BIODIVERSITY RESEARCH

Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion

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ABSTRACT

Aim Urbanization as a major global trend profoundly changes biodiversity patterns, and homogenization of urban biota due to expanding exotic species and declining native species is of increasing concern. Previous studies on this topic have mostly taken place at large scales that include high habitat heterogeneity. Here, we aimed at disentangling the effects of urbanization and plant invasion on species composition through the analysis of similarity patterns of urban plant assemblages at the community scale where species interact.

Location Berlin, Germany.

Methods We analysed how different levels of urbanization, specific components of the urban matrix and the dominance of a native (*Betula pendula*) versus an exotic tree species (*Robinia pseudoacacia*) affect alpha and beta diversity of urban woodland understorey vegetation in sixty-eight 100-m^2 plots.

Results Exotic dominance reduced alpha diversity, but not beta diversity of the total species pool. Comparing beta diversity among different species groups revealed significant but divergent effects of exotic dominance, habitat connectivity and levels of urbanization in native and non-native species assemblages. In particular, urbanity proved to homogenize the native species pool, whereas the beta diversity of the non-native species pool showed a more pronounced response to exotic dominance.

Main conclusions Our data provide evidence that both the urban context and the dominance of exotic species can modify homogenization processes at the community level. These novel insights into the mechanisms of biotic homogenization of urban floras may contribute to mitigating the effects of urbanization on biodiversity.

Keywords
Alpha diversity, beta diversity, *Betula pendula*, invasive species, *Robinia pseudoacacia*, urban forest.

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INTRODUCTION

Urbanization is a major global trend (UN, 2008) that profoundly affects biodiversity at different scales (Grimm *et al.*, 2008). Urban growth may lead to the loss of habitats with high conservation value adjacent to cities (Hansen *et al.*, 2005; McDonald *et al.*, 2008; Radeloff *et al.*, 2010). Moreover within cities, species assemblages are severely changed for two main reasons. First, intensive urban land use associated with habitat fragmentation (Bierwagen, 2007; Schleicher *et al.*, 2011) and changes in ecosystem functioning (Alberti, 2005) leads to a decline in native habitat specialists (Chocholoušková & Pyšek, 2003; Knapp *et al.*, 2010; Duncan *et al.*, 2011). Second, a range of socio-economic activities, in particular gardening, foster the influx of exotic species (Dehnen-Schmutz *et al.*, 2007; Niinemets & Peñuelas, 2008; Essl *et al.*, 2011; Kowarik, 2011). Consequently, many urban floras show a high proportion of exotic species which may reach levels of up to 60%, both at the city scale (Pyšek, 1998) and at the community scale (Kowarik, 1995).

Given that the influx of the same suite of increasingly abundant non-native species coincides with the extirpation of specialized native species, urban floras are expected to become more similar (Kühn & Klotz, 2006; McKinney, 2006). Correspondingly, urbanization as a driver of biotic homogenization – the process of increasing taxonomic, genetic or functional similarities of formerly distinct regional biota (McKinney & Lockwood, 1999; Olden & Rooney, 2006; Qian & Ricklefs, 2006) – is a topic of increasing concern.

While there is a growing evidence for urbanization effects on similarity patterns, homogenization studies have yielded divergent results thus far, differing in the addressed taxa (Kühn & Klotz, 2006; Marchetti *et al.*, 2006; Luck & Smallbone, 2011), regions (La Sorte *et al.*, 2008), species groups (Kühn & Klotz, 2006; Knapp *et al.*, 2008; Ricotta *et al.*, 2012) and habitats addressed (Bühler & Roth, 2011). Previous studies ranged widely in scale, from continental (La Sorte *et al.*, 2007, 2008) to local (Wania *et al.*, 2006; Bühler & Roth, 2011), but were mostly based on data sets from heterogeneous environmental settings such as total cities (Ricotta *et al.*, 2012), counties (Schwartz *et al.*, 2006) or grid cells (Kühn & Klotz, 2006).

This heterogeneity implies an important limitation for homogenization studies because habitat heterogeneity and land use history are believed to strongly influence urban biodiversity patterns (Kühn *et al.*, 2004; Kowarik, 2011; Ramalho & Hobbs, 2012) and may also overlay interrelated effects of species losses or gains on the similarity of species assemblages.

To disentangle the effects of habitat heterogeneity at larger spatial scales on the composition of species assemblages from the role of urbanization, we aimed to explore homogenization at the community scale where species interact. This scale is crucial for conservation issues as it is here that the mechanisms function that largely determine population establishment and thus the survival of species in urban settings. As stochastic processes may be more important than biotic interactions in shaping disturbed urban species assemblages (Ramalho & Hobbs, 2012), we chose urban woodland patches as a model system – expecting a more pronounced role of biotic interactions in late successional stages compared to early successional stages. Moreover, we excluded old forest remnants encapsulated in the urban matrix owing to the pronounced time-lags in their response to changed environmental conditions (Ramalho & Hobbs, 2012).

