fig. 4). Site age had little impact in both cities, but did occur in many models (32% of models in Berlin, 50% in Bremen) (Fig. 3).

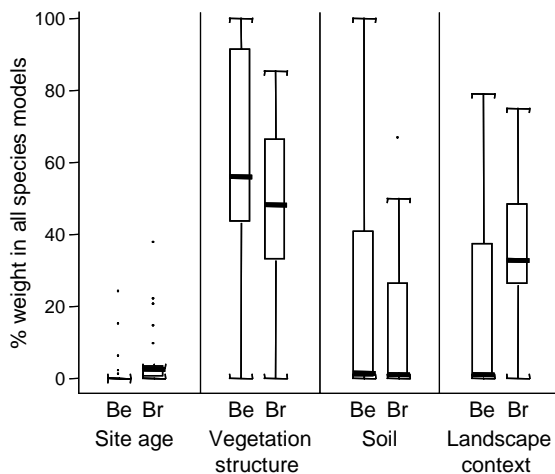


Fig. 4. Range and distribution of factor weights within species models. For each factor, the left boxplot represents Berlin models (Be), the right boxplot Bremen models (Br).

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 3). 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.

Some pronounced differences between Berlin and Bremen became apparent when landscape context parameters were considered (Table 3). 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 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 6 (Berlin) and Fig. 7 (Bremen) illustrate the modifying influence of landscape context. Four

Table 3. Summary of species responses to driving factors. We considered negative (–), positive (+) and unimodal (∩) responses. Numbers of variable or response occurrences in averaged models. NA denotes not available.

| | 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 and 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 and 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 |

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 Fig. 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 (Fig. 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 (Fig. 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. *Anacratagallia 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 (Fig. 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. *Macrosteles ossianilssoni*)

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 Fig. 6 (Berlin) and Fig. 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.

Discussion

Relative importance and ecological relevance of main driving factors

Vegetation parameters and site age

Our results clearly indicate that vegetation structure was the most influential factor for the communities of

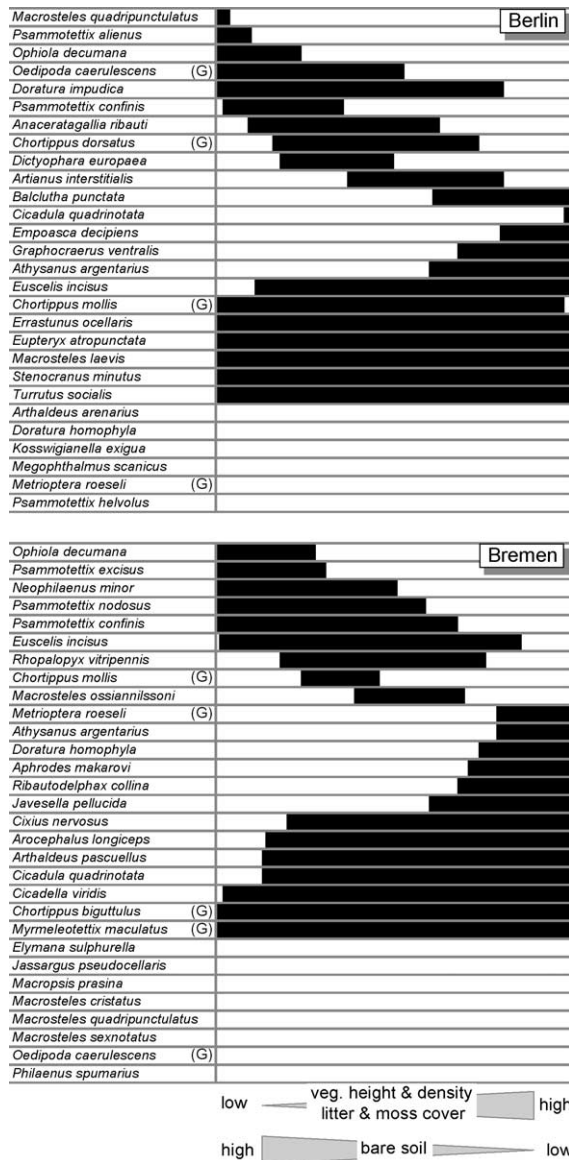


Fig. 5. Occurrence of species (black bars), based on single species habitat models, on a vegetation gradient. The gradient runs from low to high vegetation height and density, from low to high moss and litter cover, and from high to low proportions of bare soil. "Low" refers to the 5%-percentiles of 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 yr, cover of host plants to high values. All other variables are fixed to their arithmetic mean. (G) = grasshopper species.

