Landscape Ecol (2009) 24:929–941
DOI 10.1007/s10980-009-9371-7

RESEARCH ARTICLE

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

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Received: 10 October 2008 / Accepted: 2 June 2009 / Published online: 16 June 2009

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

Keywords Dynamic landscape · Species distribution model · Habitat model · Urban brownfields · Model averaging · Landscape context · Conservation planning · Succession

Introduction

In dynamic landscapes, species are facing habitats of changing quality and location. Landscape dynamics

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Electronic supplementary material The online version of this article (doi:10.1007/s10980-009-9371-7) contains supplementary material, which is available to authorized users.

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can arise from land use, succession, or natural disturbances like wind, fire or flood. Often, habitat destruction for one species allows for habitat creation for another.

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

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

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

We use species distribution models (SDMs; also called habitat suitability models or habitat models) to analyse the response of plant and insect biodiversity to spatio-temporal changes in habitat quality. SDMs are statistical models which relate species incidence or abundance to environmental predictors, and have become an important and frequently applied tool in ecology as well as in conservation biology in recent years (Guisan and Thuiller 2005).

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

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

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

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

Methods

Approach

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

Modelling shell

Our modelling shell is based on a grid-based geographic information system, which divides the study area (see below) into 63,000 raster cells of size 12.5 m by 12.5 m. The shell consists of three modules. In the scenario creation module the proportion of potential habitat patches (i.e. brownfield proportion) and the age distribution of these patches (resulting from different paces of abandonment and redevelopment, i.e. different turnover rates) are set. The location of potential habitat is assigned randomly. Site age is drawn randomly for every lot from an exponential distribution with mean value $1/\lambda$, representing a certain average turnover rate.

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

Within the evaluation module, modelling results are rated from the nature conservation perspective. First, species richness as the total number of occurring plant and insect species in the study area is calculated. To ignore unviably small populations, a species must occur on at least 0.1% of the raster cells. Second, an average rarity value over all brownfield cells is calculated. To this end, a regional rarity value ranging from 1 (very common) to 5 (very rare) was assigned to every species (see Figs. 5, 6) on the basis of distribution atlases [plants and grasshoppers (Bundesamt für Naturschutz 2004; Hochkirch and Klugkist 1998)] or, in case of leafhoppers, expert knowledge (Robert Biedermann). For all species, the number of occupied cells is multiplied by the species' rarity value. The result is summed over all species, divided by the total number of brownfield cells, and normalised by dividing it by the sum of rarity values over all species. Third, the response of every single species to the spatio-temporal configuration is calculated as the proportion of occupied brownfield cells.

Study area and sampling design

The study area is located in the city of Bremen in north-west Germany. Sampling plots were restricted to brownfield sites, consisting of previously developed land, abandoned railroads, and vacant areas within industrial and logistics centres. Soil at the sampling plots comprised mainly of sandy landfills. Plots were chosen in a random stratified way along three gradients: site age, site size and soil moisture. At 133 plots, presence/absence of all vascular plant species within an area of 16 m^2, and of leafhoppers and grasshoppers within an area of 225 m^2 was sampled. Leafhoppers were recorded by swepnet sampling and grasshoppers by acoustic monitoring and visual inspection (*Oedipoda caerulescens*). At the plots, soil water budget parameters, soil nutrients

Table 1 Predictor variables for the species distribution models, their scale, and aggregation to groups used in Fig. 1

Predictor variables	Scale	Aggregated predictor group
Coefficient of permeability	Plot	Soil
Air porosity	Plot	Soil
Field capacity	Plot	Soil
Plant available water at field capacity	Plot	Soil
Plant available water over the year	Plot	Soil
Effective cation exchange capacity	Plot	Soil
pH (in $CaCO_3$)	Plot	Soil
Plant available phosphorus (P)	Plot	Soil
Plant available potassium (K)	Plot	Soil
Calcium carbonate ($CaCO_3$)	Plot	Soil
Brick rubble	Plot	Soil
Site age	Plot	Site age
Current disturbance	Plot	Site age
Vegetation structure (PLS regression)	Plot	Vegetation
Site age (9 classes)	Landscape	Landscape context site age
Vegetation type (4 classes, regression trees)	Landscape	Landscape context vegetation type
Brownfield ratio	Landscape	Landscape context brownfield ratio

status (P, K, and cation exchange capacity), pH, and calcium carbonate content were measured (Table 1). A detailed description of sampling methods is given in Schadek et al. (2009) and Strauss and Biedermann (2006). Site age, as time since initiation of succession, was derived from a time series of aerial photographs. All samples were taken in 2003.