Exotic species may be both drivers of and respondents to biotic homogenization (Kühn & Klotz, 2006). In addition to the regional spread of common exotic species, local dominance of an exotic species may add to the homogenization effect of urbanization by competitive suppression of native species. We therefore combined two approaches to include effects of plant invasions on urban similarity patterns. First, we sampled two types of urban woodlands, one dominated by a native tree species (*Betula pendula* R.; henceforth *Betula*) and the other by an exotic tree species (*Robinia pseudoacacia* L.; henceforth *Robinia*) – one of the top 100 woody

plant invaders world-wide (Cronk & Fuller, 1995). Second, we calculated floristic dissimilarity separately for total species, native species and non-native species in understorey vegetation based on pairwise comparisons of plots of either woodland type. This combined approach enabled us to test for compositional differences in native and non-native species assemblages in response to invasion of a dominant exotic, or native, pioneer tree and to assess whether and how urbanity shapes these responses among species groups.

In particular, we addressed the following study questions: (1) Does alpha diversity of the species groups differ among native *Betula* and exotic *Robinia* stands? (2) Does exotic dominance in *Robinia* stands lead to homogenization, that is, reduced beta diversity, in comparison with *Betula* woodlands? (3) Does urbanity influence homogenization of the species groups within *Robinia* and *Betula* stands? (4) Are there combined effects of urban matrix components and *Robinia* invasion on beta diversity that may affect the species groups differently?

METHODS

Study area

The study was carried out in Berlin, Germany, a city with 3.5 million inhabitants and an area of 892 km². In the natural landscape at the urban fringe, sandy, nutrient-poor soils prevail, whereas within the built-up areas, soils predominantly reflect severe anthropogenic disturbance. Spontaneous urban woodlands, often dominated by either the native *Betula* or the exotic *Robinia*, have frequently developed on debris or gravel (e.g. Kunick, 1987; Kowarik, 1995). Overall, Berlin represents a complex urban matrix, comprising a variety of land uses, roughly 54% built-up areas, 21% woodlands, 12% green spaces, 6% water, 5% grasslands and 2% arable fields (SenStadt, 2008).

Study design

Ideally, biotic homogenization should be tracked over time by comparing historical and recent data. As such data are often unavailable, comparing invaded sites to nearby uninvaded sites is a common approach to provide a spatial analogue to temporal changes in communities before and after invasion (Sax, 2002a; Hejda *et al.*, 2009). We thus relate current differences in diversity patterns of urban woods to homogenization of urban plant assemblages.

Using the area-wide habitat mapping of the federal state Berlin (SenStadt, 2008), we randomly selected 34 pairs of woodland patches: one patch of the pair was dominated by the non-native *Robinia* and the other one by the native *Betula*. Both woodland types result from spontaneous succession and are distributed over the total area of Berlin (Fig. 1). *Betula* is a frequent pioneer of temperate forests in Europe and one of the most successful species in spontaneous succession on man-made sites (Prach, 1994). *Robinia*, a forest

Figure 1 Location of the 34 plot pairs in Berlin. Enlarged square: example of a single pair of plots within the matrix of urban land use patches (black patch: *Robinia pseudoacacia* plot; grey patch: *Betula pendula* plot).

pioneer native to North America (Boring & Swank, 1984), is known to strongly change species composition in its non-native range, mostly due to symbiotic nitrogen influxes (Dzwonko & Loster, 1997; Von Holle *et al.*, 2006).

We visually ascertained that the two patches within a given pair were approximately of the same age and belonged to the same habitat type (i.e. pioneer forest and pre-forest; soil conditions; SenStadt, 2008) to guarantee similar environmental conditions. Pairs that were assigned to the same habitat type were separated by a minimum distance of 1000 m to avoid spatial autocorrelation.

Within each woodland patch, we established a 10 × 10 m² study plot, randomly located in the core area at a distance of > 5 m from the border of the patch to counteract edge effects. Between both plots of a pair, we kept a minimum distance of 20 m between the edges to preclude neighbouring effects, in particular nitrogen influx from *Robinia* stands. At the same time, we did not exceed a distance of 500 m to assure similar environmental conditions for the pair.

