

Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients

Moritz von der Lippe* and Ingo Kowarik

Institute of Ecology, Technical University of Berlin, Rothenburgstr.12, D-12165 Berlin, Germany

ABSTRACT

Urban areas are among the land use types with the highest richness in plant species. A main feature of urban floras is the high proportion of non-native species with often divergent distribution patterns along urban–rural gradients. Urban impacts on plant species richness are usually associated with increasing human activity along rural-to-urban gradients. As an important stimulus of urban plant diversity, human-mediated seed dispersal may drive the process of increasing the similarity between urban and rural floras by moving species across urban–rural gradients. We used long motorway tunnels as sampling sites for propagules that are released by vehicles to test for the impact of traffic on seed dispersal along an urban–rural gradient. Opposite lanes of the tunnels are separated by solid walls, allowing us to differentiate seed deposition associated with traffic into vs. out of the city. Both the magnitude of seed deposition and the species richness in seed samples from two motorway tunnels were higher in lanes leading out of the city, indicating an ‘export’ of urban biodiversity by traffic. As proportions of seeds of non-native species were also higher in the outbound lanes, traffic may foster invasion processes starting from cities to the surrounding landscapes. Indicator species analysis revealed that only a few species were confined to samples from lanes leading into the city, while mostly species of urban habitats were significantly associated with samples from the outbound lanes. The findings demonstrate that dispersal by traffic reflects different seed sources that are associated with different traffic directions, and traffic may thus exchange propagules along the urban–rural gradient.

Keyword

Homogenization, plant invasions, roadside flora, traffic, urban–rural gradient, vehicle plant dispersal.

*Correspondence: Moritz von der Lippe, Institute of Ecology, Technical University of Berlin, Rothenburgstr.12, D-12165 Berlin, Germany. Tel: (+ 49) 30 314 71194; Fax: (+ 49) 30 314 71355; E-mail: moritz.vdlippe@tu-berlin.de

INTRODUCTION

The ongoing growth of urban agglomerations leads to far-reaching changes in biodiversity, including the loss of forests and other natural areas. In the USA, urbanization endangers more species and is more geographically ubiquitous than other human activities (Czech *et al.*, 2000; McKinney, 2002; Hansen *et al.*, 2005). On the other hand, for a variety of taxonomical groups, it has been widely found that urban areas are more species rich than their surroundings (Pyšek, 1998; McKinney, 2002).

Studies on the contribution of urbanization to the homogenization of floras across various spatial scales are somewhat contradictory. It has long been assumed that it is mainly the higher richness of non-native species in cities that makes different urban floras more similar (Bartlott *et al.*, 1999). If there is a similar set of species that is well adapted to urban conditions

occurring in urban areas worldwide, a trend towards a global homogenization of urban floras is to be expected (McKinney, 2004, 2006). However, at regional and local scales invasion of non-native species is not necessarily the most important driver for biotic homogenization along urban–rural gradients. Some recent studies have demonstrated that both native and non-native species richness is higher in urban areas (Kühn *et al.*, 2004; Wania *et al.*, 2006) and that urban native floras are even more similar than rural native floras in a countrywide comparison (Kühn & Klotz, 2006).

Yet, extirpations due to urbanization disproportionately affect the native flora (DeCandido *et al.*, 2004; Schwartz *et al.*, 2006). As urbanized areas represent refuges for numerous endangered native species (Pyšek, 1998), specific knowledge about the causes of urban species richness and the processes that lead to the homogenization of urban floras are crucial for the effective protection of urban biodiversity.

It is still not entirely understood how mechanisms of homogenization and differentiation of urban floras work in detail, mainly because of the complex interactions of different factors that are hard to separate. Many studies revealed positive correlations between habitat variability in cities and plant species richness (Kowarik, 1995; Kühn *et al.*, 2004; Wania *et al.*, 2006). There is also evidence that cities are not randomly distributed but were founded in areas of high natural species richness and high geological diversity (Kühn *et al.*, 2004). High urban species richness could, in this respect at least, partially be attributed to remnants of (semi) natural habitats.

