Dispersal traits determine plant response to habitat connectivity in an urban landscape

Springer

Springer

RESEARCH ARTICLE

Dispersal traits determine plant response to habitat connectivity in an urban landscape

Andrea Schleicher · Robert Biedermann · Michael Kleyer

Abstract Identification of trait syndromes that make species vulnerable to habitat fragmentation is essential in predicting biodiversity change. Plants are considered particularly vulnerable if their capacities for persistence in and for dispersal among local habitats are low. Here we investigated the influence of easily measured functional traits on the presence of 45 plant species in an urban landscape in north-west Germany where patches were separated by distances consistent with regular plant dispersal range. To describe the spatial configuration of patches we calculated species-specific patch connectivities. Then we assessed plant connectivity responses in distribution models calculated from connectivities and environmental predictors. Twenty (45%) of the analysed species showed a positive connectivity response after accounting for species-specific habitat requirements. These species differed from non-responsive species by functional traits associated with dispersal, including reduced seed numbers and higher terminal velocities relative to non-responsive species. Persistence traits played however no role which we attribute to the environmental conditions of urban habitats and their spatiotemporal characteristics. Our study underlines that even ruderal plants experience dispersal limitation and demonstrates that easily measured functional traits may be used as indicators of fragmentation vulnerability in urban systems allowing generalizations to larger species sets.

Keywords Assembly rules · Dispersal limitation · Habitat fragmentation · Local persistence · Model averaging · Plant functional traits · Spatial autocorrelation

A. Schleicher · R. Biedermann · M. Kleyer
Landscape Ecology Group, Institute of Biology and Environmental Sciences, University of Oldenburg, 26111 Oldenburg, Germany

A. Schleicher (✉)
ANUVA Landscape Planning, Allersberger Strasse 185, 90461 Nürnberg, Germany
e-mail: andrea.schleicher@uni-oldenburg.de

Introduction

Habitat fragmentation is considered one of the main factors leading to loss of biodiversity. When habitats become increasingly dissected, species are confronted with habitats of reduced size, extended isolation and novel ecological boundaries with major consequences for their regional persistence (Fahrig 2003; Ewers and Didham 2006). However, functional differences among species may result in different responses to fragmentation. Therefore, identification of species trait syndromes with increased vulnerability to fragmentation is pivotal in predicting biodiversity in fragmented landscapes (Henle et al. 2004; Ozinga et al. 2009).

Response to fragmentation depends on local extinction risk and the potential to rescue declining populations via (re-) colonization (Vos et al. 2001; Johst et al. 2002). Plants will be most vulnerable to fragmentation if their capacities for local persistence and dispersal among patches are low. Translated to a functional perspective, this means that traits enabling a species to survive within and to move between habitat patches confer the ability to maintain viable (meta-) populations in fragmented landscapes (Johst et al. 2002; Verheyen et al. 2004).

The ability of plants to colonize suitable habitats depends on both dispersal range and the number of potential dispersers (Johst et al. 2002; Nathan 2006). This underlines the functional relevance of two types of plant traits. First, dispersal range is determined by traits such as terminal velocity (TV) or floating capacity of fruits, which have been used to describe the species-specific component of seed dispersal kernels (e.g. Tackenberg et al. 2003). TV is the maximum rate at which a seed with its appendices (dispersule) can fall in still air. If vertical air velocity exceeds TV the dispersule can be uplifted and dispersed for large distances (Nathan et al. 2002; Tackenberg et al. 2003). Second, the number of seeds a plant can generate indicates the number of potential dispersers. The production of many seeds may increase the chance of colonization even if the dispersal range is limited (Grashof-Bokdam and Geertsema 1998; Butaye et al. 2001; Tackenberg et al. 2003; Soons et al. 2005; Bossuyt and Honnay 2006).

By contrast, relationships between local persistence ability and plant functional traits are widely recognized as highly ecosystem dependent. Under ample resource conditions species are favored that are able to grow and reproduce in the presence of competitors (Goldberg and Barton 1992; Suding et al. 2003). In stressful environments, however it is important to cope with physically low resource levels. Consequently, a shift from traits conferring high competitive ability towards stress tolerance traits occurs along a gradient of decreasing productivity (Campbell and Grime 1992; Foster 2001; Crowley and McLetchie 2002). Shifts in leaf and stem trait expressions are expected, e.g. from high to low specific leaf area, canopy height and leaf size (Díaz et al. 2004). Increasing stress or disturbance may further select trait expressions that enable plants to bridge periods of unsuitable habitat conditions (e.g.

persistent seed banks) or rapidly regenerate between disturbance events (e.g. short life span).

In this study, we investigated the role of plant functional traits in response to habitat fragmentation in an urban environment. We assumed that traits supporting local persistence and dispersal influence plant response to fragmentation. Specifically, we hypothesized that species responding to fragmentation will display trait expressions that indicate the following: (i) decreased dispersal range and lower dispersal probability; (ii) decreased capacity to persist locally via seed banks; and (iii) decreased ability to tolerate stress, disturbance or competition relative to species less sensitive to the effects of fragmentation. We assumed that species with traits indicating (ii) or (iii) are more susceptible to temporal variations in habitat quality which may lead to local extinctions. As a consequence, their populations may become more dissected than those of species with higher tolerance of stress, disturbance or competition.

Previous studies have documented not only vast discrepancies regarding the commonness of fragmentation effects. Within large species data sets, responsiveness to fragmentation ranged between rare responses (e.g. Dupré and Ehrlén 2002; Krauss et al. 2004) to connectivity being the main predictor (Bastin and Thomas 1999; Piessens et al. 2005). Studies have also reported a variety of relationships between fragmentation vulnerability and functional traits, which seems to exceed the expected variability between ecosystems. For instance, although Kolb and Diekmann (2005) and Dupré and Ehrlén (2002) conducted their studies in deciduous forests with similar fragmentation characteristics, Kolb and Diekmann identified many more traits responding to fragmentation, including canopy height and seed longevity. These discrepancies may to some extent be explained by differences in methodology (Freckleton and Watkinson 2002; Tremlová and Münzbergová 2007).