Data collection

Vegetation data

Within each plot, all vascular plant species were recorded between early May and July 2010 by the same persons to ensure equal sampling intensity and sampling of spring ephemerals. Species abundance was estimated using the methodology of Braun-Blanquet (1964). All species were identified using standard literature for the German flora (Jäger & Werner, 2005). We also visually estimated the canopy cover as this factor usually strongly affects regeneration processes in the ground layer. Tree species taller than 5 m in height were excluded from the statistical analyses as these had served as the criterion for patch selection. We differentiated between

native and non-native species according to the BioFlor database (Klotz *et al.*, 2002). The group of non-natives combined archaeophytes (pre-1492 introductions) and neophytes (post-1492 introductions) to obtain sufficient species numbers for statistical analysis notwithstanding their possibly different ecological response (e.g. La Sorte *et al.*, 2008).

Land use and habitat data

To explore the influence of the urban matrix on species assemblages, we identified the proportions of land use types in the surroundings of the study plots using related information from the official habitat map of Berlin (SenStadt, 2008). All values were calculated for the joint area of two 500-m buffers around the study plots of a pair. We determined the proportion of impervious surface, which included built-up area and road area. By subtracting road area, which is mapped separately, we obtained the built-up area, which was used to indicate different degrees of urbanity (hereafter referred to as *urbanity*). Following Knapp *et al.* (2009), we differentiated three classes of urbanity according to the proportion of built-up area: low ($\leq$ 0.13), medium (> 0.13, $\leq$ 0.34) and high (> 0.34). This approach led to a nearly balanced design with 11 or 12 study plots per urbanity class.

Furthermore, we included the proportions of railway and road area as matrix variables. The Hanski index for woodland connectivity (Hanski, 1994) between each plot and the ten nearest patches with the same woody vegetation was determined to assess the degree of isolation of the studied patch. Both the proportions of railway and road areas and the Hanski index may play important roles in the homogenization of urban floras as they imply possible dispersal opportunities for organisms (Bierwagen, 2007). As roads and the Hanski index for *Betula* forests were not explanatory in the resulting models, data are not shown. Land cover calculation

was performed using PatchAnalyst as an extension of Arc-View GIS 9.2 software (ESRI®ArcMap 9.2, ESRI, Redlands, CA, USA).

Statistical analyses

As a measure of alpha diversity, we calculated total species richness as well as richness of both native and non-native species at the plot level. Moreover, we determined Shannon index and Simpson reciprocal index for each study plot; the latter is very suitable for the assessment of compositional differences (Lennon *et al.*, 2001). We computed the reciprocal value of the Simpson index, as suggested by Kindt & Coe (2005) for biological communities with low diversity, and the Shannon evenness index. Beta diversity as a measure of species composition dissimilarity among communities is frequently evaluated using Jaccard's coefficient, which is based on presence/absence data (Olden & Rooney, 2006). It is an adequate and straightforward measure for capturing the variation in community structure among a set of sample units within a given habitat type (Anderson *et al.*, 2011) as is the case in our study. A possible bias of the Jaccard's index by large richness differences as stated by Koleff *et al.* (2003) was not expected in our study because we performed only comparisons within the same forest type. In this paper, we used Jaccard's distance, which shows the dissimilarity among species assemblages and is very adequate for detecting underlying ecological gradients (Faith *et al.*, 1987). A plot-based beta-diversity index was calculated using the average pairwise Jaccard's distance of each study plot compared to all other plots of the same group (Vellend *et al.*, 2007), that is, to either all *Robinia* or all *Betula* plots. We did not apply β_{sim}, another frequently used dissimilarity measure, due to its sensitivity to small numbers of shared and unshared species (Koleff *et al.*, 2003) which was the case in the non-native species pool.

We tested for significant differences in alpha-diversity indices of *Robinia* and *Betula* plots using Welch *t*-tests which is frequently used for data sets with unequal sample variances (Ruxton, 2006). Values of Shannon evenness and Simpson indices were ln-transformed prior to analyses to normalize data. We furthermore tested the correlation between the richness of natives and non-natives based on Spearman rank correlations for both forest types separately.

Because beta-diversity metrics are computed from pairwise comparisons of overlapping species pools, they lack independence. Differences in beta diversity between *Robinia* and *Betula* plots were therefore tested with a one-way permutation test, based on 9999 Monte Carlo permutations. All alpha- and beta-diversity calculations were performed separately both for species groups (total species pool, natives and non-natives) and for *Robinia* and *Betula* plots.

The impact of urbanity on alpha-diversity indices was tested by ANOVA followed by a Tukey's HSD post hoc test in case of significant results. To test for influences of urbanity on beta diversity, we assigned each pair of *Robinia* and *Betula* plots to one of the three urbanity classes and performed an approximative K-sample permutation test, based on 9999 Monte Carlo permutations, followed by a Nemenyi–Damico–Wolfe–Dunn (NDWD) post hoc test (for details see Hollander & Wolfe, 1999).