Among the processes that drive plant invasions, the intensity of human activity is of particular importance in urban areas, as it results in an expansion of dispersal pathways and modes of introduction for non-native species (Kowarik, 1995). Two main vectors act at the regional scale, which is most important as the interface between urban and suburban habitats and could be related to homogenization. First, human activity increases non-native species richness by multiple accidental introductions and deliberate plantings that are closely associated with the implementation of urban land uses (Kowarik, 2003). As suburbanization leads to an export of specific urban land uses along urban–rural gradients (Robinson *et al.*, 2005), the related invasion foci are exported too. Second, cities provide a broad array of dispersal pathways that may enhance the transfer of non-native species from urban to rural habitats. Strong evidence exists for railways or roads as migration corridors for species (Ernst, 1998; Tikka *et al.*, 2001; Kowarik & von der Lippe, 2007). At the same time, vectors that might facilitate plant dispersal culminate in urban agglomerations. Among such vectors, vehicles have been shown to promote dispersal by adhesion in urban areas (Wace, 1977; Hodkinson & Thompson, 1997) as well as in suburban (Zwaenepoel *et al.*, 2006) and rural environments (Schmidt, 1989).

Yet, the question of whether and in what way traffic-aided dispersal promotes homogenization or differentiation of urban floras has not been studied, as previous approaches failed to differentiate the direction and spatial effectiveness of dispersal events by vehicles.

Our approach aims to differentiate the role of traffic as a vector of plant dispersal along an urban–suburban gradient and to specify the vector tempo and strength as suggested by Carlton & Ruiz (2005). The focus of this study is the transport of propagules along an urban-to-suburban gradient and the contribution of such transport to the homogenization of urban and rural floras. If there is a relevant ongoing impact of traffic on homogenization at the local scale, we would expect an exchange of species between urban and suburban sites, i.e. a traffic-mediated import of propagules into and an export of propagules out of the city. An export of non-native species that are confined to typical urban habitats could affect homogenization by supporting invasion of suburban habitats. In a companion study we have shown, that long-distance seed dispersal by vehicles particularly favours the spread of non-native plant species, which could have far reaching implications for the homogenization of floras in urban areas (von der Lippe & Kowarik, 2007).

To assess the homogenizing potential of seed transport by vehicles, we compare the species composition of seeds that were deposited by vehicles along opposite lanes of two motorway tunnels across an urban-to-suburban gradient. We use tunnels as sampling sites that are isolated from dispersal pathways other than traffic. By contrasting seed samples of the lanes towards the inner city with those leading out of the city, we address the following questions:

- 1 Is seed deposition and species richness of the seed samples different for opposite directions of traffic?
- 2 Is the high non-native species richness of urban habitats reflected in a higher proportion of non-native species in seeds transported out of the city?
- 3 Are species of typical urban habitats more frequent in samples from lanes leading out of the city and is there an equivalent import of seeds typical of rural habitats?

METHODS

We used two long (750 and 1050 m) motorway tunnels in Berlin, Germany, as sampling sites to insulate seed samples from other dispersal vectors than traffic. The tunnels are located on the same motorway leading from the inner city to the north-west outskirts of Berlin at a distance of 2 km from each other. The lanes had no relevant slope in both tunnels. The first tunnel is situated closer to the inner city ('urban tunnel') in a dense residential housing area. Both entrances of the urban tunnel are close to an airport district that includes huge areas of dry short-grass meadows. The second ('suburban tunnel') is located in a mid-density housing area with a high proportion of urban wasteland and railroad areas in the surroundings. The suburban tunnel is about 4 km from the city border, and traffic flow towards the city centre originates from the outer Berlin motorway ring, which is completely located in the rural surroundings of the city. The opposing lanes in both tunnels are divided along their entire lengths by solid walls and thus provide independent samples for both directions of traffic.

Special ground seed traps consisting of a flat, 1.9-m-long container (1.9 × 0.08 × 0.05 m) of sheet metal and a removable funnel (sampling surface 0.22 m²) of aluminium for protection from airflow (von der Lippe & Kowarik, 2007) were set up inside the tunnels beyond a buffer zone of 150 m from the tunnel entrances. Five traps for each lane were installed on the ground to collect the seed rain directly at the road verges, providing five replicates at each sampling date. Traps were aligned parallel to the road in a distance of approximately 1.5 m from the gutter and with a gap of 2 m between each two traps. Two additional PVC seed traps with 15 cm diameter (0.07 m² sampling surface) were deployed 1.5 m above the ground traps during two sampling periods to control for possible seed deposition by wind dispersal. No relevant impact of above ground wind dispersal inside the tunnels was revealed, as no seeds were collected in these traps.

For the determination of species, the seed samples were germinated in a glasshouse according to Ter Heerd *et al.* (1996) under a tent of garden fleece to avoid seed influx by wind. Samples were concentrated by wet sieving with a 0.2-mm-mesh

Table 1 Species richness and seed numbers in seed samples ($n = 20$) from lanes of two motorway tunnels, grouped by traffic direction along the urban–rural gradient and native status of the species. The last row displays seed numbers of non-native species with arable crops removed from the samples.