The relevance of dispersal limitation for biodiversity patterns is highly dependent on the study scale (Gilbert and Lechowicz 2004; Girdler and Barrie 2008). For instance, field and modelling studies have demonstrated that dispersal by wind rarely covers distances of more than 100 m, whereas dispersal across larger distances becomes increasingly dependent on stochastic factors (Higgins et al. 2003; Tackenberg et al. 2003; Soons et al. 2004). Regarding that much previous work has focused on habitat

patches separated by several kilometres (e.g. Dupré and Ehrlén 2002; Kolb and Diekmann 2005; Piessens et al. 2005), the rarity and unpredictability of dispersal events is likely to have hampered the detection of relevant functional characteristics. In addition, incorrect assumptions on matrix uninhabitability and habitat suitability may obscure the influence of fragmentation. Discriminating suitable and unsuitable habitats is particularly problematic in plants that do not have easily identified niches (Freckleton and Watkinson 2001; Ehrlén et al. 2006). Consequently, habitat suitability should be estimated for each species separately, rather than assuming identical niche requirements for species inhabiting a given habitat type. For instance, regarding all forest fragments as suitable habitat for understorey species is error-prone as subtle differences in e.g. soil acidity may suffice to make a habitat uninhabitable for a subset (e.g. Dupré and Ehrlén 2002). Ruling out undetected incidences in the matrix is facilitated in urban environments. These are particularly suited for fragmentation studies because impervious surfaces represent an uninhabitable matrix that is clearly distinguished from potential habitats. From a statistical point of view, the effects of spatial autocorrelation (SAuC) should be considered when distinguishing unsuitable from uncolonized habitat. SAuC is well-known to result in erroneous assessment of significant explanatory variables violating the assumption of independent samples (Legendre and Legendre 2006; Dormann et al. 2007). However it becomes more than a statistical issue in empirical studies regarding dispersal limitation. Spatially clustered plant species occurrences are not necessarily generated by dispersal but may simply reflect spatially autocorrelated suitable habitats (Legendre and Legendre 2006). Therefore, the effects of dispersal limitations must be separated from the effects of spatially autocorrelated environmental conditions.

In this study, we explicitly aimed to overcome the obscuring effects arising from the above-mentioned methodological challenges. Therefore, we investigated the relationship between plant functional traits and fragmentation vulnerability at a scale that corresponds to the dispersal range most commonly observed for wind-dispersed plants. We predicted that clear differences among species would emerge in an urban landscape in which impervious surfaces help to rule out matrix effects, and when the spatial analysis of patch configuration is based on the specific habitat requirements of each single species. Additionally, we developed a methodology that separates dispersal limitation and habitat unsuitability, and accounts for the effects of SAuC. This approach enabled us to identify easily measured functional traits corresponding to fragmentation vulnerability, which may be tested and subsequently applied to different groups of taxa.

Methods

Study area

The study was conducted at an industrial park at the city of Bremen, Germany (53°05′N, 8°44′E, mean annual temperature 8.8°C, mean annual precipitation 694 mm: Deutscher Wetterdienst 2006/2007) which constituted an artificial island habitat. The area had been created by filling the original marshland with about 2 m of sand in a step-by-step procedure starting in the 1970s. By 2006, this process had generated a patch network of about 4.0 km^2 and an age gradient spanning almost 40 years.

In determining habitat connectivity, the likelihood of missing species occurrences in the surrounding landscape composed of moist grassland was small due to the strong contrast with the land-fills in terms of environmental conditions and species composition. The study area itself was divided into an uninhabitable matrix and habitable patches. Patches with impervious surfaces and, accordingly, without any plant occurrences (e.g. buildings, paved structures) were considered uninhabitable by plants and categorized as uninhabitable matrix. By contrast, all structures with pervious surfaces that were either vegetated or open (e.g. wastelands, road verges railroad tracks) were considered as potential habitat. Patch geometries were mapped in a geographic information system (GIS), whereby patches larger than 100 × 100 m were split into smaller equally sized patches.

Between May and September 2006 we visited all resulting 958 patches and collected presence/absence data of 52 plant species. Species selection aimed at satisfying the statistical requirement of a minimum of ten occurrences which has been advised for logistic

regression analysis (Steyerberg et al. 2001). That is, we collected data on those species which had been observed with a minimum occurrence frequency of ten in a previous study (Schadek et al. 2009). As an inverse measure of isolation, we determined species-specific connectivity for each patch as proposed by Hanski (1994). The connectivity S of patch i to all patches j was calculated as follows:

$$S_i = \sum_{j \neq i} \exp(-\alpha \cdot d_{ij}) \cdot A_j^b$$

where A_j is the area of patch j, d_{ij} is the distance between the centroids of patches i and j, and $b = 0.5$ following the recommendations of Moilanen and Nieminen (2002). We used $\alpha = 0.02$, which corresponds to a migration distance of 100 m as a realistic value for intermediate and frequently observed dispersal range of many wind-dispersed plants (Tackenberg et al. 2003; Soons et al. 2004). Furthermore, Moilanen and Nieminen (2002) report that connectivity is not highly sensitive to the value of α. Centre to centre distances between patches and patch areas were obtained using GIS (ESRI Inc. 2006).

To disentangle suitable from unsuitable habitats for each species we calculated species distribution models with the following variables: soil texture (paved, coarse-grained, fine-grained), degree of shrub encroachment, typical disturbance regime and patch age. Patch age was estimated as age since soil deposition based on chronosequences of aerial photos since 1974 and field observations.