To analyse the joint effects of *Robinia* invasion, urban matrix variables and tree canopy cover on alpha and beta diversity, we performed boosted regression tree (BRT) analyses (Elith *et al.*, 2008). We used BRT because of its high predictive power and its flexibility in handling both categorical and metric predictors. BRTs rank the relative importance of each predictor variable and display the individual effects of each variable in partial dependence plots. Species richness and mean Jaccard's distance of each plot to all other plots of the same forest type were used as dependent variables, while urbanity, proportion of railway areas, Hanski index for *Robinia* stands, tree canopy cover and *Robinia* invasion (categorical, *Robinia* versus *Betula* plots) were included as predictors in the models shown earlier.

All statistical tests were conducted with R, version 2.7.2 (R Development Core Team, 2008); diversity indices and dissimilarity measures were computed with the *vegan* community analysis package (Oksanen *et al.*, 2009). NDWD test was calculated using the package *multcomp*, while BRTs were calculated with the package *gbm* and additional scripts provided by Elith *et al.* (2008).

RESULTS

Alpha diversity

Species richness clearly differed between woodland types. Total species number of the combined shrub and herb layers was higher in *Betula* than in *Robinia* plots, and this also held true for the groups of native and non-native species (Table 1). Correspondingly, average total species richness as well as average richness of native and non-native species was significantly higher in woodlands dominated by the native tree species compared with exotic stands (Table 2). The richness in native species correlated significantly with the richness in non-native species in both woodland types ($\rho = 0.444$, $P = 0.009$ in *Robinia* plots; $\rho = 0.752$, $P < 0.001$ in *Betula* plots).

Shannon and Simpson indices for alpha diversity also showed significantly higher values for total and native species in *Betula* plots than in *Robinia*, but no significant differences were detected for non-native species (Table 2). Differences in evenness were less pronounced. The evenness of total and non-native species was significantly higher in *Robinia* plots than in *Betula* plots.

Beta diversity

For the total species pool we found no significant differences in beta diversity between *Robinia* and *Betula* plots (Table 3).

Table 1 Overall species numbers found in urban woodland plots (100 m²) in Berlin, dominated by non-native *Robinia pseudoacacia* (n = 34) and native *Betula pendula* (n = 34), respectively

	Robinia		*Betula*	
	Total number	%	Total number	%
Total species	165	100	213	100
Native species	100	61	136	64
Non-native species	65	39	77	36

Table 2 Mean alpha-diversity indices calculated for total species, native species and non-native species of *Robinia pseudoacacia* plots (n = 34) and *Betula pendula* plots (n = 34), and results of Welch *t*-tests for differences between means

	Mean			
	Robinia	*Betula*	*t*	*P*
Total species				
Richness	20.85	30.94	4.72	< 0.001
Shannon	2.02	2.34	2.99	0.004
Inverse Simpson	5.48	7.51	2.33	0.023
Evenness	0.39	0.37	−2.46	0.01
Native species				
Richness	14.29	22.35	5.67	< 0.001
Shannon	1.72	2.14	4.17	< 0.001
Inverse Simpson	4.41	6.61	3.59	< 0.001
Evenness	0.43	0.42	−1.82	0.07
Non-native species				
Richness	6.56	8.59	2.13	0.037
Shannon	1.16	1.31	1.13	0.26
Inverse Simpson	2.78	3.35	0.91	0.37
Evenness	0.58	0.52	−2.6	0.01

This means that the dominance of an exotic tree species did not result in homogenization of associated species assemblages compared to stands of a dominant native tree species at similar urban sites. However, comparisons of native and non-native species groups revealed divergent results (Table 3). For native species, beta diversity was slightly but significantly higher in *Robinia* compared with *Betula* plots, whereas for non-native species, we found a lower beta diversity in the *Robinia* plots.

Effects of urbanity on alpha and beta diversity

Alpha-diversity indices were by trend highest in the intermediate urbanity classes and lowest in the high urbanity class, but the results for species richness were not significant and other indices showed no consistent statistical pattern (data not shown).