	Inbound lanes			Outbound lanes		
	Urban tunnel	Suburban tunnel	Both tunnels	Urban tunnel	Suburban tunnel	Both tunnels
Total species number	64	85	101	97	125	151
Native species	31	42	48	54	65	78
Non-native species	33	43	53	43	60	73
Seeds of native species	274	744	1018	479	1053	1532
Seeds of non-native species	425	900	1325	325	684	1009
Seeds of non-native species excl. crops	80	274	354	259	497	756

sieve and spread out thinly (<0.5 cm) in germination trays (32 × 50 cm) over sterilized potting soil. Germination trays were kept in a temperature-controlled (min. 15 °C; max. 30 °C) glasshouse for 12 months and watered as necessary to keep the soil surface moist. After identification, seedlings were removed from the germination trays. Seedlings that could not be identified were potted and grown until identification was possible. Species nomenclature follows Wisskirchen & Haeupler (1998).

Data analysis

We compared species richness and seed deposition between opposite lanes by a two-way ANOVA with direction of traffic flow and location of tunnel as fixed effects, separately for native and non-native species. Square-root-transformed richness or seed counts of either native or non-native species were used as dependent variables. We also conducted ANOVAs with the proportion of non-native species and seed counts of non-natives as response variables, transformed by arcsine square root.

As seeds of agricultural crops (*Triticum aestivum*, *Secale cereale*, and *Brassica napus*) played a dominant role in the vehicle-born flora, we performed separate analyses for non-native species both with and without agricultural crop species.

To test whether particular species were related to a particular direction of traffic, we used indicator species analysis (Dufrene & Legendre, 1997), which takes into account both the relative abundance and the relative frequency of each species in both groups compared and thus allows different sampling sizes between groups. To account for large differences in the magnitude of seed deposition between the two tunnels, the seed counts of species from each trap were standardized by division through the total seed number in the trap. The same analysis was carried out after grouping species according to habitat type. Species affiliations with habitats were derived from the BIOLFLOR database on biological and ecological traits of the German flora (Haeupler, 2002). Habitats were aggregated to the highest hierarchical level. One species could be assigned to different habitat types but was only counted once if it occurred in different sublevels of the aggregated habitat. Alpine habitats and bogs were excluded from the analysis as very few species in the tunnel samples could be assigned to them.

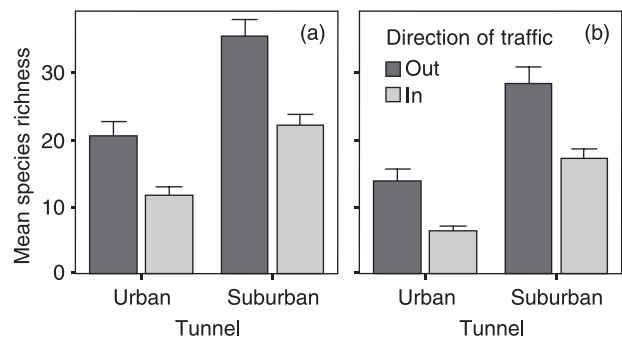


Figure 1 Mean species richness of seed samples from two motorway tunnels along lanes travelling out of (*out*) and into (*in*) the city ($n = 5$ per lane). (a): native species (b): non-native species. Error bars indicate 1 SE.

RESULTS

The seed deposition by vehicles differed markedly between the urban and suburban tunnel and for the opposite motorway lanes (Table 1). Native and non-native species richness of the tunnel samples was significantly higher in lanes leading out of the city compared to the inbound lanes (Fig. 1, $F_{1,16} = 34.57$, $P < 0.001$ for native species; $F_{1,16} = 31.87$, $P < 0.001$ for non-native species). Samples of the suburban tunnel had significantly more species than those of the urban tunnel (Fig. 1, $F_{1,16} = 46.56$, $P < 0.001$ for native species; $F_{1,16} = 61.44$, $P < 0.001$ for non-native species),

Similarly to species richness, the magnitude of seed deposition by native species was significantly higher in lanes leading out of the city (Fig. 2a, $F_{1,16} = 8.46$, $P = 0.01$) and in the suburban tunnel ($F_{1,16} = 33.65$, $P < 0.001$). For non-native species, we also observed a higher seed deposition in the suburban tunnel ($F_{1,16} = 138.81$, $P < 0.001$), but more seeds were deposited in the inbound tunnels – the opposite result as was found for non-native species richness (Fig. 2b, $F_{1,16} = 19.06$, $P < 0.001$). This is mainly an effect of the predominance of seeds from the cereals wheat and rye in samples of the inbound lanes. If all seeds of arable crops are excluded from the samples (including rapeseed that was more abundant in the outbound lanes), the pattern of

