Consequences of rapid urbanization on plant diversity in a Western Siberian city

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CONTENTS

SUMMARY

Plant communities respond sensitively to urban sprawl and are therefore considered as indicators for human-induced changes in habitats and landscapes. Ecological effects of urbanization on local plant diversity have been studied in various regions. However, these processes are poorly understood in rapidly growing cities in Western Siberia. In the city of Pavlodar in Kazakhstan, Western Siberia, recent anthropogenic degradation of the original ecosystems occurred as a result of enforced land-use changes (Virgin Land Campaign by the former Soviet Union) and expanding urbanization (from a few thousands to 355,000 inhabitants in 2015). The impacts of these changes on plant diversity may differ between the city core, the suburban zone and rural surroundings. One effect is the spread of alien plant species, which in turn profoundly influence native vegetation. This thesis consists of three studies conducted to investigate the consequences of urbanization for local plant communities in the region of Pavlodar. I considered species richness of native and alien plants, species composition and plant species characteristics (mainly frequencies of different plant life forms) in relation to different urban impacts.

The aim of the first study was to examine changes in plant species composition and abundance along an urban-rural gradient. Plant diversity and abundance as well as the percentage of alien species were recorded in plots on four 20-km long transect lines running from the city centre to the rural surroundings. Various habitat and landscape characteristics were assessed along the transect lines to describe the urban-rural gradient. The results showed that plant diversity increased with increasing distance to the city centre, which contrasts diversity patterns reported from European cities. The percentage of alien species decreased from 45% in the city centre to 23% in the rural surroundings. Local plant species richness, community structure and plant traits were partly influenced by habitat and landscape characteristics, which in turn were altered by recent land-use change.

Vehicles are an important vector for the dispersal of alien plants. Roads with high traffic densities in urban regions may facilitate the invasion of alien plants. The aim of the second project was to examine the effects of road type and distance to the city centre on native and alien plant species in both the aboveground vegetation and soil seed bank of road verges in the surroundings of Pavlodar. I investigated roadside vegetation at 12 sites along roads with two different traffic densities (national and local roads) and at two distances to the city centre (city edge and rural surrounding). At the same sites, the soil seed bank was also examined using the seedling-emergency method. I demonstrated that the type of road

and distance to the city centre influence the proportion of alien species in the aboveground vegetation. In the soil seed bank, seed species richness was affected by the distance to the city, while measures of alien seed diversity were affected by both the type of road and distance to the city. The increase of alien plant species along national roads and at the edge of the city could be explained by the propagule transportation through vehicles as well as by specific conditions in the roadside verges. Analysis of plant species composition indicates a delayed response of the soil seed bank to the establishment of alien species. Furthermore, the frequencies of different plant life forms differed between the two road types and were influenced by the distance to the city.

Within the expanding area of the city, new forests were planted for wind protection and to damp extreme climatic conditions between 1960 and 1970. Nowadays, urban forests no longer properly managed, and the increasing needs of people for recreation have to be fulfilled by visiting floodplain forests in the suburban zone. The third study aimed to assess the frequency of forest visitors, their characteristics and activities, and to quantify the effects of recreation disturbance (trampling, damage to ground vegetation and damage to trees and shrubs) and other human-mediated disturbance (waste deposits, soil disturbance, removal of leaf litter layer and ground fire) on the vegetation and plant characteristics of urban and suburban forests in Pavlodar. In urban forests, total plant species richness was reduced by recreation disturbance. In suburban forests, recreation disturbance and other human-mediated disturbance enhanced the colonization success of alien plants. Plant life forms were affected to a different extent by recreation disturbance and other human-mediated disturbances in urban and suburban forests.

To my knowledge, the results of this thesis provide the first evidence on effects of urbanization processes on the biodiversity in Western Siberia. Adequate management actions are required to prevent further degradation of original ecosystems in this Western Siberian city. These findings may contribute that aspects of human well-being and nature are better considered in future planning processes in this region.

GENERAL INTRODUCTION

The growing human population together with an increasing level of consumption and urban sprawl are the most important drivers of ecosystem degradation. Growing cities modify land cover, reduce the area of natural habitats, affect ecosystem functioning and contribute to the loss of biodiversity (Elmqvist et al., 2013).

Plant communities are vulnerable to environmental changes, therefore plant species richness is frequently used as a proxy for biodiversity. Furthermore, changes in plant species richness and composition indicate the alteration in ecosystem function (McIntyre et al., 1999). Biodiversity patterns have been largely examined in studies from European, North American and Australian cities (reviewed by Niemelä et al., 2011; Aronson et al., 2014). However, little is known on the impact of urbanization in Central Asia and Western Siberia. In particular European regions, plant assemblages have been reported to adapt to urban conditions and to develop strategies without a significant loss of species diversity (Kühn et al., 2004; Croci et al., 2008). However, a decrease in plant species richness and diversity has frequently occurred in urban centres (McKinney, 2002). Due to the geographical bias and the contrasting findings, a global analysis of the environmental impacts of urbanization is still lacking (McDonald and Marcotullio, 2011). Species diversity in urban settings largely depends on land use, urban growth, landscape characteristics, human social-economic issues, and political and historical conditions (Niemelä et al., 2011).

This thesis provides the first empirical evidence of the impact of land use changes and urban expansion on the biodiversity in a Western Siberian city in Kazakhstan, Central Asia. In 1954–1963, the traditional land use has been changed very rapidly in this region by the former USSR's Virgin Land Campaign, which caused a dramatic impact on the social and economical development. Pavlodar in northern-eastern Kazakhstan was chosen as one of the centres of the Campaign because of the existing traffic infrastructure system and the potentially fertile arable soils. During the Campaign, approximately 200,000 people were transferred to the state farms in the Pavlodar region (an increase of the population by 37% during the first two years), which led to a pronounced shortage of housing (Insebaev et al., 2007). However, due to the failure of the Campaign, large areas of intensive farming have been abandoned by now (De Beurs and Henebry, 2004). Consequently, the Campaign accelerated industrial and economical development. People settled in the city of Pavlodar, which increased from a few thousands to 355,000 inhabitants by 2014 (Committee of Statistics of the Republic of Kazakhstan, 2015). Nowadays the Pavlodar region includes several huge industrial agglomerates, and the share of the urban population increased by almost 70%. In the rural surroundings, free-grazing livestock husbandry and crop production continued in smaller areas and at a lower intensity. A major part of the investigation area was originally dry bunch feather-grass (*Stipa* ssp.) or fescue (*Festuca* ssp.) steppe, while the western side of the city is situated close to a 12–15 km wide floodplain of the river Irtysh with forb-rich meadows and floodplain forests. Specific factors that impacted the ecosystems include an uncontrolled grazing, burning of vegetation due to the dry climate, deposition of waste and increased traffic density.