In contrast, urbanity significantly influenced beta diversity of native species in both woodland types and of total species

Table 3 Comparison of mean Jaccard's distance as a measure of beta diversity between all *Robinia pseudoacacia* plots and between all *Betula pendula* plots

|	Mean beta diversity			
	Robinia	*Betula*	*z* Value	*P*
Total species	0.82	0.82	−0.32	0.75
Native species	0.81	0.80	−2.07	0.037
Non-native species	0.83	0.86	3.9	< 0.001

Range of Jaccard's distance: 0–1 with 0 = minimal beta diversity and 1 = maximum beta diversity. Results from one-way permutation test.

in *Betula* plots. Beta diversity in the intermediate urbanity class mostly showed the lowest values, while highest dissimilarity was found in plots with low urbanity in their surroundings and the lowest proportion of built-up area (Fig. 2). However, beta diversity of non-native species was not affected by urbanity in either of the woodland types (Table 4). Corresponding to overall beta diversity, the total and native species pools of *Robinia* stands showed higher Jaccard's distance values than those of *Betula* stands in the plots that had been assigned to intermediate or high urbanity classes (Fig. 2).

Joint effects of exotic dominance and urban matrix components on alpha and beta diversity

The joint effect of *Robinia* invasion, urban matrix components and canopy cover on alpha and beta diversity of *Robinia* and *Betula* plots was analysed using BRTs. In accordance with the analyses on differences in alpha diversity among forest types and urbanity classes, the BRTs for species richness showed a pronounced impact of exotic dominance in the total and the native species pool with urban matrix variables contributing only minor percentages to the explained deviance (explained deviance: 31% and relative importance of *Robinia* invasion: 63% for the total species pool; 61% and 45% for the native species, respectively). In contrast, the richness of the non-native species pool could not be predicted by forest type and matrix variables using BRT models due to low explained deviance (< 1%).

The analyses of beta diversity revealed that *Robinia* invasion had nearly no relative effect on the mean beta diversity of the total species and native species pools (Fig. 3a,b). In contrast, *Robinia* invasion was the most important predictor for beta diversity in non-native species (Fig. 3c). Mean beta diversity in the total and native species pools was strongly influenced by the proportion of built-up area around the plots with the highest beta diversity at low proportions and the lowest beta diversity at intermediate levels of building density (Fig. 3a,b). Increasing proportion of railway areas generally enhanced beta diversity in all species groups, but for total and native species, there was an additional peak of
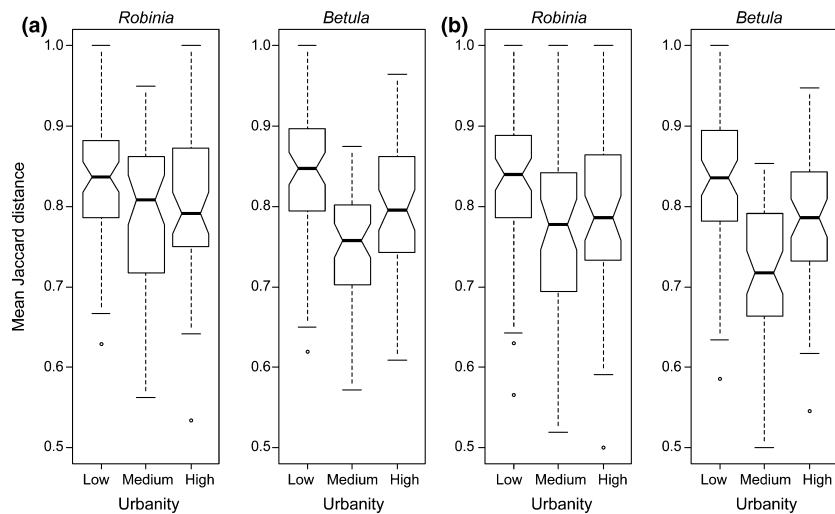
Figure 2 Influence of urbanity (low = 12 study plots, medium = 11 study plots and high = 11 study plots) on the dissimilarity (mean Jaccard's distance) of species assemblages of urban woodland plots dominated by either non-native *Robinia pseudoacacia* or native *Betula pendula* for (a) total species pool of *R. pseudoacacia* plots (NDWD test: *P* = 0.054) and *B. pendula* plots (NDWD test: *P* < 0.001) and (b) the native species pool of *R. pseudoacacia* plots (NDWD test: *P* < 0.005) and *B. pendula* plots (NDWD test: *P* < 0.001). Different lower-case letters indicate significant differences. There were no significant differences for non-native species (data not shown). NDWD, Nemenyi–Damico–Wolfe–Dunn post hoc test (Hollander & Wolfe, 1999).