Disturbance regimes in ruderal sites are often hard to describe. In many patches, irregularly used parkings, deposits of construction material, small spots of spontaneous vegetation, etc., indicated fine mosaics of spatially and temporally varying disturbance regimes. Patches with such heterogenous disturbance regimes were excluded and subsequent analyses were performed on a subset of 268 patches which were characterised by either absent or spatially homogeneous disturbances. The latter were broadly classified into (i) infrequently disturbed (by e.g. vehicles) and (ii) frequently disturbed (e.g. mowing) based on several years' observations. However, connectivities of the species in the 268 patches were calculated from occupancy data of all 958 patches.

Due to the large number we could not directly record soil properties for each patch ($n = 268$). Instead we calculated average Ellenberg values which often show a close correlation with corresponding measurements of environmental variables (Schaffers and Sykora 2000) and have proven suitable to assess local environmental habitat conditions (Ozinga et al. 2004; Verheyen et al. 2004). We considered Ellenberg values for soil moisture (F), nutrients (N) and reaction since a former study had indicated that soil acidity and nutrient availability were most suitable to describe community composition in the study area (see Schadek et al. 2009). However, Ellenberg values for moisture and nutrients were correlated (Pearson correlation: $r = 0.58$) and exhibited similar variability among sites, mean F-value $= 4.71 \pm 0.58$, mean N-value $= 4.84 \pm 0.78$). A constrained redundancy analysis further indicated that Ellenberg values for moisture explained most variability among sites (correlation coefficient with 1st axis: $r = -0.60$), whereas Ellenberg values for nutrients also covaried with other explanatory variables, such as shrub encroachment and patch age (Fig. 1). To reduce multi-collinearity among explanatory variables we only included Ellenberg values for soil moisture and reaction into subsequent analyses. The average Ellenberg value of a patch was calculated from the values of the species present in the patch as obtained from Ellenberg (1986). The species whose incidence was to be predicted by the Ellenberg values was omitted from the calculation to avoid circularity.

Functional trait data

Seed dispersal is inherently hard to quantify (Cain et al. 2000). In our study area, dispersal by ground-dwelling animals appeared unlikely due to fenced properties, heavy traffic on the roads adjacent to the patches, and frequent recreational use by locals. During several years of observation, we only noted rabbits whose contribution to plant dispersal could not be assessed. Likewise, dispersal by birds could not be determined. However, as the abundance and diversity of bird species was relatively low and the dispersal syndromes of the plant seeds did not include specific adaptations for bird dispersal (e.g. fleshy fruits) we concluded that bird dispersal was of minor importance and considered wind to be the most important dispersal vector. By contrast, the seeds of many grasses had awns which cannot only promote animal dispersal but also wind dispersal. Given the

Fig. 1 Ordination diagram of the first two axes of the constrained redundancy analysis (RDA) of 258 patches on local environmental variables (disturbance, patch age, shrub encroachment, soil texture, and Ellenberg values for moisture (F), nutrients (N) and soil reaction (R). *Grey dots* indicate patches, *letters* indicate species (for abbreviations see Appendix 1—Supplementary material). For clarity, only species are shown with correlation coefficient with axis-scores >0.05. *Arrows* represent the constraining environmental variables. Axes inertias are given in *parentheses*
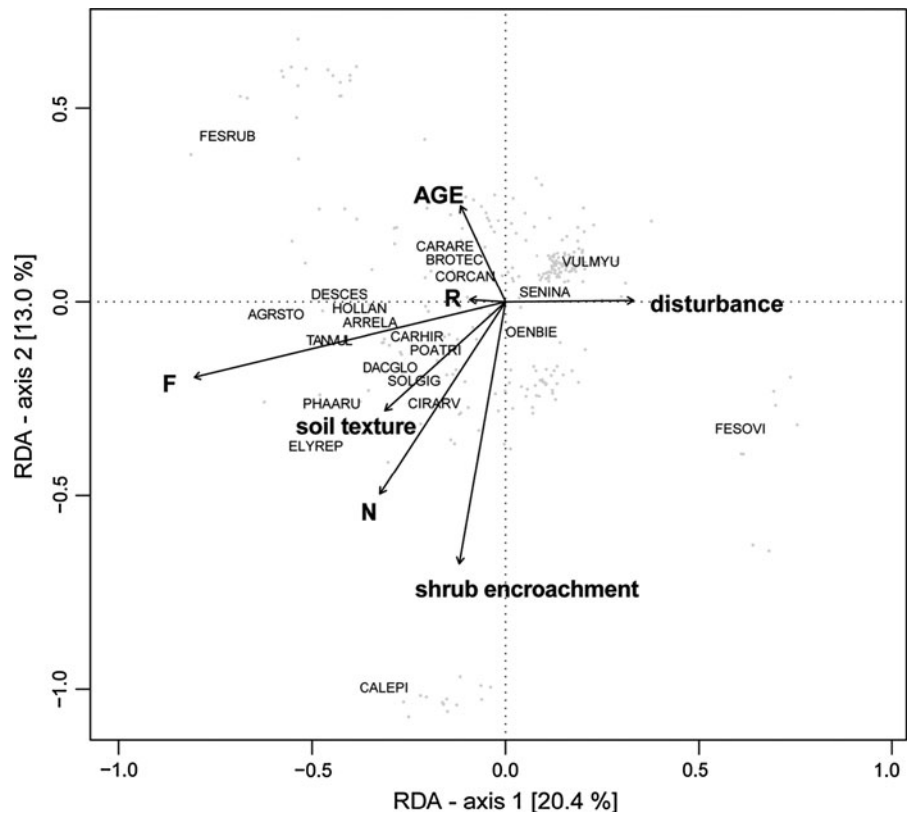
absence of large herbivores, wind was assumed to be the most prevalent dispersal vector in this urban landscape.