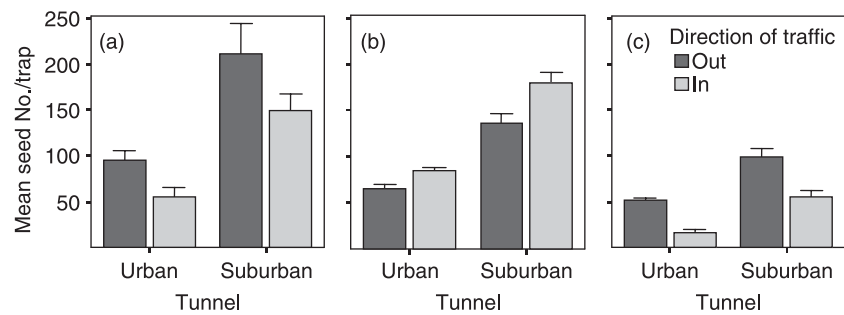


Figure 2 Mean seed deposition in seed traps inside two motorway tunnels along lanes travelling out of (*out*) and into (*in*) the city ($n = 5$ per lane). (a): native species (b): total non-native species (c): non-native species without arable crops. Error bars indicate 1 SE.

Table 2 Results of indicator species analysis for opposite directions of traffic flow (into vs. out of the city). Only species with significant indicator values (IV) are shown.

Species	Indicated direction	Observed indicator value (IV)	IV from randomized groups		
			Mean	SD	<i>P</i>
<i>Betula pendula</i>	In	63.7	54	2.99	0.0038
<i>Galium aparine</i>	In	50.0	22.8	8.57	0.0316
<i>Poa compressa</i>	Out	62.7	31.1	9.3	0.0122
<i>Festuca brevipila</i>	Out	60.0	31	9.32	0.0174
<i>Lycium barbarum</i>	Out	56.7	28.6	9.34	0.0175
<i>Chenopodium album</i>	Out	64.8	54	4.74	0.0233
<i>Agrostis capillaris</i>	Out	58.1	36.3	9.35	0.0317
<i>Oenothera biennis</i> agg.	Out	68.1	48.3	8.63	0.0323
<i>Achillea millefolium</i>	Out	43.3	25.1	9.21	0.0335
<i>Herniaria glabra</i>	Out	64.0	47.7	7.92	0.0445

seed deposition for non-native species is consistent with that of species richness: there is a higher seed deposition of non-native species in lanes leading out of the city than into the city (Fig. 2c, $F_{1,16} = 54.68$, $P < 0.001$).

The proportion of non-native species from all species in the samples was not significantly different between opposite lanes ($F_{1,16} = 0.32$, $P < 0.58$). However, when arable crops were excluded, the share of seeds of non-native species from the total seeds deposited was significantly higher for samples from the outbound lanes ($F_{1,16} = 18.52$, $P = 0.001$). Hence, the export of seeds from non-native species out of the city by vehicles was not only higher in numbers than the import, it was also higher in relation to their overall proportion.

In the indicator species analysis, 10 species could be shown to significantly indicate a particular direction of traffic. While eight species were associated with the samples of lanes leading out of the city, only two species, *Galium aparine* and *Betula pendula*, were significantly associated with the incoming lanes (Table 2). The higher number of indicators for the outbound lane is most likely due to the higher species richness in this direction (Table 1). Most species indicating the outbound lane were typical species of ruderal urban habitats such as *Poa compressa*, *Chenopodium album*, *Oenothera biennis* agg., and *Herniaria glabra*. Species of dry grassland habitats, including *Festuca brevipila*, *Agrostis capillaris*, and *Achillea millefolium*, also prevailed in

the samples of the outbound lanes. One woody species, *Lycium barbarum*, was related to the outbound lane. *O. biennis* agg., *C. album*, and *H. glabra* reached the highest indicator values.

The tunnel flora represents a broad variety of different habitat types, including elements of both urban-industrial vegetation and seminatural communities (Fig. 3). Among the habitat types, most species of the tunnel flora can be assigned to ruderal ecotones and grassland habitats. Species of woodlands, weed communities, and urban vegetation are also well represented in the samples.