Application of urban-rural gradients is a common approach to assess the effects of urbanization on biodiversity (McDonnell and Hahs, 2008; Burton et al., 2009). Specific urban conditions, such as the density of built-up area or proportion of natural habitats, are usually highly correlated with the distance to city centre (Du Toit and Cilliers, 2011). Previous studies revealed that the diversity of native and alien species as well as species composition in the communities change along the urban-rural gradient (see for example Ranta, 2012). However, the patterns of reported changes might differ among the regions, leading to the diverse interpretations (McKinney, 2006, 2008; Aronson et al., 2014). **Chapter I** presents the results of a field survey of the vegetation along a 20-km long urban-rural gradient in the city of Pavlodar and its surroundings. In addition to the distance to city centre, I used habitat and landscape characteristics (e.g., distance from the study site to the nearest built-up area, land-use type, percentage cover of wasteland or cropland) to analyse the effects of urbanization on plant diversity (species richness and diversity indexes), percentage of alien species, community composition and plant species characteristics (various plant life forms and evolutionary strategies). In this study, I emphasised the influence of land-use modifications owing to the Virgin Land Campaign on the frequencies of plant species.

Urbanization leads to an increased number and proportion of alien species in plant communities (Pyšek, 1998; Zisenis, 2015). The importance of vehicles as a dispersal vectors for alien plants was documented by Von der Lippe and Kowarik (2007, 2008), Fowler et al. (2008), and Ansong and Pickering (2013). Road verges provide areas of disturbed habitats for the establishment of alien plants (Arévalo et al., 2010). High traffic densities result in a strong pressure of alien propagules in roadside verges (Von der Lippe and Kowarik, 2008). Moreover, plant invasion processes might be influenced by the type of road (Joly et al., 2011). In my study region, the traffic density has increased very recently (in the past two decades). Distances of hundreds of kilometres between cities in Kazakhstan and an intensive movement of people potentially promote the transport of alien plants from remote biogeographic regions and may lead to the changes in the composition of local flora. In the cities, additional sources for the introduction of alien species in roadside verges may occur (Hodkinson and Thompson, 1997). In the **Chapter II**, I investigated roadside verges along the two types of roads with different traffic densities (national and local roads) and at two different distances to the city centre (city edge and rural surroundings). I examined the effects of road type and distance to the city centre on both the aboveground vegetation and soil seed bank of roadside verges, considering the abundance and composition of alien and native plant species. Besides that, I tested whether plant life forms and seed traits differed between roads of different type and distance to the city.

The values of urban ecosystems for human well-being are increasingly recognized in numerous studies (Bolund and Hunhammar, 1999; Dwyer et al., 2000). Urban forests provide highly valuable recreational resources (Konijnendijk et al., 2005). In general, forests in urban areas are subject to recreation and other anthropogenic disturbances, which affect plant diversity (see for example Hamberg et al., 2008; Hegetschweiler et al., 2009). However, the preservation of natural diversity in these ecosystems may not always be respected by the local authorities as well as by the general public. In northern-eastern Kazakhstan, urban forests, which have been planted in Soviet period, are hardly maintained nowadays. Suburban floodplain forests, restricted to the western edge of Pavlodar, may be the preferred areas for recreation of urban citizens. The aim of the **Chapter III** was to examine the effects of recreational use on plant diversity in urban and suburban forests. I assessed the frequencies of forest visitors, their characteristics and activities as well as the existing recreation disturbance and other human mediated disturbance, and analyzed the potential effects of these human factors on vegetation parameters (species richness and number of alien species) and various plant life forms in 14 urban and 11 suburban forests. In this study, the effects of the extent of vegetation cover, habitat and landscape characteristics and forest area on the vegetation were also considered. I took into consideration positive or negative personal perceptions of forest visitors to draw the conclusions from this study.

The final section of this thesis, the **General Discussion**, discusses the most important findings of the three chapters and their implications for sciences as well as for the management actions in the study region.

References

Ansong, M., Pickering, C., 2013. Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. PLoS ONE 8(11)e:80275.

Arévalo, J. R., Otto, R., Escudero, C., Fernández-Lugo, S., Arteaga, M., Delgado, J. D., Fernández-Palacios, J. M., 2010. Do anthropogenic corridors homogenize plant communities at a local scale? A case studied in Tenerife (Canary Islands). Plant Ecol 209, 23–35.

Aronson, M. F., La Sorte, F. A. Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B. et al., 2014. A global analysis of the impact of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proc R Soc B 281, 1–8.

Bolund, P., Hunhammar, S., 1999. Ecosystem services in urban areas. Ecol Econ 29, 293–301.

Burton, M. L., Samuelson, L. J., McKenzie, M. D., 2009. Riparian wood plant traits across an urban-rural land use gradient and implications for watershed function with urbanization. Landsc Urban Plan 90, 42–55.

Committee of Statistics of the Republic of Kazakhstan, 2015. Pavlodar region. http://www.stat.gov.kz/faces/homePage.htm.

Croci, S., Butet, A., George, A., Aguejdad, R., Clergeau, P., 2008. Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. Landsc Ecol 23, 1171–1186.

De Beurs, K., Henebry, G., 2004. Land surface phenology, climatic variation, and institutional change: analysing agricultural land cover change in Kazakhstan. Remote Sens Environ 89, 497–509.

Du Toit, M. J., Cilliers, S. S., 2011. Aspects influencing the selection of representative urbanization measures to quantify urban-rural gradients. Landsc Ecol, 26, 169–181.

Dwyer, J. F., Nowak, D. J., Noble, M. H., Sisinni, S. M., 2000. Connecting people with ecosystems in the 21st century: an assessment of our nation's urban forests. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland.

Elmqvist, T., Fragkias, M., Goodness, J. et al. (Eds.), 2013. Urbanization, biodiversity and ecosystem services: challenges and opportunities. A global assessment. Springer Open.

Fowler, J. F., Sieg, C. H., Dickson, B. G., Saab, V., 2008. Exotic plant species diversity: influence of roads and prescribed fire in Arizona ponderosa pine forests. Rangeland Ecol Manage 61, 284–293.