Table 4 Effect of urbanity on mean Jaccard's distance within *Robinia pseudoacacia* and *Betula pendula* stands based on the comparison of three urbanity classes (< 0.13 proportion of built-up area in 500-m buffer around study plot = low urbanity; 0.13–0.34 of built-up area = intermediate urbanity; > 0.34 of built-up area = high urbanity)

	Robinia		*Betula*	
	maxT	*P*	maxT	*P*
Total species	2.33	0.052	5.19	< 0.001
Native species	2.67	0.017	5.87	< 0.001
Non-native species	0.47	0.883	2.13	0.082

maxT and significance levels of approximate K-sample permutation test for total, native and non-native species pools.

beta diversity at extremely low proportions of railway area. Hanski connectivity between plots and *Robinia* forests increased beta diversity after a slight decrease at intermediate connectivity for all species as well as for native species. In contrast, non-native beta diversity peaked at intermediate connectivity and declined strongly at higher levels.

DISCUSSION

Effects of biotic homogenization are strongly scale dependent (Sax & Gaines, 2003). However, it has not yet been tested whether results from previous urban homogenization studies – addressing larger spatial scales – also hold true at the community scale. Using urban woodlands as model systems, this study for the first time explored homogenization effects in urban

plant assemblages at the community level. We found different responses in species groups to urbanization and revealed joint effects of urban matrix features and the local dominance of a non-native species on floristic homogenization.

Alpha diversity

In contrast to non-urban studies (Michelsen *et al.*, 1996; Sax, 2002a), our data show markedly higher species richness for native compared with exotic woodlands; also, the values for diversity indices for total and native species were higher in native woodlands. The capacity of *Robinia* – as also reported from other dominant non-native tree species of urban environments (Castro-Díez *et al.*, 2009) – to increase nitrogen availability for associated species may be expected to enhance the species turnover compared to *Betula* stands and promote a less diverse suite of N-demanding species, ultimately resulting in lower species richness and diversity in the understorey.

Interestingly, the native woodland plots had both more native and non-native species than the exotic woodland plots, and the species numbers of both groups were positively correlated. This adds evidence to the 'rich get richer' hypothesis, which posits a positive correlation between native and exotic species richness (Stohlgren *et al.*, 2003), although this has rarely been tested for forest types (but see Sax, 2002b). Hence, the same factors that reduced native species numbers in *Robinia* stands presumably also reduced non-native species richness.

Yet, our results clearly contrast with another study from rural settings that found a higher richness, due to a higher number of non-natives, in *Robinia* stands compared with
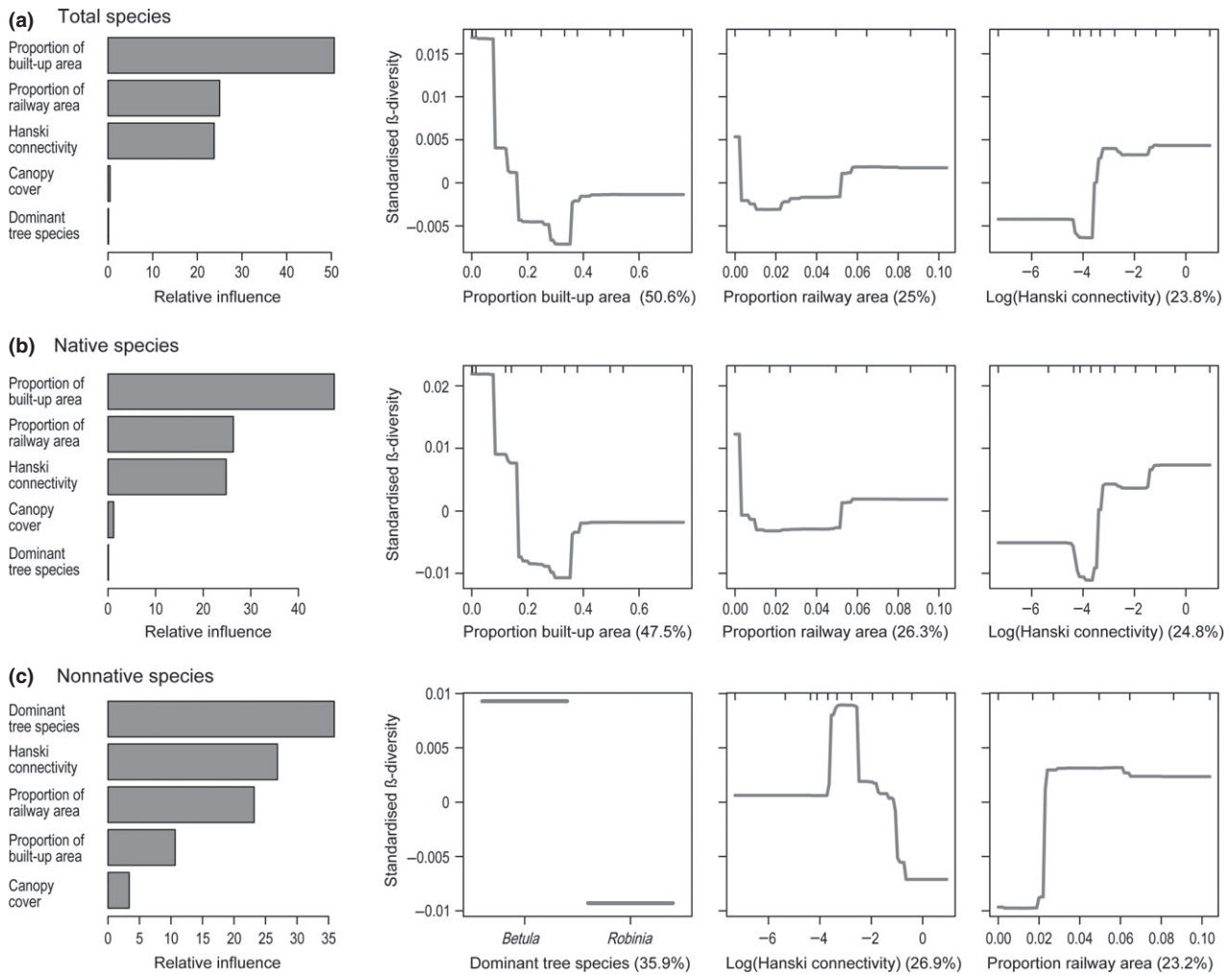
Figure 3 Relative variable importance plots and partial dependency plots for boosted regression tree analyses showing the size and direction of effects of matrix and site-related predictors on beta diversity based on Jaccard's distance for (a) the total species pool (cv correlation = 0.37; SE = 0.13, explained deviance: 0.27); (b) the native species (cv correlation = 0.41; SE = 0.11, explained deviance: 0.36); (c) the non-native species (cv correlation = 0.34; SE = 0.13, explained deviance: 0.34).