Species of five habitat types showed significant affiliations with one direction of traffic. Lanes leading into the city can be characterized by woodland species (Fig. 3, Table 3). Lanes leading out of the city were significantly indicated by species of ruderal ecotones, weed communities, urban habitats, and dry meadows (Fig. 3, Table 3). The highest indicator values were found for species of dry meadows, woodlands, and weed communities.

DISCUSSION

Vectors driving invasion processes and changes in biodiversity patterns can be characterized by their cause (i.e. accidental or deliberate transport), their route, their tempo and strength, and

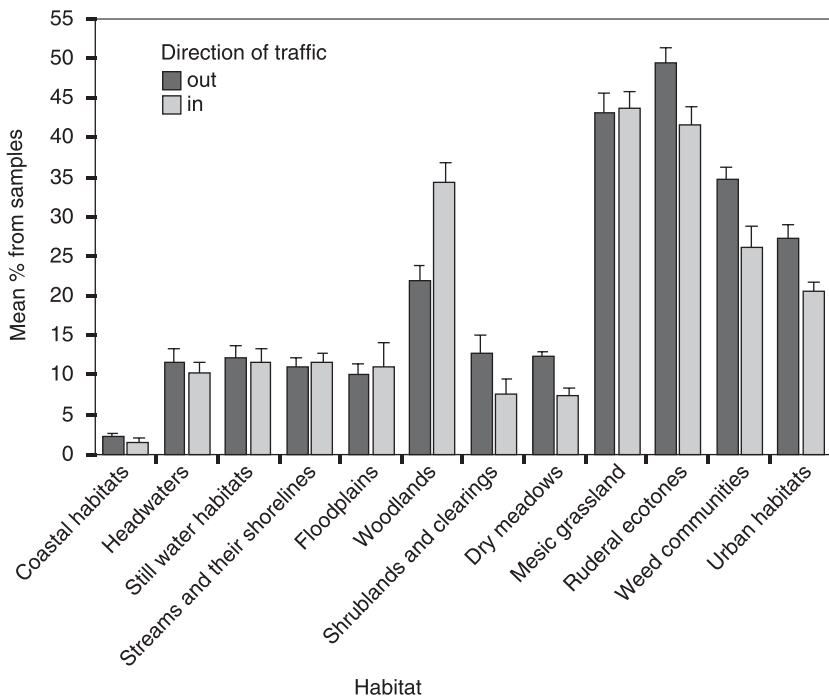


Figure 3 Proportion of species representing different habitat types in seed samples from opposite lanes of two motorway tunnels. Species could be assigned to more than one habitat type.

Table 3 Results of indicator species analysis with species grouped by their affiliation with different habitat types. Seed counts of all species in the samples representing one habitat type were aggregated. Species could be assigned to more than one habitat type. Species groups significantly indicating one direction of traffic are in bold.

Habitats indicated	No. of species in group	Indicated direction	Observed indicator value (IV)	IV from randomized groups		P
				Mean	SD	
Coastal habitats	3	Out	57.9	50.9	6.45	0.1376
Headwaters	4	Out	53.4	53.9	2.95	0.5057
Still water habitats	13	Out	51.3	54	2.96	0.7929
Streams and their shorelines	20	In	51.2	52.9	2.17	0.7471
Floodplains	29	In	52.5	56.5	3.89	0.8279
Woodlands	18	In	61.1	53	2.3	0.0018
Shrublands and clearings	16	Out	62.9	56.3	4.49	0.0956
Dry meadows	34	Out	62.6	53.3	2.46	0.0007
Mesic grassland	64	In	50.2	51.4	1.18	0.8925
Ruderal ecotones	69	Out	54.3	51.5	1.2	0.0142
Weed communities	56	Out	57	52.4	1.8	0.0114
Urban habitats	64	Out	56.8	52.1	1.63	0.0045

IV, indicator values.

finally by the species that are being transported (Carlton & Ruiz, 2005). As we have shown elsewhere, vehicles are seed-dispersal vectors that can transport a high magnitude of propagules and that act effectively at the regional scale, dispersing seeds over long distances (von der Lippe & Kowarik, 2007). The focus of this study was primarily on the route and the species involved as these characteristics most affect the ability of the vector to move species along the urban–suburban gradient.

Quantitative differences in seed deposition at opposing lanes

Seed transport by vehicles travelling in opposite directions along the urban–suburban gradient varied greatly with respect to species richness, the magnitude of seed deposition, and the proportion of non-native species. Seed samples from opposite lanes also differed in species composition, and single species and

species groups that are representative of different habitat types served as indicators of travel direction. Seed dispersal by vehicles can thus in general be related to species exchange between cities and their surroundings.