Hamberg, L., Lehvävirta, S., Malmivaara-Lämsä, M., Rita, H., Kotze, D. J., 2008. The effects of habitat edges and trampling on understorey vegetation in urban forests in Helsinki, Finland. Appl Veg Sci 11, 83–98.

Hegetschweiler, K. T., van Loon, N., Ryser, A., Rusterholz, H.-P., Baur, B., 2009. Effects of fireplace use on forest vegetation and amount of woody debris in suburban forests in Northwestern Switzerland. Environ Manage 43, 299–310.

Hodkinson, D. J., Thompson, K., 1997. Plant dispersal: the role of man. J Appl Ecol 34, 1484–1496.

Joly, M., Bertrand, P., Gbangou, R. Y., White, M.-C., Dubé, J., Lavoie, C., 2011. Paving the way for invasive species: road type and the spread of common ragweed (*Ambrosia artemisiifolia*). Environ Manage 48, 514–522.

Insebaev, T. A., Azerbaev, A. D., Abdrakhmanova, A. D., Randuk, I. V., Shegenova, Z. K., 2007. Павлодарская область: страницы истории (1938–2008) (Pavlodar region: pages of history (1938–2008)). S. Torajgyrov Pavlodar State University, Pavlodar. (In Kazakh and Russian).

Konijnendijk, C. C., Nilsson, K., Randrup, T. B., Schipperijn, J. (Eds.), 2005. Urban Forests and Trees. Springer, Heidelberg.

Kühn, I., Brandl, R., Klotz S., 2004. The flora of German cities is naturally species rich. Evol Ecol Res 6, 749–764.

McDonald, R., Marcotullio, P., 2011. Global effects of urbanization on ecosystem services. In: Niemelä, J., Breuste, J., Elmqvist, T., Guntenspergen, G., James, P., McIntyre, N. (Eds.). Urban ecology: patterns, processes and applications. Oxford University Press, Oxford.

McDonnell, M. J., Hahs, A. K., 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landsc Ecol 23, 1143–1155.

McIntyre, S., Lavorel, S., Landsberg, J., Forbes, T. D. A., 1999. Disturbance response in vegetation – towards a global perspective on functional traits. J Veg Sci 10, 621–630.

McKinney, M. L., 2002. Urbanization, biodiversity, and conservation. BioScience 52, 883-890.

McKinney, M. L., 2006. Urbanization as a major cause of biotic homogenization. Biol

Conserv 127, 247–260.

McKinney, M. L., 2008. Effects of urbanization on species richness: A review of plants and animals. Urban Ecosyst 11, 161–176.

Niemelä, J., Breuste, J., Elmqvist, T., Guntenspergen, G., James, P., McIntyre, N. (Eds.), 2011. Urban ecology: patterns, processes and applications. Oxford University Press, Oxford.

Pyšek, P., 1998. Alien and native species in Central European urban floras: a quantitative comparison. J Biogeogr 25, 155–163.

Ranta, P., 2012. Urban ecosystems – Response to disturbances, resilience and ecological memory. Dissertation. Environmentalica Fennica, Helsinki.

Von der Lippe, M., Kowarik, I., 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv Biol 21, 986–996.

Von der Lippe, M., Kowarik, I., 2008. Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients. Diversity Distrib 14, 18–25.

Zisenis, M., 2015. Alien plant species: A real fear for urban ecosystems in Europe? Urban Ecosyst 18, 355–370.

Chapter I

Changes in plant diversity along an urban–rural gradient in an expanding city in Kazakhstan, Western Siberia

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Research Paper

Changes in plant diversity along an urban–rural gradient in an expanding city in Kazakhstan, Western Siberia

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HIGHLIGHTS

- We compared plant diversity along urban–rural gradients in Kazakhstan.
- Species richness increased from the city centre to the rural surroundings.
- Plant community structure changed along urban–rural gradients.
- Changes in species characteristics can partly be explained by landscape features.

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ABSTRACT

Plant communities respond sensitively to urban expansion and therefore serve as indicators for human land use. An urban–rural gradient approach was used to examine changes in plant species composition and abundance related to human-altered habitats in the Western Siberian city of Pavlodar (Kazakhstan). This region is characterized by harsh continental environmental conditions and recent anthropogenic degradation of the original steppe grasslands as a result of enforced land-use changes (Virgin Land Campaign) and rapidly expanding urbanization. Plant diversity and abundance as well as the percentage of alien species were recorded in plots on four 20-km long transect lines running from the city centre to the rural surroundings. Various habitat and landscape characteristics were assessed along the transect lines to describe the urban–rural gradient. Based on the results of a principal component analysis considering these landscape characteristics the variable "distance to the city centre" was used as proxy for the urban–rural gradient. Plant diversity increased with increasing distance to the city centre and was also influenced by the type of land use (ornamentally managed, agricultural or unmanaged land) and the percentage cover of built-up area within a 500 m radius. The percentage of alien species decreased from 45% in the city centre to 23% in the rural surroundings. The percentage of species belonging to different plant life forms and to different evolutionary strategies were affected by different landscape characteristics. The study showed that the combined effects of expanding urbanization and agricultural land-use changes altered the plant species composition.

1. Introduction

In a rapidly urbanizing world, knowledge of ecosystem responses to urbanization is a need to ensure that cities are planned for the well-being of residents and nature (Niemelä, 2011). A combination of processes or drivers including habitat transformation, fragmentation, specific urban environmental conditions and human preferences are assumed to shape plant communities in urban areas (Williams et al., 2009). However, the magnitude of the different drivers may differ depending on the region or even the city (Niemelä, 2011).

Effects of urbanization can be examined through studies across urban–rural gradients (Burton, Samuelson, & Pan, 2009; McDonnell & Hahs, 2008; Van Heezik, Smyth, & Mathieu, 2008; Weng, 2007). Such gradients, from densely built city centres to increasingly rural surroundings occur all over the world. In many cases, however, there are highly complex indirect gradients (e.g., Du Toit & Cilliers, 2011; Hahs & McDonnell, 2006). Cities include unique habitats (e.g., domestic gardens, parks, roadside verges) that are subject to high anthropogenic impacts (e.g., fertilizers, pesticides,

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trampling, noise and artificial light). Studies on plant and insect communities revealed that species composition is changing along the urban–rural gradient, while the diversity of native species is usually reduced in urban areas but shows a peak in suburban area compared to the rural surroundings (e.g., McKinney, 2008; Ranta, 2012). In contrast, the number of alien (non-native) species is often increased in urban areas (Pyšek, 1998; Ranta, 2012). Urbanization promotes dispersal of exotic species, resulting in a gradual replacement of native biotas (McKinney, 2002). In a global perspective, this process diminishes floral and faunal distinctions among regions (Olden & Poff, 2004). Urbanization may lead to biotic homogenization (McKinney, 2006, but see Aronson et al., 2014).