native forests with the same land use history (Von Holle *et al.*, 2006). These results support the invasional meltdown hypothesis, which claims that secondary invasions are promoted by positive interactions among invaders (Simberloff, 2006; Von Holle *et al.*, 2006). Our contradictory results can be explained by the fact that nitrogen availability is often higher – and therefore not limiting – in urban habitats than in the surroundings (Chocholoušková & Pyšek, 2003; Alberti, 2005) and certainly also compared to the nutrient-poor sandy soils that prevailed in the study area of Von Holle *et al.* (2006). A study from northern Italy revealed no pronounced effects of *Robinia* on biodiversity indices of understorey vegetation in a rural environment compared to young native pioneer forests (Sitzia *et al.*, 2012). Despite trends similar to our study in the total and native species, alpha-diversity indices of the native forests were clearly lower and therefore more similar to *Robinia* forests than in the urban area of Berlin.

Beta diversity

The marked decline of alpha diversity in the exotic stands corresponds to a general pattern showing a reduction in the diversity of resident species assemblages owing to invading species (Vilà *et al.*, 2011). In contrast to our expectations, the strong decrease in total species richness and alpha-diversity measures due to *Robinia* dominance at the plot level did not go along with a general decline in beta diversity at the community scale. We found no homogenizing effect and consequently similar beta diversity of *Robinia* stands for the total species pool and, for native species, even an increase in beta diversity, compared to native *Betula* woodlands. As the decline in species richness was most pronounced for native species, this opposing result for beta diversity can only be explained by a random suppression of native species in the exotic woodland plots. Increased values of Jaccard's distance along with a decline in alpha diversity indicate that native

species previously present in different plots become extirpated in some, but not in others. On the other hand, the beta diversity of non-native species was significantly lower in *Robinia* plots, which points to a homogenizing effect of the dominant invader on the associated non-native species assemblages. Hence, in contrast to its effect on native species, *Robinia* seems to facilitate a common non-native species pool as already suggested by Von Holle *et al.* (2006). Again, there was no evidence for homogenization in understorey species pools of Italian *Robinia* stands due to overall lower beta diversity in young pioneer forests (Sitzia *et al.*, 2012).

Our data show that the loss of native species in exotic woodland patches does not translate to biotic homogenization in associated native species assemblages but does in communities of non-native species. While non-native species were found to enhance differentiation of urban floras at larger spatial scales (Kühn & Klotz, 2006), our study clearly demonstrates that such findings on urban similarity patterns cannot be generalized for the community scale.

Effects of urbanity on alpha and beta diversity

Alpha diversity was not significantly influenced by urbanity. In particular, we found no evidence for differences in species richness among urbanity classes. In contrast, our results illustrate that the homogenization effects of increasing urbanity at large spatial scales (Kühn & Klotz, 2006) are also detectable at the community scale: the highest beta diversity of total and native species mostly corresponded to the lowest urbanity class (Fig. 2). As an unexpected result, this did not hold for similarity patterns in non-native species. We found homogenization effects in non-native species assemblages of the *Robinia* stands (see above), but these appear to occur independently of the urbanization level in the plot surroundings.