Urban areas often show a higher floristic diversity than the adjacent landscape. Consistently, the higher seed deposition and species richness in lanes leading out of the city (Figs 1 and 2) illustrated the high urban plant diversity of Berlin (Zerbe *et al.*, 2003). Traffic as a dispersal vector thus appears to reflect quantitative and qualitative differences in source floras at the local to regional scale. This indicates that traffic is not a vector of even dispersion of propagules in space but of spatially explicit, directed transport processes. The differentiation of roadside floras supports this conclusion, as vegetation of different highways in the same region can be characterized by distinct assemblages (Rentch *et al.*, 2005), which shows that homogenizing effects are not so strong as to equalize differences in site conditions and regional propagule sources. To determine whether traffic dispersal has the potential to homogenize or differentiate urban floras, however, it is necessary to consider the composition of the seeds that are exchanged.

The higher quantitative share of non-native species related to outbound lanes gives evidence to the assumption that cities can act as starting points of invasion processes, involving traffic as an effective support for rapid migration of plant species. This is in accordance with findings of increasing plant invasions due to urban land use at the local scale (Borgmann & Rodewald, 2005). As the invasion of wetlands and semiarid grassland habitats by harmful exotic plant species can be related to nearby roads (Choi & Bury, 2003; Gelbard & Belnap, 2003), seed export of non-native species out of the city can in fact contribute to the homogenization of seminatural habitats in the suburban or rural surroundings of the city. As there was no significant difference in the proportion of non-native species between the opposing lanes, the proportionately higher seed deposition along the outbound lanes must be related to higher propagule pressure of non-native species in the city centre.

Species composition of seed samples from opposing lanes

Only two species in the indicator species analysis were characteristic of samples from the inbound lanes (Table 2). Both, *G. aparine* and *B. pendula*, are not exclusively confined to rural or seminatural communities but also occur in urban habitats. Nevertheless, *G. aparine* is a nitrophyte of mesic to moist sites, which possibly occur less frequently towards the city centre due to an increasing proportion of compacted and well-drained soils.

The affiliation of the indicator species of the outbound lanes with urban habitats was much higher. All eight indicator species occur frequently in urban habitats and some are especially adapted to habitats of compacted soils (*P. compressa*, *H. glabra*) and areas subject to intense disturbance (*C. album*) that are typical of the city centre. The three indicator species that are representative of short-grass meadows (*F. brevipila*, *A. capillaris*, and *A. millefolium*) frequently occur on fallow land in Berlin, which,

due to the often prevailing sandy soils, is similar to dry acidic grassland habitats. These species, however, also occur in seminatural grasslands that are primarily distributed in the rural surroundings of the city as well as in the suburban area. It is thus striking that there is a significantly higher export of these species in the outbound lanes. This might be due to the high representation of dry grassland in the surroundings of the urban tunnel, especially in the large area of the airport district. Another possible origin could be seed mixtures for urban lawns and roadside embankments, which frequently include all three species. This points to an important implication when assessing the risks that are associated with urban-to-rural seed transport: the chance of gene flow between urban and non-urban populations of the same species also increases. At the infraspecific level, the provenances of urban populations that descend from seed mixtures can be quite different from the regional species pool. Due to German regulations, the seed mixtures mostly contain cultivars instead of regional provenances of a given species. Hence, an export of native species can be an unwanted effect if traits of domesticated taxa are transferred to wild populations. We therefore hypothesize that homogenization across urban–rural gradients may also occur on a subspecies level with consequences for genetic diversity.

The results of the indicator analysis using species groups that are associated with different habitats are consistent with those at the species level but allow for more general conclusions (Fig. 3, Table 3). The tunnel flora includes species of different habitats that cannot be exclusively assigned to ruderal or urban-industrial communities. Species confined to urban habitats only reach the fourth order of all seeds deposited. However, edge habitats and disturbed weed communities, which contribute the first and third orders of seeds in the samples, represent typical urban habitats and share a high number of species with the category of urban habitats. The high proportion of woodland and grassland species reflects the ability of traffic to promote non-standard dispersal events for species of rather undisturbed sites, such as *Pinus sylvestris*, *Veronica chamaedris*, or *Deschampsia cespitosa*, that are not commonly associated with anthropogenic dispersal.