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

Species distribution models

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

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

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

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

Community models

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

The relative importance of predictors for the plant and insect communities was assessed by summing, for each group of variables (soil, site age or vegetation at the plot; site age, vegetation type or brownfield ratio in the landscape context; Table 1), the AIC_c-weights of all models that contained the variable as demonstrated by Strauss and Biedermann (2006).

Modelling scenarios

Using the modelling shell, brownfield proportion was varied between 10 and 90% to analyse species response to available habitat area. The impact of the pace of brownfield turnover was assessed by setting mean site age of brownfields to 3, 6, 10, 15, and 20 years, respectively. The maximum age of a site was restricted to 50 years, as this was the maximum value found in the field data set. Soil properties at the study area could not be spatially predicted in this study. But as artificial landfills are the main soil type at the study sites, soil properties do not vary much between sites. Nutrient and soil water parameters were assigned to the brownfield sites according to the estimated most similar sampling plot. We applied the modelling shell in 45 scenarios (every combination of brownfield proportion and age distribution) in 500 replicates per setting to industrial areas in Bremen with a total area of about 9,850 ha.

Results

Single species models

For 88% of the insect species with prevalence $\geq$10% distribution models could be constructed, whereas only about 55% of the plant species, which passed the prevalence threshold, could be modelled. Model performance according to R^2_{Ncor} ranged from >0.2 to >0.41, which is good for logistic regression models (Table 2). Most of the SDMs reached $\mathrm{AUC}_{\mathrm{cor}}$ values exceeding 0.8, some of them exceeded 0.9, which is regarded as outstanding (Hosmer and Lemeshow 2000).

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

Table 2 Overview of habitat model performance

Number of modelled species (prevalence > 10%):	Plants 38 (60)	Leafhoppers 36 (41)	Grasshoppers 7 (8)
R^2_{Ncor}			
Median	0.28	0.37	0.35
q 25	0.23	0.27	0.26
q 75	0.38	0.41	0.40
$\mathrm{AUC}_{\mathrm{cor}}$			
Median	0.82	0.84	0.86
q 25	0.78	0.81	0.82
q 75	0.87	0.87	0.88
Kappa			
Median	0.51	0.58	0.56
q 25	0.45	0.50	0.54
q 75	0.57	0.64	0.60
CCR			
Median	0.85	0.87	0.85
q 25	0.76	0.80	0.83
q 75	0.89	0.92	0.90

AUC_{cor} and R^2_{Ncor} corrected by bootstrap validation, *kappa* Cohen's kappa, *CCR* correct classification rate, *q 25, q 75* 25% and 75% percentile

Community models

Performance of the community models was of satisfactory quality (Table 3). Concerning sensitivity, CCR, and Cohen's kappa, species composition predictions were better than chance predictions for the majority of plots. Due to the rather low prevalence of several species, chance predictions for specificity (i.e. correct absences) were high, resulting in low proportions of plots for which the community models exceeded these high values (only 26 and 47% for plants and insects, respectively).

The most important predictors for the plant community model were soil parameters, which accounted for about 50% of the predictor weights (Fig. 1, grey boxes). At least one predictor of each plant SDM was a soil parameter. Site age at the plot and in the landscape context both accounted for about 20% of the predictor weights and were involved in approx. 80 and 70% of the models, respectively.

As opposed to that, the leafhopper and grasshopper community was mainly driven by vegetation at the plot, vegetation type and site age in the landscape context, which made up about 25% of the predictor weights and were involved in about 90% of the species models, each (Fig. 1, white boxes). Site age at the plot and soil parameters played only a minor role (about 11 and 15%, respectively), but were involved in about 60 and 80% of the habitat models.

Landscape modelling scenarios

For each brownfield turnover rate (mean site age of 3, 6, 10, 15, and 20 years, respectively), the variance in the results over the 500 replicates per setting decreased with increasing brownfield proportion (Figs. 2, 3, 4). The higher the proportion of brownfield area, the smaller was the mean age of brownfield sites (i.e. the faster the turnover) above which co-occurrence of all plant species was predicted in nearly every replicate simulation run (Fig. 2). Insects reacted similarly, but additionally, at slow turnover (mean age of 20 years), occurrence of all species together was predicted only for very large proportions of brownfield area.