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

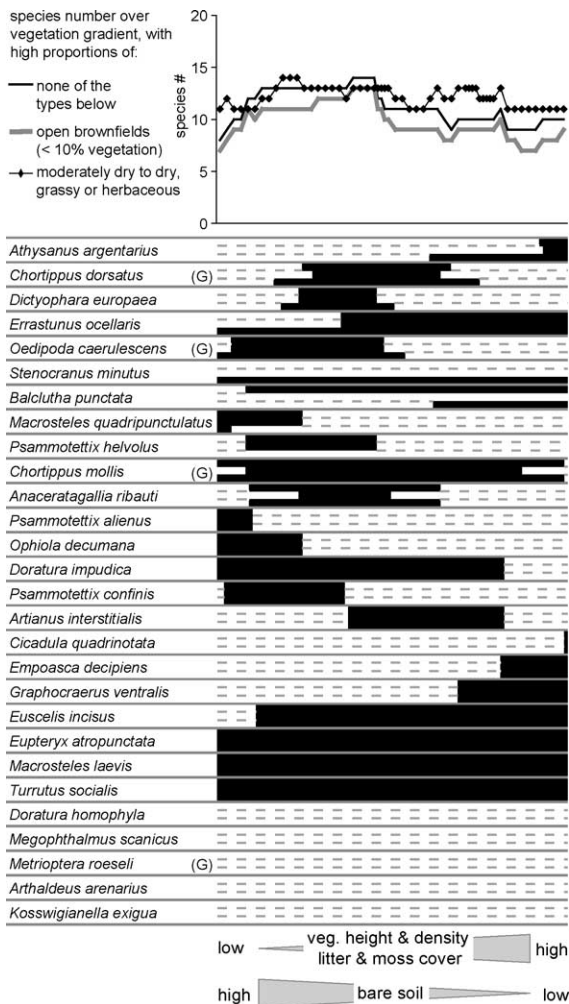


Fig. 6. Berlin community: influence of landscape context on the occurrence of species on a vegetation gradient (for gradient details see Fig. 5). For each species, three bars indicate species occurrence with either low (5%-percentile) proportions of open, grassy and herbaceous brownfields (upper bar), 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.

importance for both leafhoppers (Brown et al. 1992, Morris 2000) and grasshoppers (Brocksieper 1978, Detzel 1998, Ingrisch and 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



Fig. 7. Same as Fig. 6, but for the Bremen community. In addition, a fourth landscape context condition is shown (high proportions of moist to wet brownfields).

characteristics (Rebele 1994, Hollier et al. 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 and 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 and 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 and 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, particularly in Bremen. As the majority of leafhoppers feeds on grasses (Morris 2000), this relationship is reasonable. Sanderson (1992) found higher species diversities in leafhoppers 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 led 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 and Bennett 2004).

Soil parameters

Even though in some studies soil parameters were found to strongly influence leafhoppers (Cherrill and Rushton 1993) and grasshoppers (Ingrisch and 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 (Brown et al. 1992, Steffan-Dewenter and Tscharntke 1997, Purtauf et al. 2004) 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 >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 and 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 Pepler-Lisbach and 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. Generalizations should not be made before transferability of the models has been tested with independent data (Vaughan and 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.

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 generalizations cannot be made until the models have successfully been transferred to independent data.

Acknowledgements – This study was conducted as part of the TEMPO-project and was financially supported by the German Ministry of Education and Research (BMBF, grant 01LM0210). We thank Ute Schadek for providing soil and plant composition data and Nora Lange for providing leafhopper data and the brownfield type map for Berlin.