Urbanization effects on biodiversity have mainly been studied in cities of Europe, North America and Australia (Aronson et al., 2014). Very little is known on the impact of urbanization in Central Asia and Western Siberia. The aim of this study was to explore different factors that influence the vegetation pattern in the agglomerate of Pavlodar, a city in north-eastern Kazakhstan. The people of this region experienced very rapid changes in the traditional husbandry system with a dramatic impact on the social and economical development as a result of the Virgin Land Campaign in 1954–1963 (see Study area). The Campaign altered original habitats resulting in significant ecosystem changes together with the increased urbanization have so far not been investigated. We aimed to disentangle habitat and landscape factors that may influence plants communities in the expanding city of Pavlodar. We also investigated whether life form and evolutionary strategy types of plants are affected by urbanization. We determined the urban–rural gradient based on 14 habitat and landscape characteristics using principal component analysis.

In particular, we addressed the following questions:

(1) Do plant species diversity and the proportion of alien (non-native) species change along the urban–rural gradient in the developing city of Pavlodar?
(2) Which habitat and landscape variables influence plant diversity and species composition along the urban–rural gradient?
(3) Do life form and evolutionary strategies of plants change along the urban–rural gradient?

2. Methods

2.1. Study area

The study was conducted in the city of Pavlodar (331,000 inhabitants) and its surroundings in northern-eastern Kazakhstan (Fig. 1). Pavlodar was chosen as one of the centres of the Virgin Land Campaign in 1954–1963 because of the existing traffic infrastructure system and the potentially fertile arable soils. During the Campaign, the area of crop cultivation in the region increased from 0.8 to 2.8 million hectares. Approximately 200,000 people were transferred to the state farms in the Pavlodar region (an increase of the population by 37% during the first two years), which led to a pronounced shortage of housing (Insebaev et al., 2007). However, due to the failure of the Campaign large areas of intensive farming have been abandoned by now (De Beurs & Henebry, 2004). Consequently, the Campaign accelerated industrial and economical development. Nowadays the Pavlodar region includes several huge industrial agglomerates, and the share of the urban population increased by almost 70%. Specific factors that impacted the ecosystems include an uncontrolled intensive grazing, burning of grassland vegetation due to the dry climate, deposition of waste and contamination by petroleum products from pipelines and traffic.

Situated at the eastern embankment of the river Irtysh in the Western Siberian Plateau at the elevation of 125–150 m above sea level, Pavlodar has a dry continental climate with a mean annual precipitation of 228 mm and a mean annual temperature of 2.1 °C (National Hydrometeorological Service of the Republic of Kazakhstan, 2011). Mean January temperature is −18.1 °C (minimum temperature: −47 °C) and mean July temperature 21.3 °C (maximum temperature: 42 °C). There is usually a constant snow cover (depth 12–14 cm) from the beginning of November to the beginning of April.

The Irtysh valley runs from south to north. The width of river Irtysh varies from 500–800 m at low water level to 1200–1500 m during the flood period in spring. The eastern embankment of the river is formed by a 25–50 m high slope, while the western bank of the river passes into a 12–15 km wide floodplain with several small streams. The bedrock of the study area consists of eroded Pliocene deposits covered by a Pleistocene layer of sand, gravel and loess loam, sometimes with pebble stones (Kalinina, 1961). A major part of the investigation area was originally dry bunch feather-grass (*Stipa* ssp.) or fescue (*Festuca* ssp.) steppe, while in the flood plain a forb-rich meadow steppe occurred (Rachkovskaya & Bragina, 2012).

2.2. Sampling design and plant survey

Plant surveys were carried out between late June and early August 2012. Four 20 km-long transect lines were installed, beginning in the centre of Pavlodar (52°16.58′ N, 76°56.26′ E) and running in the four main directions (N, E, S, W) from the city centre into the rural surroundings (Fig. 1). The western transect line crossed the Irtysh valley with its alluvial floodplains, while the other three transect lines covered residential and agricultural areas in originally dry steppe-like grassland. Plant surveys were made at distances of 2 km along each transect line resulting in 4 × 10 sites plus the common site in the centre of Pavlodar city (in total 41 sites). At each site four sampling plots, measuring 5 m × 5 m and situated 20 m from each other, were installed.

Species richness of vascular plants, their abundance and vegetation cover (%) were recorded in each plot. Spontaneously growing species were only recorded. Abundance of plant species was assessed using the Braun-Blanquet method (1964). Abundance classes were transformed as follows: *r*: 0.01%; +0.1%; 1:5%; 2:17.5%, 3:37.5%; 4:62.5% and 5:87.5%. Plant species were identified following Pavlov (1956–1966) and Goloskokov (1972). Nomenclature was adjusted following Czerepanov (1995). Information on non-native (alien) plant species was obtained from Nurmukhambetova (2002), Kamkin (2009) and Leonova (2010). Information on the species composition of the original vegetation cover was extracted from Lavrenko (1991). A Red Data List of plants in Kazakhstan is not yet available. Therefore the conservation status of plants was derived from the Red List of Kazakh SSR (Bikov, 1981).

2.3. Habitat and landscape structure characteristics

For each sampling site, the intensity of disturbance and type of land use were assessed in the field (Table 1). For the intensity of disturbance, the impact of each of ten different types of disturbance was visually estimated in each plot using the four categories: absent (0), low (1), moderate (2) and high (3) (Appendix A). The scores of the 10 types of disturbance were added for each plot and the mean of four plots was calculated as a semi-quantitative measure of the overall intensity of disturbance for each sampling site. The type of land use was assigned to one of three categories (Table 1).