The average plant rarity value over all brownfield cells increased slightly with increasing brownfield proportion but remained constant for insects (Fig. 3). With increasing turnover average plant rarity value

Table 3 Overview of community model performance

	Plant community				Insect community			
	Sens	Spec	CCR	Kappa	Sens	Spec	CCR	Kappa
Median	0.70	0.89	0.84	0.54	0.79	0.90	0.86	0.66
q 25	0.57	0.83	0.79	0.40	0.70	0.82	0.81	0.53
q 75	0.86	0.93	0.89	0.67	0.85	0.94	0.91	0.72
% sig	63	26	65	72	71	47	89	89

Sens sensitivity, *spec* specificity, *CCR* correct classification rate, *kappa* Cohen's kappa, *q 25, q 75* 25% and 75% percentile, *% sig* percentage of plots with significantly better than chance species composition predictions

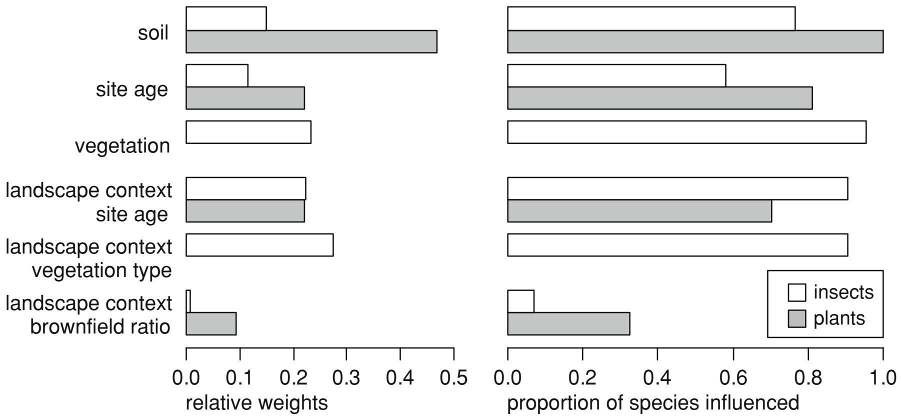

Fig. 1 Relative weights of environmental factor groups in the community model (*left*) and ratio of species influenced by at least one factor of the groups (*right*). Plants are indicated by *grey*, insects by *white boxes*; vegetation parameters at plot and landscape scale were only used in the insect species models