References

- Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. – *Ecol. Modell.* 157: 101–118.
- Bellmann, H. 1993. Die Stimmen der heimischen Heuschrecken. – Naturbuchverlag.
- Biedermann, R. 2002. Mating success in the spittlebug *Cercopis sanguinolenta* (Scopoli, 1763) (Homoptera, Cercopidae): the role of body size and mobility. – *J. Ethol.* 20: 13–18.
- Biedermann, R. and Niedringhaus, R. 2004. Die Zikaden Deutschlands. – Wissenschaftlich Akademischer Buchvertrieb-Frönd.
- Brocksieper, R. 1978. Der Einfluß des Mikroklimas auf die Verbreitung der Laubheuschrecken, Grillen und Feldheuschrecken im Siebengebirge und auf dem Rodderberg bei Bonn (Orthoptera: Saltatoria). – *Decheniana-Beihefte* 21: 1–141.
- Brown, V. K. and Southwood, T. R. E. 1987. Secondary succession: patterns and strategies. – In: Gray, A. J. et al. (eds), *Colonization, succession, and stability. The 26th Symp. of the British Ecological Society held jointly with the Linnean Society of London.* Blackwell, p. 482.
- Brown, V. K. et al. 1992. Community organisation in leaf hoppers. – *Oikos* 65: 97–106.
- Burnham, K. P. 1998. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.
- Cherrill, A. J. and Rushton, S. P. 1993. The Auchenorhyncha of an unimproved moorland in northern England. – *Ecol. Entomol.* 18: 95–103.
- Cronin, J. 2004. Host-parasitoid extinction and colonization in a fragmented prairie landscape. – *Oecologia* 139: 503–514.
- Cushman, S. A. and McGarigal, K. 2004. Patterns in the species-environment relationship depend on both scale and choice of response variables. – *Oikos* 105: 117–124.
- Detzel, P. 1998. Die Heuschrecken Baden-Württembergs. – Ulmer.
- Ellenberg, H. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. – Goltze.
- Eversham, B. C. et al. 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. – *Ann. Zool. Fenn.* 33: 149–156.
- Eyre, M. D. et al. 2003. Beetles (Coleoptera) on brownfield sites in England: an important conservation resource? – *J. Insect Conserv.* 7: 223–231.
- Ferrier, S. et al. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. – *Biodiv. Conserv.* 11: 2275–2307.
- Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence-absence models. – *Environ. Conserv.* 24: 38–49.
- Finnern, H. et al. 1996. Bodenkundliche Kartieranleitung. – Schweizerbart.