Four habitat and seven landscape characteristics were derived from satellite maps (Google Earth, 2013). Habitat characteristics included the distance of the sampling site to the nearest building or built-up area, the distance to the nearest road, the distance to the nearest wooded area and the distance to the nearest water

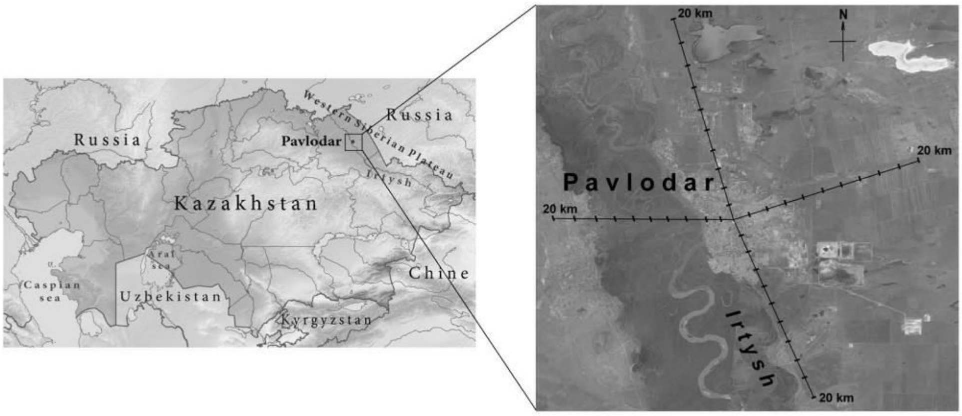

Fig. 1. Location of the study area in north-eastern Kazakhstan, showing the four transect lines. The western transect line cover the floodplain of river Irtysh, while the other three transect lines were situated in originally dry steppe grassland.

body (Table 1). The percentage cover of built-up area and traffic infrastructure within a radius of 200 m and 500 m around each sampling site were determined using the pixel counting function of Adobe Photoshop, version 10.0.1 (estimated to the nearest 5%). In the same way, we assessed the percentage cover of wasteland, cropland, woodland, grassland and water bodies within a radius of 200 m and 500 m around each sampling site (Table 1).

Table 1
List of habitat and landscape variables used in PCA, GLM and ANCOVA analyses.

Variables codes	Definition
Direction	Four directions (N, E, S, W) of the transect lines running from the urban centre into the rural surroundings
Distance	Distance from the city centre (km)
Habitat characteristics:	
Disturbance	Intensity of disturbance: score of 10 types of disturbances (Appendix A) were added for each plot and the mean of each plot was calculated
Land use	Three land-use types: ORN–ornamental management by urban services AGR–agricultural use of steppe and floodplains for pastures (free browsing herds of cattle, sheep and horses), mowing, cultivation of cereals, private gardens UNM–rough herbage (unmanaged land)
DistBuild	Distance from the study site to the nearest building or built-up area (m)
DistRoad	Distance from the study site to the nearest road (m)
DistWood	Distance from the study site to the nearest wooded area (m)
DistWater	Distance from the study site to the nearest water body (m)
Landscape characteristics:	Cover (in %) of different landscape elements within a radius of 200 m and 500 m around each study site
Build200/500	buildings–including residential areas, industrial and rural settlements
Traf200/500	traffic infrastructure–roads, railway trails, parking areas and pedestrian paths
Waste200/500	wasteland–trampled spots, industrial land, landfills and waste deposits, salted and eroded patches and other spots with bare soil
Crop200/500	cropland–arable fields and private gardens
Wood200/500	woodland–planted and natural occurrences of trees and bushes
Grass200/500	grassland–unwooded natural remnants (occasionally grazed pastures and abandoned pastures), including floodplains, also lawns
Water200/500	water–river Irtysh and small channels and ditches

2.4. Plant species characteristics

Based on available data bases (BioFlor Version 1.1 (Klotz, Kühn, & Durka, 2002); Open atlas of vascular plants of Russia and adjacent countries) and information collected by local botanists, data on plant life form and evolutionary strategy types were compiled. The plant species recorded were assigned to one of the four life forms (geophytes, chamaephytes, therophytes and hemicryptophytes; Raunkiaer, 1934). Similarly, the plant species were categorized according to the evolutionary strategy types of (Grime, 1979; R+, C+, S+ and CRS) following Graae and Sunde (2000). In the statistical analyses, however, only species with R+, C+ and S+ strategies were considered.

2.5. Statistical analyses

Principal component analysis (PCA) is a multivariate analysis that reduces a large number of variables down to a smaller number of relatively independent components associated with a set of specific variables. The values of the 14 habitat and landscape variables (see Table 1; transformed for normality, land use was excluded) were used as input for a PCA. The PCA revealed three distinct components (Appendix B), which explained together 65.7% of the variance in habitat and landscape variables. The first component was associated with distance to the city centre, distance to the nearest built-up area, area of buildings, area of traffic infrastructure, wasteland area and grassland area. All these variables were highly intercorrelated with distance to the city centre (Appendix C). Therefore, in further analyses, distance to the city centre was used as a proxy for the urban–rural gradient in this recently expanding town.

The 12 shrub and 8 tree species recorded in the 40 sampling sites were not considered in the data analyses because most of them were planted. Three measures of plant diversity were used (species richness, Shannon index and evenness). Generalized linear models with Poisson distributed errors and log-link function for species richness and ANCOVA for Shannon index and evenness were applied to examine potential effects of the direction of the transect line, distance from the city centre to the rural surroundings and habitat and landscape variables (Table 2). To avoid pseudoreplicates, we omitted data from the central site in all analyses (reducing the number of sites to 40). To assess the effects of these variables on the percentage of alien species, generalized linear models with binomial distributed errors and log-link function were used. Log-transformations were applied to explanatory variables to fit normal distributions (Table 2). The direction of transect lines, distance and

Table 2
Summary of GLM and ANCOVA analyses showing the effect of habitat and landscape characteristics on plant diversity measures and percentage of alien species along transect lines running from the centre of Pavlodar, Kazakhstan, to the rural surroundings. Data are shown for all four transect lines and for three transect lines excluding the western one covering the floodplain of river Irtysh.