We used seed TV as a species-specific measure of wind dispersal. Such a simple approach is adequate in herbaceous vegetation where wind turbulances play a minor role (Fenner and Thompson 2004). TV was measured by K. Thompson using seed material collected in the field according to Askew et al. (1997). Seed releasing height was not used because this trait was strongly correlated with canopy height (see below).

Seed production is often considered a variable trait increasing with productivity. The high number of patches made it logistically impossible to determine seed production per patch. Instead, seed number per species was used to estimate dispersal probability. Seed number was calculated as the average number of seeds per shoot/ramet of ten individuals which were collected from ten patches covering the full range of the species-specific habitat conditions. Generally, site productivity was comparative low and had only minor effects on species distribution (Fig. 1). Therefore, we

considered the effects of patch productivity on seed number to be rather small.

Species ability to persist locally was evaluated by two sets of traits. Local persistence under disturbance was described by life span and seed bank longevity index (Bekker et al. 1998) the latter quantifying the capacity of a species to maintain a population at a site from the available seed bank. Ability to persist in either resource-poor or resource-rich environments was assessed by specific leaf area, seed mass, leaf size and canopy height (Westoby et al. 2002). Local trait information had been collected in a previous study in the area (Schadek 2006) with the exception of plant life span and seed longevity index which were extracted from the LEDA Traitbase (Kleyer et al. 2008). All traits were collected according to the LEDA Traitbase standards (see www.leda-traitbase.org). Species nomenclature followed Jäger and Werner (2002).

Statistical analysis

To determine the response of each species to connectivity we combined a habitat modelling approach with

a methodology to handle SAuC. Our approach involved altogether five steps which can be summarized as follows: We first determined the response of species to environmental variables and connectivity following Strauss and Biedermann (2006, steps 1 and 2). Then we performed two tests aiming to account for the effects of SAuC. In a first test, we addressed the problem of biased variable estimates arising from spatial data dependency (step 3). The second test specifically aimed at ensuring that our measure of connectivity did not simply reflect autocorrelated environmental conditions (step 4). In a last step, we applied model averaging following Burnham and Anderson (2002) to merge adequate habitat models into one averaged model per species. The single steps will be described in the following in more detail.

As a first step, we calculated univariate logistic regression models for each species. Thereby we tested for either sigmoid or unimodal relationships between species occurrence, abiotic patch parameters and species-specific connectivity (Strauss and Biedermann 2006). Patch age and connectivities were log-transformed before use in the logistic regressions.

In the second step, we calculated multiple models for all possible combinations of the significant variables identified from the univariate models to avoid spurious inclusion of variables (Strauss and Biedermann 2006). Multiple models were only chosen for further analyses if the following criteria were met: (i) the model performed better than any model of a lower hierarchy; and (ii) if coefficients significantly differed from zero ($P < 0.05$).

As a third step, we corrected for biased parameter estimates resulting from spatial data dependency by capturing the spatial patch configuration in spatial vectors and adding them to the model (Dray et al. 2006; Dormann et al. 2007). We computed global Moran's tests to determine if spatial structure was present in the model residuals. Second-order stationarity assumption was verified by visually checking variograms for a sill and additionally applying Levene's test for variance equality on three different patch groupings (Legendre and Legendre 2006): (i) based on increasing x-coordinates; (ii) based on increasing y-coordinates; and (iii) based on boundaries as imposed by road and railway infrastructure. If the second-order stationarity assumption was not accepted, we considered models with a P-value > 0.01 of any coefficient likely to be erroneously significant and treated them like models with

residuals exhibiting a significant spatial structure according to Moran's test. If spatial structure was detected in the residuals, we applied spatial eigenvector mapping (SEVM) (Dray et al. 2006). SEVM is particularly suitable to check variable significance because it removes residual SAuC and can deal with different error distributions such as that originating from binary response data (Griffith and Peres-Neto 2006; Dormann et al. 2007). We followed Dormann et al. (2007) and calculated spatial eigenvectors which were then incorporated into the regression model as covariates. If any model coefficient became insignificant after the addition of the SEVM vectors the model was excluded from further analysis.

To further separate dispersal effects from those of spatially autocorrelated environmental factors, we applied an additional test to models exhibiting connectivity (step 4). We assumed that connectivity captured not only spatial patterns generated by autocorrelated environmental factors but also patterns induced by dispersal processes between local population (Legendre and Legendre 2006; Dormann et al. 2007). If so, connectivity should explain species occurrences better than the SEVM vectors which are based solely on the spatial positions of the habitats. Hence, we calculated a corresponding model in that SEVM vectors replaced connectivity. If this model outperformed the connectivity model in a likelihood ratio test, we concluded that connectivity reflected spatially autocorrelated environmental factors and excluded the model from further analysis.

In a fifth step, we applied model averaging as proposed by Burnham and Anderson (2002) to all remaining multiple models for a species. Model averaging does not rely on a model selection procedure, but rather merges all entering models to a single averaged model. Each entering model is assigned a weight according to its relative performance calculated as the difference between the Akaike Information Criterion (AIC) of the entering model and the AIC of the best model. In addition to averaged coefficients, model averaging calculates a variable weight according to variable performance and number of models containing that variable. This variable weight can be used to assess the importance of a predictor relative to other predictors (Burnham and Anderson 2002) and we used connectivity weight to determine species connectivity relevance in comparison to the importance of environmental factors. Moreover, we defined two

connectivity response groups: species with a connectivity weight smaller than 1% were classified as non-responsive to connectivity, and species with a connectivity weight greater than 1% were classified as responsive to connectivity (see Appendix 1—Supplementary material).