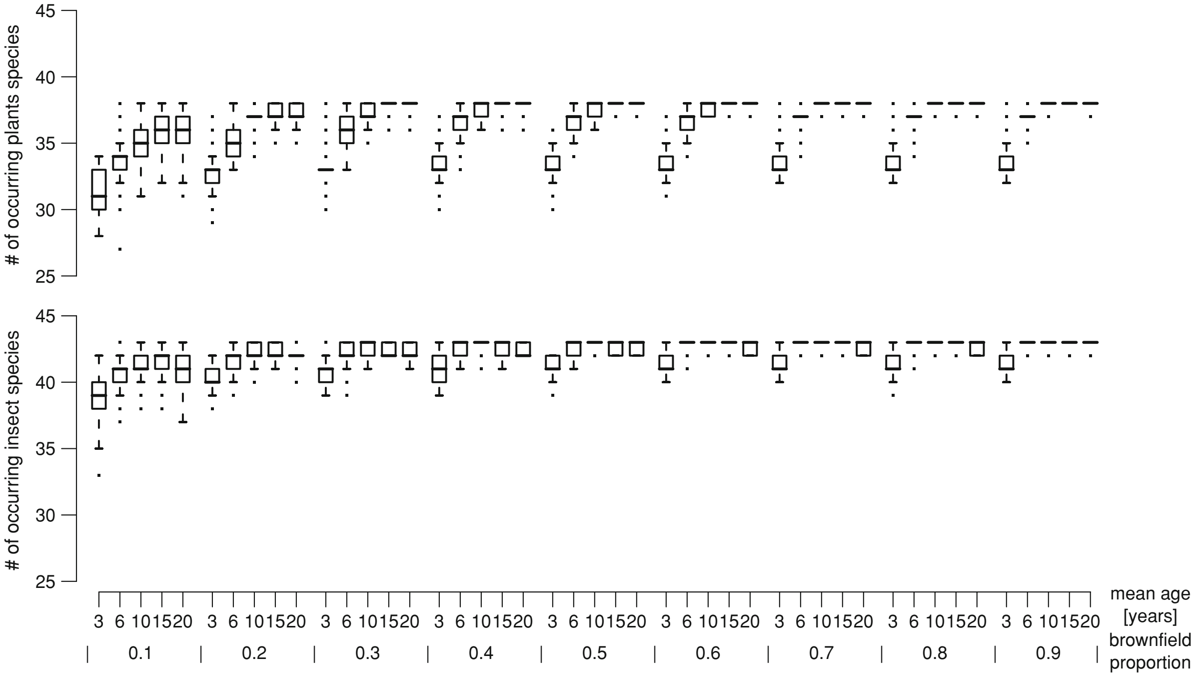

Fig. 2 Biodiversity of the plant (*top*) and insect (*bottom*) community as the total number of occurring species in the study area. The upper X-axis gives the mean brownfield age, the lower the brownfield proportion in relation to the whole study area

increased, whereas the insect rarity value decreased. A linear decrease with decreasing average site age could be found for plants, while the insect rarity value reached its maximum at a mean habitat age of 15 years.

Diverse reactions to the spatio-temporal structure were found on the single-species level (Fig. 4). *Senecio inaequidens*, for instance, benefited from increasing brownfield proportion and its occurrence decreased with increasing mean site age. As opposed to this, increasing brownfield proportion had a negative effect and turnover had no effect on *Cerastium holosteoides*. *Cicadella viridis* showed no reaction to brownfield area, but a maximum occurrence at medium mean site ages. For some species (e.g. *Aphrodes makarovi*), increasing brownfield proportion intensified the effect of turnover rate on the occurrence (causing steeper slopes), while higher site age itself had a positive impact.

Species can be grouped into those reacting positively, or reacting negatively to fast site turnover, or

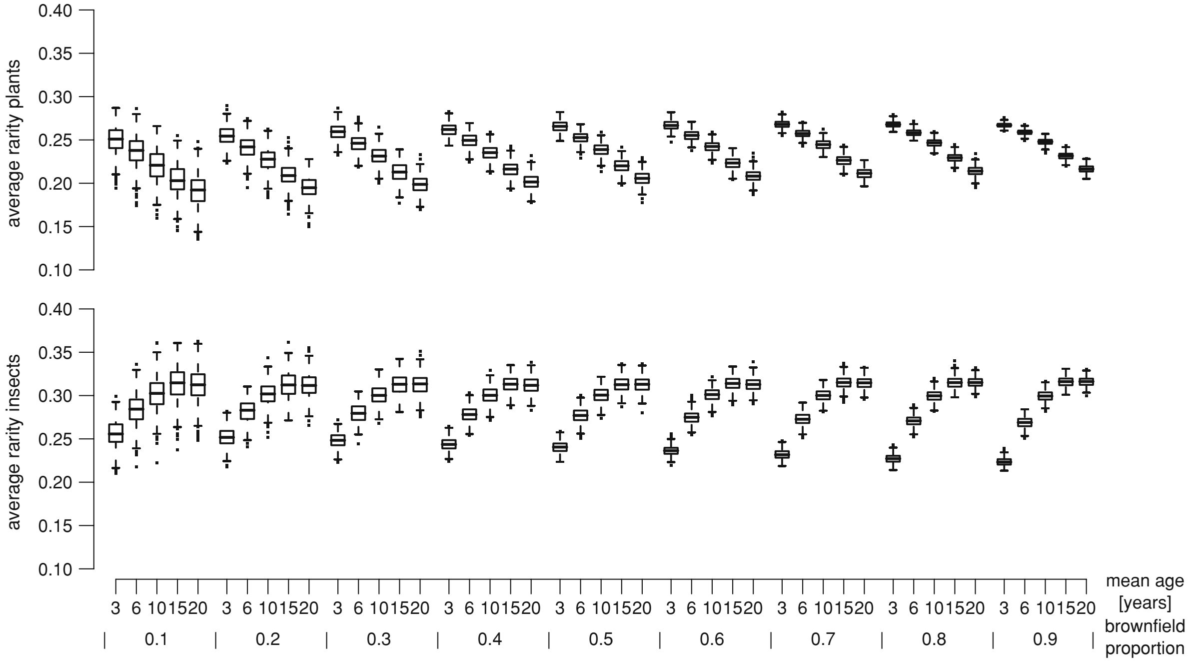

Fig. 3 Rarity of the plant (*top*) and insect (*bottom*) community, averaged over all brownfield cells. X-axis as in Fig. 2