Regarding the affiliation of species from different habitats with the opposite tunnel lanes, only woodland species significantly indicated the incoming lanes. This could be an effect of higher woodland density in the suburban surroundings of the city. The woodland group of species, however, was largely dominated by seeds of *B. pendula*, which, as already discussed, is also common in urban habitats, and because of its high seed production, a few specimens in the direct surroundings of the tunnel entrances could easily change the proportions between opposite lanes. Hence, if *B. pendula* is removed from the calculations, there appears to be no higher import of species that are strongly confined to woodland habitats. Conversely, species of three habitat types that are clearly associated with urban areas – edge habitats, disturbed weed communities, and urban-industrial habitats – indicated the outbound lanes. The prevalence of species of dry grasslands in the samples of the outbound lanes is consistent with the findings for the indicator analysis of the

species, but is based on a much larger species pool. Those species might have a closer spatial connection to roadsides near the urban centre than in the urban fringe or rural surroundings of the city, which could explain their higher transport by vehicles out of the city. In fact, dry urban habitats like airport areas, railroads, or dry urban wasteland are usually much closer to road corridors than short grass meadows in the rural surroundings of the city.

Consequences for the homogenization of urban and suburban floras

Our findings suggest a prevailing effect of 'suburbanization' of species predominant in urban habitats rather than an import of species from rural or suburban habitats that could enrich urban floras. This process could lead to homogenization within the process of suburbanization, as propagules of common ruderal and non-native species are easily dispersed from the inner city to the outskirts and to new developments in the urban fringe. This will not necessarily lead to low species diversity in the latter areas. As long as no displacement of species by invasive species takes place, the higher species richness of seeds that were transported out of the city will possibly increase species richness in suburban environments. This is consistent with findings of a suburban peak in plant biodiversity (Pyšek, 1992; McKinney, 2002) that can be attributed to the variety of habitat conditions as well as to the high potential for species to immigrate from both rural and urban communities. It means, however, that urban and suburban habitats become more similar as they share more species. Also the risk of plant invasions that can reduce native species richness is spread. Roadside plantations of non-native species in particular may act as a seed source for plant invasions along road verges. An example of this process is the frequent deposition of seeds of *Lycium barbarum*, which was significantly affiliated with the outbound lanes and is frequently planted along the sides of motorways. Since it has been shown for rural areas that roadsides can act as invasion foci for the adjacent landscape (Gelbard & Belnap, 2003), it is likely that seminatural habitats in suburban areas can also be invaded starting from roadsides.

The effectiveness of species exchange between urban and suburban habitats is fostered by the high proportion of long-distance-dispersal events caused by traffic (von der Lippe & Kowarik, 2007). According to our results, it is likely that normal distances between urban habitats and suburban environments are frequently bridged by car-borne dispersal. Homogenization by non-native plant species is most effective on a very similar regional scale as demonstrated by McKinney (2005). Also plant invasions at the regional scale are primarily driven by human-aided dispersal (Pauchard & Shea, 2006; Kowarik & von der Lippe, 2007). Thus, the combination of directed dispersal (i.e. the route of the vector) and the spatial scale over which propagules are transported along the urban–suburban gradient (i.e. the vector tempo) makes traffic an effective dispersal vector in exporting urban plant diversity to suburban sites, while also promoting plant invasions.

ACKNOWLEDGEMENTS

This study was supported by the postgraduate research and study program (DFG – GRK 780) 'Perspectives on Urban Ecology – the Example of the European Metropolis of Berlin.' We thank T. Bachmann and Y. Golopasany for technical assistance and K. Vargas for improving the English.

REFERENCES

- Bartlott, W., Biedinger, N., Braun, G., Feig, F., Kier, G. & Mutke, J. (1999) Terminological and methodological aspects of the mapping and analysis of the global biodiversity. *Acta Botanica Fennica*, **162**, 103–110.
- Borgmann, K.L. & Rodewald, A.D. (2005) Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. *Restoration Ecology*, **13**, 334–340.
- Carlton, J.T. & Ruiz, G.M. (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. *Invasive alien species* (ed. by H.A. Mooney, R.N. Mack, J.A. McNeely, L.E. Neville, P.J. Schei & J.K. Waage), pp. 36–58. Island Press, Washington.
- Choi, Y.D. & Bury, C. (2003) Process of floristic degradation in urban and suburban wetlands in northwestern Indiana, USA. *Natural Areas Journal*, **23**, 320–331.
- Czech, B., Krausman, P.R. & Devers, P.K. (2000) Economic associations among causes of species endangerment in the United States. *Bioscience*, **50**, 593–601.
- DeCandido, R., Muir, A.A. & Gargiullo, M.B. (2004) A first approximation of the historical and extant vascular flora of New York City: implications for native plant species conservation. *Journal of the Torrey Botanical Society*, **131**, 243–251.
- Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.
- Ernst, W.H.O. (1998) Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in the Netherlands: from wool alien to railway and road alien. *Acta Botanica Neerlandica*, **47**, 131–151.
- Gelbard, J.L. & Belnap, J. (2003) Roads as conduits for Exotic plant invasions in a semiarid landscape. *Conservation Biology*, **17**, 420–432.
- Haeupler, H. (2002) Die Biotope Deutschlands. *BIOLFLOR – eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland* (ed. by S. Klotz, I. Kühn & W. Durka), pp. 177–196. Bundesamt für Naturschutz, Bonn, Germany.
- Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H. & Jones, A. (2005) Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications*, **15**, 1893–1905.
- Hodkinson, D.J. & Thompson, K. (1997) Plant dispersal: the role of man. *Journal of Applied Ecology*, **34**, 1484–1496.
- Kowarik, I. (1995) On the role of alien species in urban flora and vegetation. *Plant invasions – general aspects and special*