Trait relationships were analyzed using Spearman correlation coefficients or Kolmogorov–Smirnov tests and differences between connectivity response groups with Wilcoxon–Mann–Whitney and χ^2 tests. Seed mass and seed number were log-transformed prior to analysis. Interactions between responsive functional traits were calculated by generating the products or quotients and comparing the obtained values between the connectivity response groups. Species models were calculated using the statistical programming software R (R Development Core Team 2005) and other statistical analyses were performed in SPSS 15.0 for Windows (SPSS Inc. 2006).

Results

Importance of habitat isolation versus habitat suitability

For 45 out of 52 species our analysis yielded averaged models with Nagelkerke's $R^2 > 0.1$. All models with Nagelkerke's $R^2 < 0.1$ were omitted from subsequent analyses. Within the remaining models Nagelkerke's R^2 ranged between 0.11 and 0.33 (mean: 0.20, see Appendix 1—Supplementary material). Model averaging provides variable weights that can be used to assess variable importance (Burnham and Anderson 2002). Accordingly, we derived a given species connectivity response from the weight of the connectivity variable in the species model. Out of 45 remaining species, 25 species (56%) possessed connectivity weights >1% and were classified as "responsive to connectivity" while the other 20 species were determined "non-responsive" (see Fig. 2; Appendix 1—Supplementary material). The average connectivity weight of the 25 responsive species was 27% suggesting that the explanatory power of connectivity across all species was lower than the cumulative power of the environmental variables (Fig. 2). However, connectivity weight showed high variability among species ranging from 2% (*Tripleurospermum maritima*) to 100% (*Arrhenaterum elatius*).
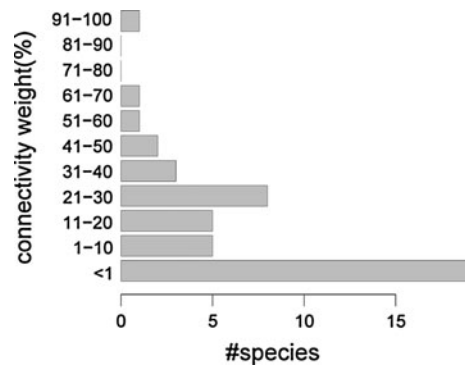
Fig. 2 Frequency of connectivity weights for the studied species

SAuC correction highly reduced the number of adequate models that entered the averaged model of a species. However, this resulted in only minor changes to the averaged models in terms of model goodness and presence of model parameters. When comparing models with and without application of the SAuC correction (steps 3 and 4 in "Methods") the connectivity weights of 14 species were changed by the correction (seven decreases and seven increases, see Appendix 1—Supplementary material). The connectivity weights of *Betula pendula*, *Sisymbrium altissimum* and *Taraxacum officinale* decreased below the threshold of 1.0% resulting in their reclassification from responsive to non-responsive.

Functional traits and connectivity

Increasing life span was positively correlated with leaf size but negatively with seed longevity index (Table 1). A negative correlation was observed between seed mass and seed number, and seed number was also positively correlated with canopy height. TV increased with seed mass and decreased with seed number.

Species responsive to connectivity did not differ from non-responsive species in canopy height, leaf size, specific leaf area, life span or seed longevity index (Table 2). However, responsive species showed significantly lower seed numbers and higher terminal velocities than non-responsive species, while the differences in seed mass were not significant (Fig. 3). Subsequent analysis revealed that the clearest distinction between connectivity response groups was obtained when combining seed number and TV in a quotient.

Table 1 Spearman correlation coefficients among plant functional traits

Functional trait	Canopy height	Specific leaf area	Leaf size	Life span	Terminal velocity	Seed longevity index	Seed mass
Specific leaf area	−0.19						
Leaf size	0.27	−0.24					
Life span	0.03	−0.08	**0.34**				
Terminal velocity	−0.21	0.13	−0.18	−0.20			
Seed longevity index	−0.04	0.23	**−0.35**	**−0.34**	−0.02		
Log seed mass	−0.20	0.07	0.03	−0.29	**0.52**	−0.12	
Log seed number	**0.33**	−0.14	0.29	0.03	**−0.40**	0.26	**−0.56**

Significant results are in boldface

Table 2 Results of two-sided Wilcoxon–Mann–Whitney tests for independent samples. General difference in plant functional traits between connectivity response groups. Log(seed number)/terminal velocity is the quotient of log transformed seed number and terminal velocity

Functional trait	P-value
Terminal velocity	**0.013**
Log seed number	**0.042**
Log seed mass	0.337
Canopy height	0.537
Specific leaf area	0.599
Leaf size	0.144
Seed longevity index	0.749
Log(seed number)/terminal velocity	**0.007**

Significant results are in boldface

Discussion

Although ruderal plants are usually considered able to quickly colonize any available suitable habitat more than half of the 52 species in our study responded to connectivity, indicating spatially structured plant distributions. We hypothesized that response to connectivity could be explained by species traits associated with dispersal ability and local persistence. The species responding to connectivity exhibited significantly higher terminal velocities and lower seed numbers than non-responsive species. As a high TV corresponds to a short dispersal range both trait expressions are indicative for high dispersal capacity and support our hypothesis that species responsive to connectivity should show traits conferring low dispersal ability. The results demonstrated the relevance of TV as a marker of

dispersal range (Tackenberg et al. 2003; Nathan 2006) and seed number was indicative of the number of potential dispersers, emphasizing the relevance of two types of dispersal traits.

Additionally, we found that the clearest differentiation between connectivity response groups was obtained by the combination of seed number and TV. This observation suggests a compensatory relationship between the two traits in which high dispersal range may counterbalance low numbers of dispersers and vice versa. Our results provided empirical evidence for current plant dispersal concepts, which emphasize both the role of seed number and the duration of seed transport—indicated here by TV—for dispersal across intermediate distances (Nathan et al. 2008).