Surprisingly, we observed the lowest beta diversity for total and native species in the intermediate urbanity class. Most studies on urban–rural gradients have found that intermediate levels of urban development often reflect the greatest species richness (McDonnell & Hahs, 2008; McKinney, 2008), and at larger spatial scales, the similarity in native species in urban regions decreased with decreasing levels of urbanization (Kühn & Klotz, 2006). This pattern obviously did not translate to the community scale in our study.

Biotic homogenization in the areas of intermediate urbanity could be an outcome of increased human-mediated dispersal as here, habitat connectivity of forest habitats as seed sources and dispersal corridors such as roads (von der Lippe & Kowarik, 2008) or railway habitats (Penone *et al.*, 2012) are both at intermediate levels which may foster species exchange among forests. As only a few species dominate the pool of seeds able to be transported by human vectors such as motor vehicles (von der Lippe & Kowarik, 2007) or clothing (Pickering *et al.*, 2011), high levels of human activity are expected to support the efficient exchange of a narrow set of species between woodland patches. In the highest urbanity class, a lower connectivity between the patches may dampen this effect.

For non-native species, this phenomenon is less pronounced – presumably due to their generally lower frequencies (Chocholoušková & Pyšek, 2003) and the much stronger impact of exotic dominance in our model system.

Joint impacts of urban matrix components and exotic dominance on alpha and beta diversity

The BRT analyses support the findings on differences in alpha diversity among forest types and among urbanity classes. Total and native species richness corresponded most pronouncedly to exotic dominance, whereas the impact of the urban matrix was only weak. In the non-native species pool, neither exotic dominance nor matrix variables were decisive for richness.

The main result of the BRT analysis was that *different* parameters shape homogenization in the addressed species groups, indicating functional differences among them (Fig. 3). This would correspond to the urbanization-induced changes in functional trait representation in native and non-native species assemblages that have been found at larger spatial scales (Knapp *et al.*, 2008, 2010; Ricotta *et al.*, 2012).

The beta diversity of both the total and the native species pools clearly reflected the proportion of built-up area with the lowest beta diversity found at intermediate urbanity levels. Also, the dispersal-related parameters exhibited a pronounced impact: intermediate proportions of railway areas around the patches decreased beta diversity as did intermediate patch connectivity. These results suggest that biotic homogenization in the native species pool of our model systems was increased by components of the urban matrix including those that promote patch connectivity and species exchange. Still, the high contribution of the proportion of built-up area to homogenization in the native species group may indicate dispersal limitation, which led to a reduced species pool in plots that were located in highly urbanized surroundings.

Exotic dominance was the most important parameter for homogenization of the non-native species pool. In contrast to native species, non-native beta diversity peaked at intermediate patch connectivity while high connectivity strongly homogenized the species assemblages. This suggests the functioning of an exchange of common non-native species between urban woodland patches that appears to foster taxonomic homogenization only in highly connected patches. Results from larger spatial scales similarly illustrated a functional homogenization in species traits in urban species assemblages and an increased representation of species with traits related to a greater potential for long-distance dispersal (Knapp *et al.*, 2008, 2010).

Maintaining diverse species assemblages in steadily growing urban areas is an increasing challenge for global nature conservation. Our study illustrates that urbanization can enhance biotic homogenization also at the community scale, but with divergent responses in different species groups. In contrast to other studies at larger scales, our approach thus

provides novel insights into the mechanisms driving biotic homogenization. These include the fact that dominant exotic species may add to homogenization through facilitation or suppression of other species, which can only be observed at the community level. Moreover, we also demonstrated that the spatial context of urban habitat patches plays a crucial role in homogenization processes.

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BIOSKETCH

The authors are plant ecologists dedicated to varying aspects of vegetation dynamics and nature conservation. The cooperation of the authors aims at analysing invasion mechanisms of non-native plant species and their effects on plant biodiversity. A.C. is interested in all aspects of urban ecology and invasion biology with particular focus on non-native tree species in the city of Berlin.

Author contributions: G.T. collected field data, analysed output data and wrote the first draft of the manuscript; M.v.d.L. contributed to the study design and performed the BRT analysis; T.S. codesigned the study and, together with U.Z., collected data in the field and performed GIS analyses; I.K. stimulated the study and elaborated on the final version of the manuscript; A.C. developed the study design, collected data and analysed output data, and all authors contributed substantially to revisions.

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