- problems (ed. by P. Pyšek, K. Prach, M. Rejmánek & M. Wade), pp. 85–103. SPB. Academic Publishing, Amsterdam.
- Kowarik, I. (2003) Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. *Biological Invasions*, **5**, 293–312.
- Kowarik, I. & von der Lippe, M. (2007) Pathways in plant invasions. *Biological invasions*, Ecological Studies Vol. 193 (ed. by W. Nentwig), pp. 29–47. Springer, Berlin Heidelberg, Germany.
- Kühn, I., Brandl, R. & Klotz, S. (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, **6**, 749–764.
- Kühn, I. & Klotz, S. (2006) Urbanization and homogenization – comparing the floras of urban and rural areas in Germany. *Biological Conservation*, **127**, 292–300.
- McKinney, M.L. (2002) Urbanization, biodiversity, and conservation. *Bioscience*, **52**, 883–890.
- McKinney, M.L. (2004) Measuring floristic homogenization by non-native plants in North America. *Global Ecology and Biogeography*, **13**, 47–53.
- McKinney, M.L. (2005) Species introduced from nearby sources have a more homogenizing effect than species from distant sources: evidence from plants and fishes in the USA. *Diversity and Distributions*, **11**, 367–374.
- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.
- Pauchard, A. & Shea, K. (2006) Integrating the study of non-native plant invasions across spatial scales. *Biological Invasions*, **8**, 399–413.
- Pyšek, P. (1992) Settlement outskirts – may they be considered as ecotones? *Ekológia CSFR*, **11**, 273–286.
- Pyšek, P. (1998) Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography*, **25**, 155–163.
- Rentch, J.S., Fortney, R.H., Stephenson, S.L., Adams, H.S., Grafton, W.N. & Anderson, J.T. (2005) Vegetation–site relationships of roadside plant communities in West Virginia, USA. *Journal of Applied Ecology*, **42**, 129–138.
- Robinson, L., Newell, J.P. & Marzluff, J.A. (2005) Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. *Landscape and Urban Planning*, **71**, 51–72.
- Schmidt, W. (1989) Plant dispersal by motor cars. *Vegetatio*, **70**, 147–152.
- Schwartz, M.W., Thorne, J.H. & Viers, J.H. (2006) Biotic homogenization of the California flora in urban and urbanizing regions. *Biological Conservation*, **127**, 282–291.
- Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996) An improved method for seed bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology*, **10**, 144–151.
- Tikka, P.M., Hogmander, H. & Koski, P.S. (2001) Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology*, **16**, 659–666.
- von der Lippe, M. & Kowarik, I. (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, **21**, 986–996.
- Wace, N. (1977) Assessment of dispersal of plant species – the car-borne flora in Canberra. *Proceedings of the Ecological Society of Australia*, **10**, 167–186.
- Wania, A., Kühn, I. & Klotz, S. (2006) Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning*, **75**, 97–110.
- Wisskirchen, R. & Haeupler, H. (1998) *Standardliste der Farn- und Blütenpflanzen Deutschlands*, Ulmer, Stuttgart, Germany.
- Zerbe, S., Maurer, U., Schmitz, S. & Sukopp, H. (2003) Biodiversity in Berlin and its potential for nature conservation. *Landscape and Urban Planning*, **62**, 139–148.
- Zwaenepoel, A., Roovers, P. & Hermy, M. (2006) Motor vehicles as vectors of plant species from road verges in a suburban environment. *Basic and Applied Ecology*, **7**, 83–95.