being indifferent to mean site age (Figs. 5, 6). Some benefited strongly from fast turnover, their predicted incidences were highest at a low mean site age (e.g. *S. inaequidens*). On the other hand, there was a group of species with maximum occurrence when site turnover was low, resulting in many older sites (*A. makarovi*). A third group favoured intermediate turnover rates (e.g. *C. viridis* or *Poa trivialis* and *Rumex acetosella*). Several species were not or only marginally influenced by mean site age with constant occurrences over all scenarios (like *Poa pratensis*).

Discussion

Cumulated species distribution models to assess urban biodiversity

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

Species with very low prevalence, which may be endangered ones of special conservation interest, had to be excluded from the analysis as data was insufficient for model building. Prediction of diversity indices in response to environmental factors, regardless of species identity might seem attractive to overcome this problem. However, such an approach neglects the fact that species numbers can stay quite constant over the course of succession or be equal at different spatial locations, while the species composition varies considerably (Strauss and Biedermann 2006). Additionally, in statistical models of species numbers, important predictors for single species occurrence like isolation might be excluded from the model resulting in misleading conclusions for conservation (Bastin and Thomas 1999). This can be tracked down by the assessment of community composition with a species-specific modelling technique.

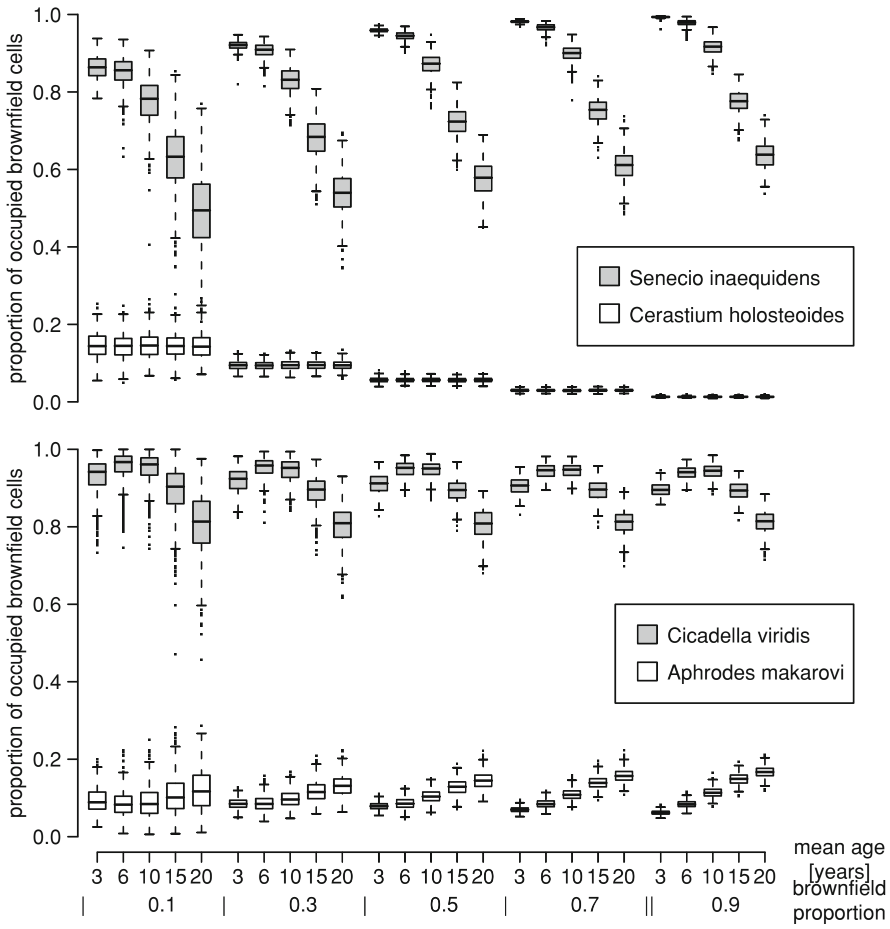

Fig. 4 Single species reaction to various brownfield turnover rates for two example plant species (*top*) and two example insect species (*bottom*)