Seed number was also relevant in empirical studies, in which distances between habitat patches by far exceeded regular dispersal ranges (e.g. Dupré and Ehrlén 2002; Verheyen et al. 2004; Kolb and Diekmann 2005). But in terms of dispersal range studies have often highlighted the role of dispersal mode. Here we provide strong empirical support of wind dispersal models predicting that TV allows a quantitative assessment of dispersal capacity across intermediate distances (Tackenberg et al. 2003; Soons et al. 2004). Across larger distances, however, these mechanistic models demonstrate an increased relevance of stochastic factors (e.g. extreme winds, weather conditions).

The second and third elements of our hypothesis were dismissed, because functional traits associated with local persistence were not related to plant response to connectivity. Life span, seed bank

Fig. 3 Relations between selected plant functional traits (terminal velocity, log seed number, log seed mass, log(seed number)/terminal velocity), and species groups based on their response to connectivity. Species were considered "responsive to connectivity" if the connectivity weight in the averaged model was >1.0. Boxplots show median, 25 and 75% quartiles, minimum and maximum, and outliers, respectively
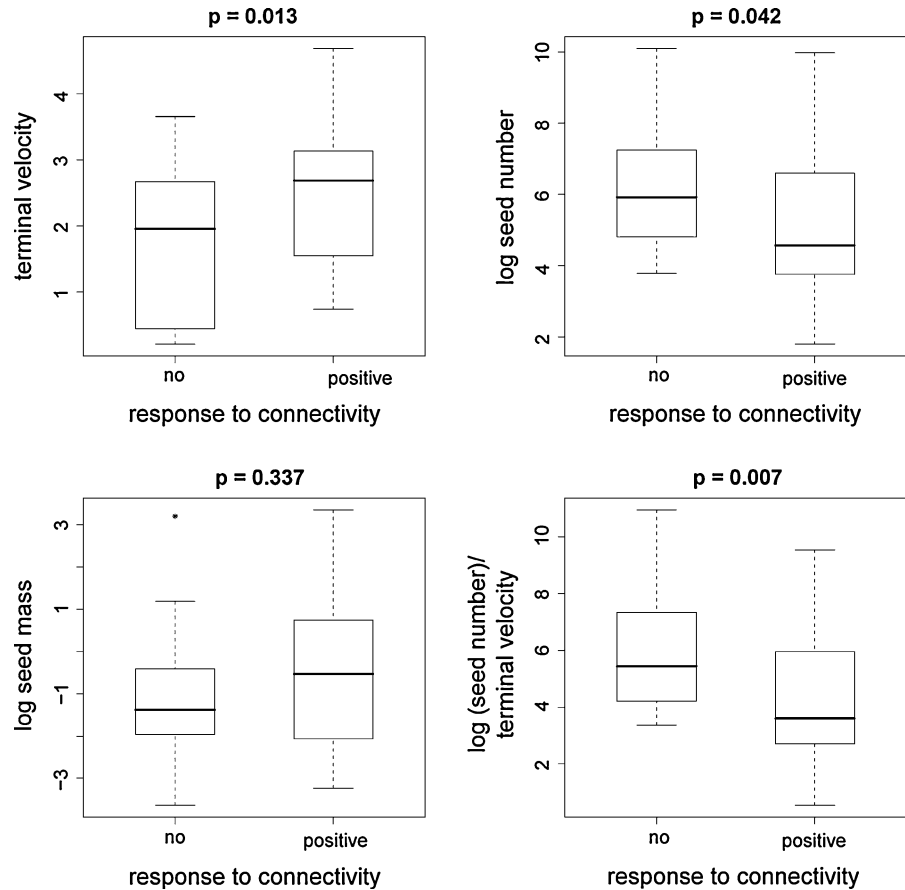
longevity, specific leaf area, canopy height or leaf size did not differ between responsive and non-responsive species. These results are inconsistent with previous empirical studies that detected relationships between fragmentation and persistence traits. For example, fragmentation vulnerability in forest ecosystems was associated with seed number, seed mass, plant height and life span (Dupré and Ehrlén 2002; Kolb and Diekmann 2005). These observations indicated the importance of functional traits associated with dispersal as well as local viability via competitive ability. By contrast, Piessens et al. (2005) showed that the ability to form persistent seed banks increased local persistence in heathland ecosystems. On national scales, Ozinga et al. (2009) found that persistent seed banks lowered the local extinction risk of plants under increased habitat fragmentation.

The particular habitat conditions and spatiotemporal dynamics of urban systems may be responsible for this discrepancy, as they minimize the chance of plant recruitment from the seed bank and for local persistence via competition. New habitats for spontaneous vegetation are often created by the transformation of former agricultural land or by the abandonment of built-up spaces with impervious surfaces (Kattwinkel et al. 2009), resulting in raw soils relatively free of buried diaspores. Moreover, habitat turnover in terms of the conversion of built-up to fallow sites and vice versa occurs irregularly and with long time intervals. In other systems, such as arable fields with old soils and short disturbance return intervals due to crop rotation, or old systems with little disturbance including forests or heathlands, persistent seed banks or competitive ability may be superior to dispersal (Schippers et al. 2001). Our results suggest, however, that dispersal ability is favourable if habitat turnover is relatively slow and new habitats are created on raw soils. Alternatively, persistence in the soil seed bank might become more important in older plots.