Dependent variables	Explanatory variables	Four transect lines	Three transect lines
Species richness[a]	Direction	$X^2 = 18.70$, df = 3, $\mathbf{p < 0.001}$	$X^2 = 2.46$, df = 2, $p = 0.29$
	Distance	$X^2 = 26.87$, df = 9, $\mathbf{p = 0.002}$	$X^2 = 34.74$, df = 9, $\mathbf{p < 0.0001}$
	Disturbance	–	–
	Land use	$X^2 = 8.13$, df = 2, $\mathbf{p = 0.017}$	$X^2 = 14.05$, df = 2, $\mathbf{p = 0.001}$
	$\text{DistRoad}^{\log}$	–	–
	$\text{DistWood}^{\log}$	$X^2 = 1.90$, df = 1, $p = 0.17$	–
	$\text{Build500}^{\log}$	$X^2 = 6.95$, df = 1, $\mathbf{p = 0.008}$	$X^2 = 5.96$, df = 1, $\mathbf{p = 0.010}$
	$\text{Traf500}^{\log}$	–	–
	$\text{Waste500}^{\log}$	$X^2 = 3.32$, df = 1, $p = 0.07$	–
	$\text{Crop500}^{\log}$	–	–
	$\text{Grass500}^{\log}$	–	–
Shannon index[b]	Direction	$F_{3,21} = 17.97$, $\mathbf{p < 0.0001}$	$F_{2,13} = 12.05$, $\mathbf{p = 0.001}$
	Distance	$F_{9,21} = 4.08$, $\mathbf{p = 0.004}$	$F_{9,13} = 4.61$, $\mathbf{p = 0.007}$
	Disturbance	–	$F_{1,13} = 1.08$, $p = 0.32$
	Land use	$F_{2,21} = 3.74$, $\mathbf{p = 0.041}$	$F_{2,13} = 5.55$, $\mathbf{p = 0.018}$
	$\text{DistRoad}^{\log}$	–	–
	$\text{DistWood}^{\log}$	$F_{1,21} = 2.79$, $p = 0.11$	$F_{1,13} = 0.98$, $p = 0.34$
	$\text{Build500}^{\log}$	$F_{1,21} = 3.80$, $p = 0.07$	–
	$\text{Traf500}^{\log}$	$F_{1,21} = 1.99$, $p = 0.17$	–
	$\text{Waste500}^{\log}$	$F_{1,21} = 5.46$, $\mathbf{p = 0.030}$	–
	$\text{Crop500}^{\log}$	–	–
	$\text{Grass500}^{\log}$	–	$F_{1,13} = 1.21$, $p = 0.29$
Evenness[c]	Direction	$F_{3,23} = 12.00$, $\mathbf{p < 0.0001}$	$F_{2,10} = 18.12$, $\mathbf{p < 0.001}$
	Distance	$F_{9,23} = 1.88$, $p = 0.11$	$F_{9,10} = 3.80$, $\mathbf{p = 0.025}$
	Disturbance	–	$F_{1,10} = 1.69$, $p = 0.22$
	Land use	$F_{2,23} = 2.62$, $p = 0.09$	$F_{2,10} = 4.18$, $\mathbf{p = 0.048}$
	$\text{DistRoad}^{\log}$	–	$F_{1,10} = 1.51$, $p = 0.25$
	$\text{DistWood}^{\log}$	$F_{1,23} = 2.46$, $p = 0.13$	$F_{1,10} = 6.65$, $\mathbf{p = 0.027}$
	$\text{Build500}^{\log}$	–	–
	$\text{Traf500}^{\log}$	$F_{1,23} = 2.73$, $p = 0.11$	$F_{1,10} = 2.59$, $p = 0.14$
	$\text{Waste500}^{\log}$	–	$F_{1,10} = 1.83$, $p = 0.21$
	$\text{Crop500}^{\log}$	–	–
	$\text{Grass500}^{\log}$	–	$F_{1,10} = 1.62$, $p = 0.23$
Percentage of aliens[d]	Direction	$X^2 = 38.86$, df = 3, $\mathbf{p < 0.0001}$	$X^2 = 1.81$, df = 2, $p = 0.40$
	Distance	$X^2 = 38.54$, df = 9, $\mathbf{p < 0.0001}$	$X^2 = 31.08$, df = 9, $\mathbf{p < 0.001}$
	Disturbance	–	$X^2 = 1.05$, df = 1, $p = 0.31$
	Land use	$X^2 = 4.33$, df = 2, $p = 0.12$	$X^2 = 7.56$, df = 2, $\mathbf{p = 0.023}$
	$\text{DistRoad}^{\log}$	$X^2 = 16.08$, df = 1, $\mathbf{p < 0.0001}$	$X^2 = 9.54$, df = 1, $\mathbf{p = 0.002}$
	$\text{DistWood}^{\log}$	–	$X^2 = 2.07$, df = 1, $p = 0.15$
	$\text{Build500}^{\log}$	$X^2 = 1.87$, df = 1, $p = 0.17$	–
	$\text{Traf500}^{\log}$	$X^2 = 0.29$, df = 1, $p = 0.59$	$X^2 = 2.50$, df = 1, $p = 0.11$
	$\text{Waste500}^{\log}$	–	–
	$\text{Crop500}^{\log}$	–	–
	$\text{Grass500}^{\log}$	$X^2 = 6.85$, df = 1, $\mathbf{p = 0.009}$	$X^2 = 7.59$, df = 1, $\mathbf{p = 0.006}$

[log] log-transformed.
– Excluded from the model.
Significant results are in bold ($p < 0.05$).
[a] GLM, poisson distributed errors
[b] ANCOVA
[c] ANCOVA, square-root transformed data
[d] GLM, binomial distributed errors

type of land use were included as factors, while assessed habitat and landscape characteristics were included as cofactors (Table 1). Three habitat and landscape characteristics were excluded from the models because of intercorrelations: distance to the nearest building (correlated with cover of buildings and distance to the nearest road), distance to the nearest water body (correlated with cover of water and distance from the city centre) and cover of wooded area (correlated with distance to the nearest wooded area). Pearson product-moment correlation coefficients were used to analyse associations between species diversity and landscape and habitat characteristics.

Previous analyses showed that the transect line running to west (crossing the floodplain of the Irtysh river) differed in plant communities from the three other transect lines running into the dry steppe zone. Therefore, all analyses were done twice: first with data from all four transect lines, and second with data from the three transect lines in the dry steppe zone. Furthermore, GLM and ANCOVA conducted at the scales of 200 and 500 m radii yielded similar results. Therefore, only the results of the analyses at the scale of 500 m are presented.

To assess whether different directions and the urban–rural gradient affect plant species composition, non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measure was applied as recommended by Austin (2013). Data were square-root transformed and Wisconsin double standardization was applied. The ordinations were fitted using the metaMDS function with default options on two dimensions in the vegan package in R (Oksanen, 2013). In a second step, landscape and habitat variables were fitted onto the ordinations of plants using the function envfit with 999 permutations in the vegan package in R (Oksanen, 2013). Landscape and habitat variables consisted of the four directions, urban–rural distances and the assessed habitat characteristics at the 500 m scale (Table 1). Plant species that occurred only in one site were excluded from the analyses.