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

Relative importance of abiotic conditions and spatio-temporal habitat configuration

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

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

The influence of landscape context variables was much stronger on leafhoppers and grasshoppers than on the plant community. Their reaction differed from that of carabid beetles on brownfields, for which only little response of a few species to these parameters has been found (Small et al. 2006). The insect

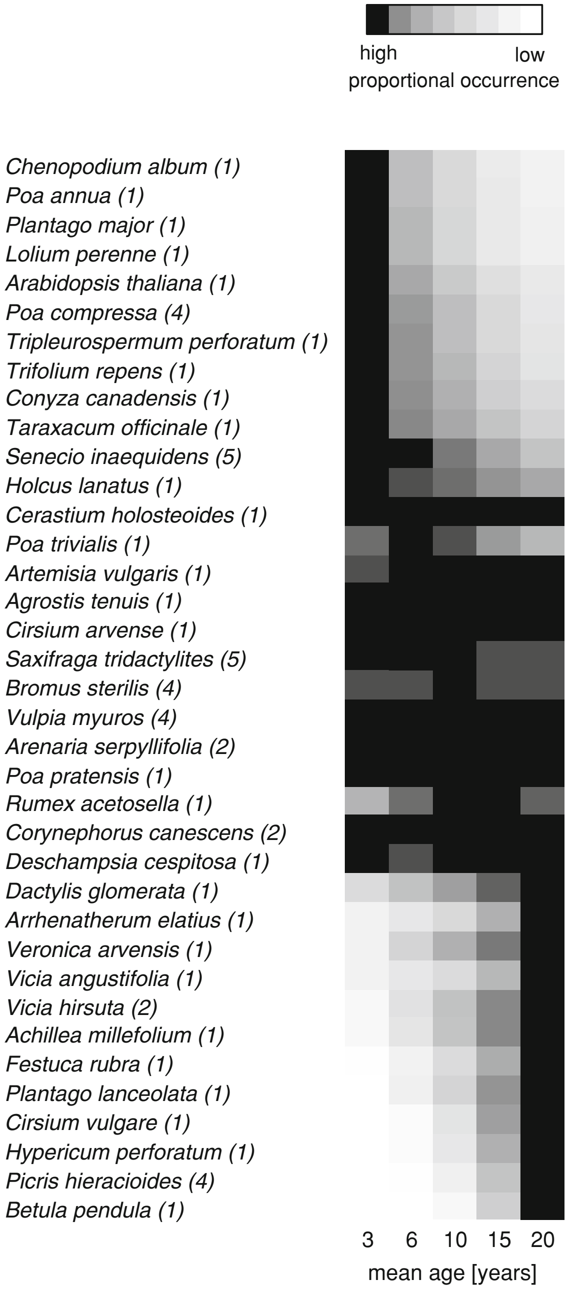

Fig. 5 Occurrence of plant species against mean site age. In *brackets*: regional rarity value. Brownfield proportion is fixed to 0.4. The graphic shows the median proportion of occupied brownfield cells for each mean site age, standardised by division by the maximum value per species