- Fisher, J. T. et al. 2005. The protean relationship between boreal forest landscape structure and red squirrel distribution at multiple spatial scales. – *Landscape Ecol.* 20: 73–82.
- Gibson, C. W. D. 1998. Brownfield: red data – the values artificial habitats have for uncommon invertebrates. – *English Nat. Res. Rep.* 273.
- Gibson, L. A. et al. 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. – *J. Appl. Ecol.* 41: 213–223.
- Gilbert, O. L. 1989. The ecology of urban habitats. – Chapman and Hall.
- Grand, J. and Mello, M. J. 2004. A multi-scale analysis of species-environment relationships: rare moths in a pitch pine-scrub oak (*Pinus rigida-Quercus ilicifolia*) community. – *Biol. Conserv.* 119: 495–506.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – *Ecol. Modell.* 135: 147–186.
- Gustafson, E. J. 1998. Quantifying landscape spatial pattern: what is the state of the art? – *Ecosystems* 1: 143–156.
- Harrell, F. E. 2001. Regression modeling strategies. – Springer.
- Heinze, G. and Schemper, M. 2002. A solution to the problem of separation in logistic regression. – *Stat. Med.* 21: 2409–2419.
- Hirzel, A. and Guisan, A. 2002. Which is the optimal sampling strategy for habitat suitability modelling. – *Ecol. Modell.* 157: 331–341.
- Holland, J. D. et al. 2004. Determining the spatial scale of species' response to habitat. – *Bioscience* 54: 227–233.
- Hollier, J. A. et al. 1994. Successional leafhopper assemblages – pattern and process. – *Ecol. Res.* 9: 185–191.
- Hosmer, D. W. and Lemeshow, S. 2000. Applied logistic regression. – Wiley.
- Ingrisch, S. and Köhler, G. 1998. Die Heuschrecken Mitteleuropas. – Westarp Wissenschaften.
- Kuhn, W. and Kleyer, M. 1999/2000. A statistical habitat model for the blue winged grasshopper (*Oedipoda caerulescens*) considering the habitat connectivity. – *Zeitschrift für Ökologie und Naturschutz* 8: 207–218.
- Manel, S. et al. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. – *J. Appl. Ecol.* 38: 921–931.
- Manly, B. F. J. 2001. Randomization, bootstrap and Monte Carlo methods in biology. – Chapman and Hall.
- Mazerolle, M. J. and Villard, M. A. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. – *Ecoscience* 6: 117–124.
- Morris, M. G. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. – *Biol. Conserv.* 95: 129–142.
- Nickel, H. 2003. The leafhoppers and planthoppers of Germany (Hemiptera, Auchenorrhyncha), patterns and strategies in a highly diverse group of phytophagous insects. – *Series Faunistica* 28, Pensoft.
- Niemelä, J. 1999. Is there a need for a theory of urban ecology? – *Urban Ecosyst.* 3: 57–65.
- Niemelä, J. et al. 2002. Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. – *Landscape Ecol.* 17: 387–401.
- Olden, J. D. 2003. A species-specific approach to modeling biological communities and its potential for conservation. – *Conserv. Biol.* 17: 854–863.
- Olden, J. D. and Jackson, D. A. 2000. Torturing data for the sake of generality: how valid are our regression models? – *Ecoscience* 7: 501–510.
- Pearce, J. and Ferrier, S. 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. – *Biol. Conserv.* 98: 33–43.
- Peppler-Lisbach, C. and Schröder, B. 2004. Predicting the species composition of *Nardus stricta* communities by logistic regression modelling. – *J. Veg. Sci.* 15: 623–634.
- Purtauf, T. et al. 2004. Carabid communities in the spatio-temporal mosaic of a rural landscape. – *Landscape Urban Plann.* 67: 185–193.
- Radford, J. Q. and Bennett, A. F. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. – *Biol. Conserv.* 117: 375–391.
- Rebele, F. 1994. Urban ecology and special features of urban ecosystems. – *Global Ecol. Biogeogr. Lett.* 4: 173–187.
- Rebele, F. and Lehmann, C. 2002. Restoration of a landfill site in Berlin, Germany by spontaneous and directed succession. – *Restor. Ecol.* 10: 340–347.
- Rushton, S. P. et al. 2004. New paradigms for modelling species distributions? – *J. Appl. Ecol.* 41: 193–200.
- Sadler, J. P. et al. 2006. Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. – *J. Biogeogr.* 33: 1126–1138.
- Sanderson, R. A. 1992. Hemiptera of naturally vegetated derelict land in north-west England. – *Entomol. Gaz.* 43: 221–226.
- Schuhmacher, O. and Fartmann, T. 2003. Wie mobil ist der Warzenbeißer? Eine populationsökologische Studie zum Ausbreitungsverhalten von *Decticus verrucivorus*. – *Naturschutz und Landschaftsplanung* 35: 20–28.
- Schwerk, A. 2000. Ecological aspects of carabid beetle coenoses (Coleoptera: Carabidae) on industrial fallow grounds in the Ruhr Valley Area. – In: Brandmayr, P. et al. (eds), Natural history and applied ecology of carabid beetles. Proc. of the 9th European Carabidologists' Meeting (26–31 July 1998, Camigliatello, Cosenza, Italy). Pensoft, pp. 277–287.
- Small, E. C. et al. 2003. Carabid beetle assemblages on urban derelict sites in Birmingham, UK. – *J. Insect Conserv.* 6: 233–246.
- Small, E. et al. 2006. Do landscape factors affect brownfield carabid assemblages? – *Sci. Total Environ.* 360: 205–222.
- Steffan-Dewenter, I. and Tschamntke, T. 1997. Early succession of butterfly and plant communities on set-aside fields. – *Oecologia* 109: 294–302.
- Sundermeier, A. 1999. Zur Vegetationsdichte der Xerothermrassen nordwestlich von Halle/Saale. – Cramer.
- Vaughan, I. P. and Ormerod, S. J. 2005. The continuing challenges of testing species distribution models. – *J. Appl. Ecol.* 42: 720–730.
- Wood, B. C. and Pullin, A. S. 2002. Persistence of species in a fragmented urban landscape: the importance of dispersal ability and habitat availability for grassland butterflies. – *Biodiv. Conserv.* 11: 1451–1468.
- Zehm, A. et al. 2003. Multiparameter analysis of vertical vegetation structure based on digital imaging processing. – *Flora* 198: 142–160.

Subject Editor: John Spence.