Studies observing plant responses to fragmentation in old systems with a constantly increasing degree of

landscape fragmentation have provided additional evidence of the confounding role of extinction debt (Grashof-Bokdam and Geertsema 1998; Helm et al. 2006; Ozinga et al. 2009). Extinction debt refers to the phenomenon that species with long life span or seed bank longevity are buffered from local extinction with the consequence that these taxa respond to habitat fragmentation with a temporal lag (Tilman et al. 1994). If so, distribution patterns will reflect historical rather than actual habitat configurations which may lead to an inaccurate conclusion that species with long term persistence ability are not affected by connectivity (Ewers and Didham 2006; Helm et al. 2006). Urban systems, however, are not characterized by long-term trends in habitat fragmentation but by oscillating habitat connectivities due to high rates of patch destruction and creation, which may reduce the importance of extinction debts.

From a methodological point of view, our study differed from previous studies in three major aspects. First, we chose a comparable fine scale corresponding to the dispersal range of wind-dispersed plants. This approach increased the likelihood of discerning uncolonized habitat patches and underestimating the role of dispersal limitation.

Second, the 52 species used in this study represent a considerable fraction (>20%) and the most common species of the total species pool. This extensive species list came at the cost of considerable heterogeneity in species requirements making it difficult to develop a sampling design and select environmental variables which are meaningful to all species. Consequently, the explanatory power of species distribution models was relatively low, a characteristic commonly observed in many multi-species studies (e.g. Krauss et al. 2004; Kolb and Diekmann 2005).

Third, our study assessed habitat suitability for the entire study site and for each species separately. In fact, the models showed marked differences among species regarding the relative importance of connectivity and environmental predictors. These differences support the observations of previous studies suggesting that although the average explanatory ability of connectivity may be small single species were strongly affected (Dirnböck and Dullinger 2004; Hérault and Honnay 2005; Prugh et al. 2008). Furthermore, calculation of species-specific models was a necessary precondition to disentangle dispersal limitation from spatially autocorrelated habitat unsuitability. For example,

B. pendula and *T. officinale* responded to connectivity without SAuC correction, but showed no response after the models were corrected. *B. pendula* and *T. officinale* are well-known for their highly effective dispersal (e.g. Grime et al. 1989). Therefore, we assume our approach was successful in separating the effects of habitat unsuitability and dispersal limitation.

Conclusion

This study demonstrated functional relationships between species-specific connectivity and easily measured traits such as seed TV and seed number. Yet, discrepancies in trait syndromes between different published studies indicate the absence of an easy, single classification of sensitivity to fragmentation across all environments, which is hardly surprising as there is enormous variation across species and habitat types.

Furthermore, the interpretation of the results of studies conducted in different environments is also hampered by the incomparability of different methods. In particular, we want to stress the importance of appropriate spatial scales, species-specific assessment of habitat suitability, and separation of SAuC of environmental conditions from dispersal effects. A consensus regarding methodological requirements to adequately describe the response of plants to habitat fragmentation may decidedly promote the identification of trait syndromes with increased vulnerability to fragmentation.

Trait data are becoming increasingly available for a large number of species (e.g. Kleyer et al. 2008) and linkages between traits and habitat configuration, as identified in our study, may allow the assessment of fragmentation vulnerability for large species data sets based on their functional traits. In the long run, this approach might be useful for the planning and design of habitat networks.

References

Askew AP, Corker D, Hodkinson DJ, Thompson K (1997) A new apparatus to measure the rate of fall of seeds. Funct Ecol 11:121–125

Bastin L, Thomas CD (1999) The distribution of plant species in urban vegetation fragments. Landscape Ecol 14:493–507

Bekker RM, Bakker JP, Grandin U, Kalamees R, Milberg P, Poschlod P, Thompson K, Willems JH (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. Funct Ecol 12:834–842

Bossuyt B, Honnay O (2006) Interactions between plant life span, seed dispersal capacity and fecundity determine metapopulation viability in a dynamic landscape. Landscape Ecol 21:1195–1205

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Butaye J, Jacquemyn H, Hermy M (2001) Differential colonization causing non-random forest plant community structure in a fragmented agricultural landscape. Ecography 24:369–380

Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. Am J Bot 87:1217–1227

Campbell BD, Grime JP (1992) An experimental test of plant strategy theory. Ecology 73:15–29

Crowley PH, McLetchie DN (2002) Trade-offs and spatial life-history strategies in classical metapopulations. Am Nat 159:190–208

Deutscher Wetterdienst 2006/2007. Mittelwerte des Niederschlags und der Temperatur für den Zeitraum 1961–1990

Díaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Díez P, Funes G, Hamzehee B, Khoshnevi M, Pérez-Harguindeguy N, Pérez-Rontomé MC, Shirvany FA, Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A, Jones G, Kowsary E, Kazemi-Saeed F, Maestro-Martínez M, Romo-Díez A, Shaw S, Siavash B, Villar-Salvador P, Zak MR (2004) The plant traits that drive ecosystems: evidence from three continents. J Veg Sci 15:295–304

Dirnböck T, Dullinger S (2004) Habitat distribution models, spatial autocorrelation, functional traits and dispersal capacity of alpine plant species. J Veg Sci 15:77–84

Dormann C, McPherson J, Araújo M, Bivand R, Boilliger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling W, Kühn I, Ohlemüller R, Peres-Neto P, Reineking B, Schröder B, Schurr F, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Model 196:483–493

Dupré C, Ehrlén J (2002) Habitat configuration, species traits and plant distributions. J Ecol 90:796–805

Ehrlén J, Münzbergová Z, Diekmann M, Eriksson O (2006) Long-term assessment of seed limitation in plants: results from an 11-year experiment. J Ecol 94:1224–1232

Ellenberg H (1986) Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Ulmer, Stuttgart

ESRI Inc. (2006) ArcMap™ version 9.2. Redlands, California

Ewers R, Didham R (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fenner M, Thompson K (2004) The ecology of seeds. Cambridge University Press, Cambridge