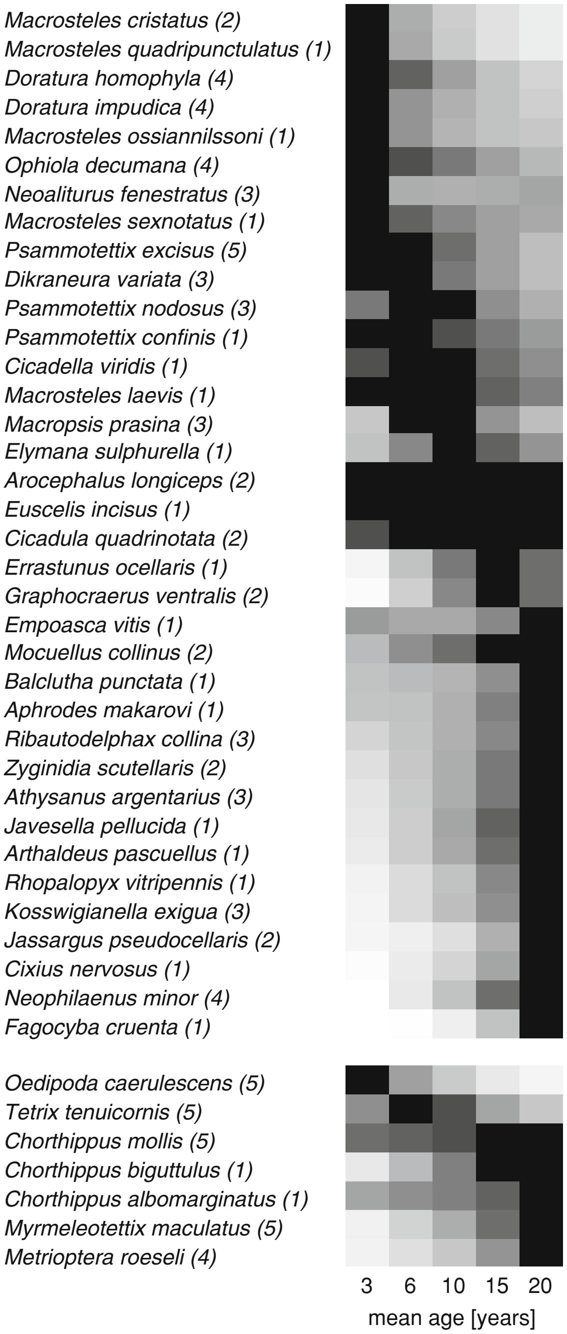

Fig. 6 Occurrence of insect species against increasing mean site age. Grouped in leafhoppers (*top*) and grasshoppers; details and legend as in Fig. 5

community was also driven by the vegetation at the site (and thus indirectly by soil parameters and site age). Carabid assemblages on urban brownfields are strongly influenced by the stage of vegetation succession as well (Small et al. 2003). Strauss and Biedermann (2006) found comparable weights of the main driving factors for grasshoppers and leafhoppers when including detailed measures of horizontal and vertical vegetation structure and host plant cover in the SDMs, although vegetation structure measures made up a greater proportion of the driver weights. Hence, PLS-dimension reduction seems to be a valid simplification in this context but contains probably less information than detailed measures.

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

On the single-species level, the response to brownfield turnover rate was very distinct and variable. This is due to the major role site age plays in determining species' response as revealed by the SDMs. Some species benefited from many young sites (i.e. a fast turnover, Figs. 5, 6), while others depended on older sites in the surrounding or at the plot. In terms of rarity no clear trend could be found on the single-species level. There were regionally rare plant species which benefited strongly from fast turnover (e.g. *Poa compressa*), but others did not show any preference (such as *Vulpia myuros*) or a positive reaction to many older sites (e.g. *Picris hiracioides*). For grasshoppers results were similar. Only regionally rare leafhoppers seemed to depend on a low mean site age, with *Neophilaenus minor* (rarity value 4) being the only rare species which, though preferring young and open habitats, benefits from many older sites in the landscape context. This contrasts the averaged findings for insect rarity which increased with decreasing turnover. It is caused by low predicted occurrences of regionally rare species depending on fast turnover resulting in many young, open sites (e.g. *Doratura impudica* and *Oedipoda caerulescens*) as opposed to high predicted incidences of rare species benefiting from slow turnover (e.g. *M. roeseli*). This difference between community and single-species results and the species dependent reaction to dynamics demonstrates that biodiversity indices alone (such as species richness) reflect effects on species communities inadequately (Olden et al. 2006) and that management decisions may depend strongly on which species is given priority (Bastin and Thomas 1999) if only single species are considered.

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

According to the results of our case study we recommend an intermediate rate of redevelopment and abandonment (mean age of 10–15 years) and a brownfield proportion of at least 40% to maintain most modelled plant, grasshopper, and leafhopper species. The actually mapped proportion of open space in our study area was 31% with an average successional site age of about 8 years. Thus, in the absence of any conservation management within the area the conditions found are already quite close to our recommendations. Furthermore, a detailed study of business areas of six German cities (including Bremen) based on the analyses of aerial photographs over the time series from 1950 to 2004 (Empter 2006) revealed that 34% of all analysed sites experienced one, 22% two, and 7% even three open periods over the whole time span. Thus, site turnover including a period of open space and free succession can indeed be found in industrial areas.

Conclusions

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

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

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

Acknowledgments 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 Cord Peppler-Lisbach for helpful comments on species fidelity to vegetation types and Ute Schadek for providing soil and plant composition data.

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