Generalized linear models with binomial distributed errors and log-link function for percentage of plant species with different life forms and evolutionary strategies as well as ANCOVA with arcsine-transformation of abundance data were used to determine potential effects of explanatory variables. All models were stepwise reduced according to Crawley (2013).

3. Results

3.1. Total species richness, frequent and rare species

A total of 160 vascular plants were recorded in the 40 sampling sites. The number of plant species recorded per site ranged from 10 to 39 (mean ± S.E. = 23.2 ± 1.2). The most frequent species were *Agropyron pectinatum* (occurred in 82.5% of all sites), *Medicago falcata* (77.5%), *Convolvulus arvensis* (72.5%), *Polygonum aviculare* (72.5%), *Artemisia absinthium* (70.0%), *Artemisia dracunculus* (60.0%), *Elytrigia repens* (60.0%) and *Berteroa incana* (55.0%). In contrast, 43 singleton species were found (occurred in only one site). Two rare species (*Iris halophilla*, *Polygonum amphibium*), recorded in the floodplain, were listed as of conservation concern on the Red List of Kazakh SSR (Bikov, 1981). *P. amphibium* was found in the two sites at the riverside situated 4 and 6 km from the city centre, *I. halophilla* in a single rural site 16 km from the city centre. Two species endemic to the Third Irtysh biogeographic vegetation region were recorded: *Serratula kirghisorum* in the floodplain and *Centaurea sibirica* in the steppe grassland. In all, 38 out of the 160 plant species recorded (23.8%) were non-native.

3.2. Determinants of plant species diversity

Results of GLM based on the data of four transect lines revealed that local plant species richness was affected by the direction of the transect line, the distance to the city centre, the type of land use and the percentage cover of built-up area (Table 2). Correlation analysis showed that local plant species richness increased with increasing distance from the city centre ($r = 0.35$, $n = 40$, $p = 0.03$; Fig. 2a) and was negatively correlated with the cover of built-up area ($r = -0.39$, $n = 40$, $p = 0.01$). With decreasing cover of built-up area, the number of plant species per site increased from 16.3 to 28.8 species. Considering land use, total plant species richness was slightly higher at agriculturally managed sites (26.5 species) than at unmanaged sites (23.1 species) and significantly higher than at ornamental sites (14.4 species) (Appendix D).

The three transect lines in the dry steppe zone (with the rather heterogeneous transect line crossing the Irtysh floodplain omitted) revealed very similar results. Distance to the city centre, type of land use and the cover of built-up area significantly influenced plant species richness, but no longer direction (Table 2). This indicates that the effect of direction in the former analysis was mainly a result of the transect line running to the west (Fig. 1).

Shannon diversity index was influenced by the direction of the transect line, the distance to the city centre ($r = 0.39$, $n = 40$, $p = 0.01$; Fig. 2b), the type of land use and the percentage cover of wasteland (Table 2). Ornamental sites were less diverse than agriculturally managed and unmanaged sites. Sites in northern and western directions contained more divers plant communities than sites in eastern and southern directions (Post-hoc test $p < 0.05$. Appendix D). The percentage of wasteland cover negatively affected

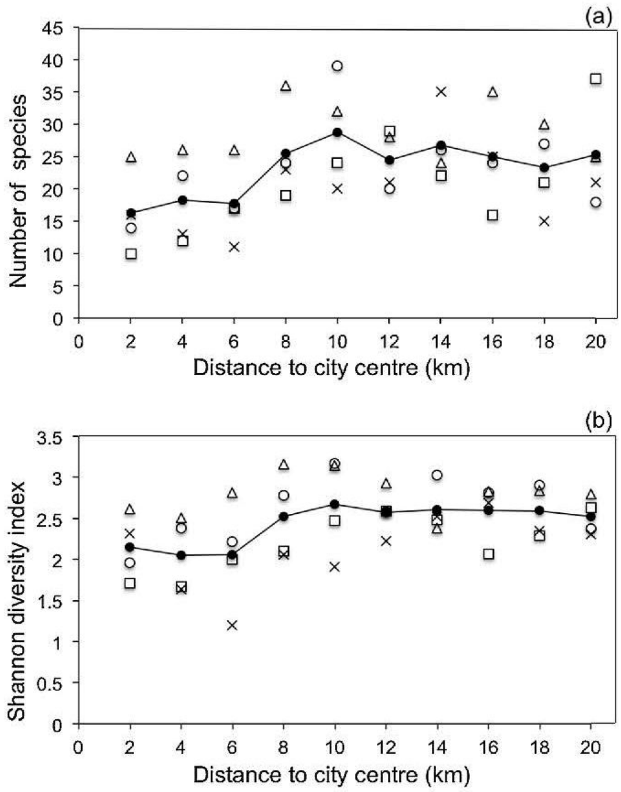

Fig. 2. Total number of plant species (a) and Shannon diversity index (b) in relation to the distance to the city centre (△ western, □ eastern, ○ northern, × southern transect line, ● average of all transect lines).

Shannon diversity (Appendix D). Interestingly, the effect of the direction of the transect line on Shannon diversity remained when only the three transect lines in the dry steppe zone were considered.

Evenness was only influenced by the direction of the transect lines (Table 2). Considering the three transect lines in the dry steppe zone, species evenness was affected by the direction of the transect line, the distance to the city centre, the type of land use and the distance to the nearest wooded area.

3.3. Percentage of alien species

The number of alien species varied from 0 to 19 species per site (mean ± S.E. = 6.9 ± 0.6). Based on the data of four transect lines, the percentage of alien species was affected by the direction of the transect lines, the distance to the city centre, the distance to the nearest road and the percentage cover of grassland in the surrounding landscape (Table 2). The percentage of alien species gradually decreased from 45% in the urban area (within 6 km from the city centre) to 23% in the rural zone ($r = -0.53$, $n = 40$, $p < 0.001$; Fig. 3). Both the number of alien species (Fig. 4a) and their percentage were higher at sites situated close to roads, and at sites with a low proportion of grassland in their surroundings (Fig. 4b).