Foster BL (2001) Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecol Lett 4:530–535

Freckleton RP, Watkinson AR (2001) Nonmanipulative determination of plant community dynamics. Trends Ecol Evol 16:301–307

Freckleton RP, Watkinson AR (2002) Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. J Ecol 90:419–434

Gilbert B, Lechowicz MJ (2004) Neutrality, niches, and dispersal in a temperate forest understory. PNAS 101:7651–7656

Girdler EB, Barrie BTC (2008) The scale-dependent importance of habitat factors and dispersal limitation in structuring Great Lakes shoreline plant communities. Plant Ecol 198:211–223

Goldberg DE, Barton AM (1992) Patterns and consequences of interspecific competition in natural communities—a review of field experiments with plants. Am Nat 139:771–801

Grashof-Bokdam CJ, Geertsema W (1998) The effect of isolation and history on colonization patterns of plant species in secondary woodland. J Biogeogr 25:837–846

Griffith DA, Peres-Neto PR (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. Ecology 87:2603–2613

Grime JP, Hodgson JG, Hunt R (1989) Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London

Hanski I (1994) A practical model of metapopulation dynamics. J Anim Ecol 63:151–162

Helm A, Hanski I, Pärtel M (2006) Slow response of plant species richness to habitat loss and fragmentation. Ecol Lett 9:72–77

Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. Biodivers Conserv 13:207–251

Hérault B, Honnay O (2005) The relative importance of local, regional and historical factors determining the distribution of plants in fragmented riverine forests: an emergent group approach. J Biogeogr 32:2069–2081

Higgins SI, Nathan R, Cain ML (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84:1945–1956

Jäger EJ, Werner K (2002) Rothmaler Exkursionsflora von Deutschland. Gefäßpflanzen: Kritischer Band. Spektrum Akademischer Verlag, Heidelberg Berlin

Johst K, Brandl R, Eber S (2002) Metapopulation persistence in dynamic landscapes: the role of dispersal distance. Oikos 98:263–270

Kattwinkel M, Strauss B, Biedermann R, Kleyer M (2009) Modelling multi-species response to landscape dynamics:

mosaic cycles support urban biodiversity. Landscape Ecol 24:929–941

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Endels P, Götzenberger L, Hodgson JG, Jackel A-K, Dannemann A, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Fitter A, Peco B (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96:1266–1274

Kolb A, Diekmann M (2005) Effects on life-history traits on responses of plant species to forest fragmentation. Conserv Biol 19:929–938

Krauss J, Klein AM, Steffan-Dewenter I, Tscharntke T (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. Biodivers Conserv 13:1427–1439

Legendre P, Legendre L (2006) Numerical ecology. Elsevier, Amsterdam

Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. Ecology 83:1131–1145

Nathan R (2006) Long-distance dispersal of plants. Science 313:786–788

Nathan R, Katul GG, Horn HS, Thomas SM, Oren R, Avissar R, Pacala SW, Levin SA (2002) Mechanisms of long-distance dispersal of seeds by wind. Nature 418:409–413

Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A (2008) Mechanisms of long-distance seed dispersal. Trends Ecol Evol 23:638–647

Ozinga WA, Bekker RM, Schminée JHJ, van Groenendael JM (2004) Dispersal potential in plant communities depends on environmental conditions. J Ecol 92:767–777

Ozinga WA, Römermann C, Bekker RM, Prinzing A, Tamis WLM, Schaminée JHJ, Hennekens SM, Thompson K, Poschlod P, Kleyer M, Bakker JP, van Groenendael JM (2009) Dispersal failure contributes to plant losses in NW Europe. Ecol Lett 12:66–74

Piessens K, Honnay O, Hermy M (2005) The role of fragment area and isolation in the conservation of heathland species. Biol Conserv 122:61–69

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. PNAS 105:20770–20775

Schadek U (2006) Plants in urban brownfields: modelling the driving factors of site conditions and of plant functional group occurrence in a dynamic environment. Dissertation, University of Oldenburg

Schadek U, Strauss B, Biedermann R, Kleyer M (2009) Plant species richness, vegetation structure and soil resources of urban brownfield sites linked to successional age. Urban Ecosyst Online First 115–126

Schaffers AP, Sykora KV (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. J Veg Sci 11:225–244

Schippers P, van Groenendael JM, Vleeshouwers LM, Hunt R (2001) Herbaceous plant strategies in disturbed habitats. Oikos 95:198–210

Soons MB, Nathan R, Katul GG (2004) Human effects on long-distance wind dispersal and colonization by grassland plants. Ecology 85:3069–3079

Soons MB, Messlink JH, Jongejans E, Heil GW (2005) Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. J Ecol 93:1214–1225

SPSS Inc. (2006) SPSS version 15.0.1 for Windows. Chicago, USA

Steyerberg EW, Harrell FE, Borsboom GJJM, Eijkemans MJC, Vergouwe Y, Habbema JDF (2001) Internal validation of predictive models: efficiency of some procedures for logistic regression analysis. J Clin Epidemiol 54:774–781

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

Suding KN, Goldberg DE, Hartman KM (2003) Relationships among species traits: separating levels of response and identifying linkages to abundance. Ecology 84:1–16

Tackenberg O, Poschlod P, Bonn S (2003) Assessment of wind dispersal potential in plant species. Ecol Monogr 73: 191–205

Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. Nature 371:65–66

Tremlová K, Münzbergová Z (2007) Importance of species traits for species distribution in fragmented landscapes. Ecology 88:965–977

Verheyen K, Vellend M, van Calster H, Peterken G, Hermy M (2004) Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. Ecology 85:3302–3312

Vos CC, Verboom J, Opdam PFM, ter Braak CJF (2001) Toward ecologically scaled landscape indices. Am Nat 157:24–41

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Syst 33:125–159