Considering the three transect lines in the dry steppe zone revealed slightly different results among transect lines. The percentage of alien species did no longer differ among transect lines. The percentage of aliens decreased from 50% in the urban area to 26% in rural surroundings ($r = -0.64$, $n = 30$, $p < 0.001$). The percentage of aliens was also affected by the type of land use (ornamental sites: 53%; agriculturally managed sites: 34%; unmanaged sites: 31%). As in the case of four directions, the percentage of alien species

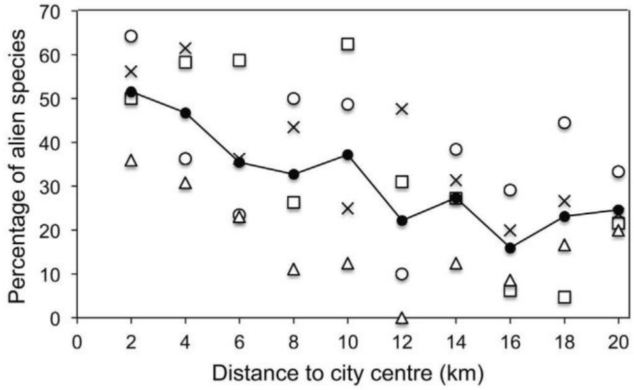

Fig. 3. Percentage of alien species in relation to the distance to city centre based on data from four transect lines (△ western, □ eastern, ○ northern, × southern transect line, ● average of all transect lines).

was positively influenced by the proximity of roads and negatively by the percentage of grassland present.

3.4. Community structure

NMDS ordination analyses based on data from the four transect lines showed that plant species composition of the western transect line significantly differed from those of the other three transect lines ($R^2 = 0.36$, $p = 0.002$; Fig. 5), and that the distance to the nearest situated building separated species composition along the first NMDS axis ($R^2 = 0.27$, $p = 0.03$; Fig. 5). Furthermore, the distance to the city centre, the percentage of grassland, wasteland and built-up area separated plant species composition along the second axis (distance: $R^2 = 0.46$, $p = 0.001$; percentage cover of grassland: $R^2 = 0.46$, $p = 0.001$; percentage cover of wasteland: $R^2 = 0.35$, $p = 0.001$; percentage cover of built-up area: $R^2 = 0.27$, $p = 0.003$; Fig. 5).

Results of the NDMS ordination excluding data from the western transect line revealed similar results. Distance to the city centre, the percentages cover of grassland, wasteland and built-up areas separated plant species on the first axis (distance: $R^2 = 0.77$, $p = 0.001$; percentage cover of grassland: $R^2 = 0.53$, $p = 0.001$; percentage cover of wasteland: $R^2 = 0.52$, $p = 0.001$; percentage cover of built-up area: $R^2 = 0.42$, $p = 0.001$). There was no significant effect of any other assessed habitat or landscape variables on plant species composition (all $p > 0.11$).

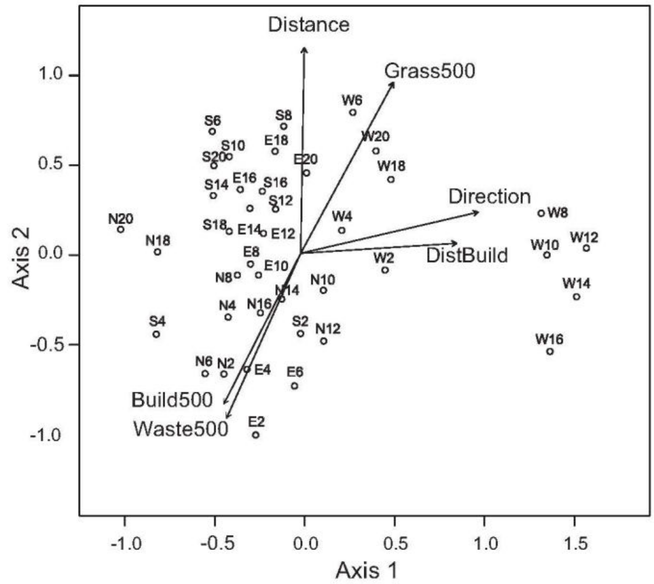

Fig. 5. NMDS ordination analysis showing plant species composition in response to habitat and landscape characteristics. The analysis is based on 40 sampling sites distributed over four transect lines.

3.5. Plant species characteristics

Results of GLM and ANCOVA based on data of four transect lines showed that geophyte abundance was affected by both the direction of the transect line and the percentage grassland cover (Appendix E). The same results were obtained when data from the western transect line were omitted. The effect of transect line was caused by higher proportions of geophytes in northern and western (floodplain) directions (Fig. 6a), where more sites were unmanaged or involved in a husbandry system (e.g., mowing, grazing, cropping). Geophytes were more abundant (up to 20%) at sites, which had a grassland cover of 20–80% in their surroundings. Considering only three transect lines, geophyte abundance increased with increasing distance from the city centre (Appendix E).

Overall, 26.9% of the recorded plant species were therophytes with an abundance of 24.5%. The percentage of therophyte species and their abundance were affected by the direction of the transect lines (Appendix E). Both therophyte species richness (not shown) and their abundance were lower in the western direction than in

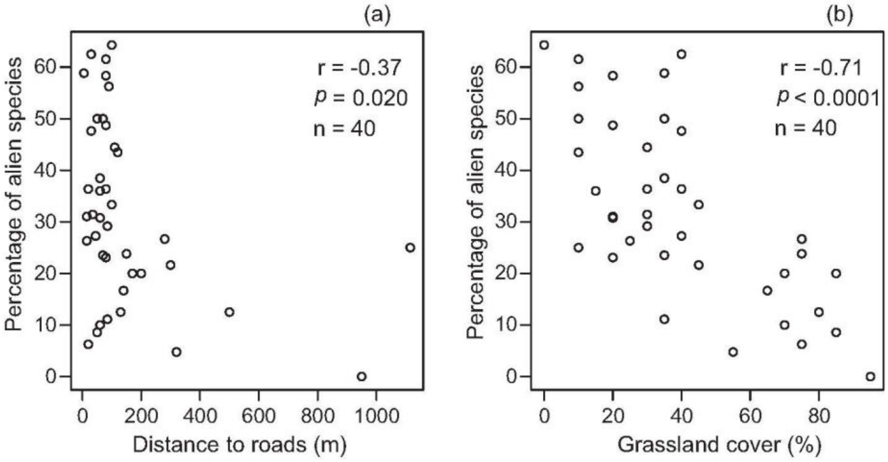

Fig. 4. Relationships between the percentage of alien species and the distance to the nearest road (a), and the percentage of grassland cover (b).

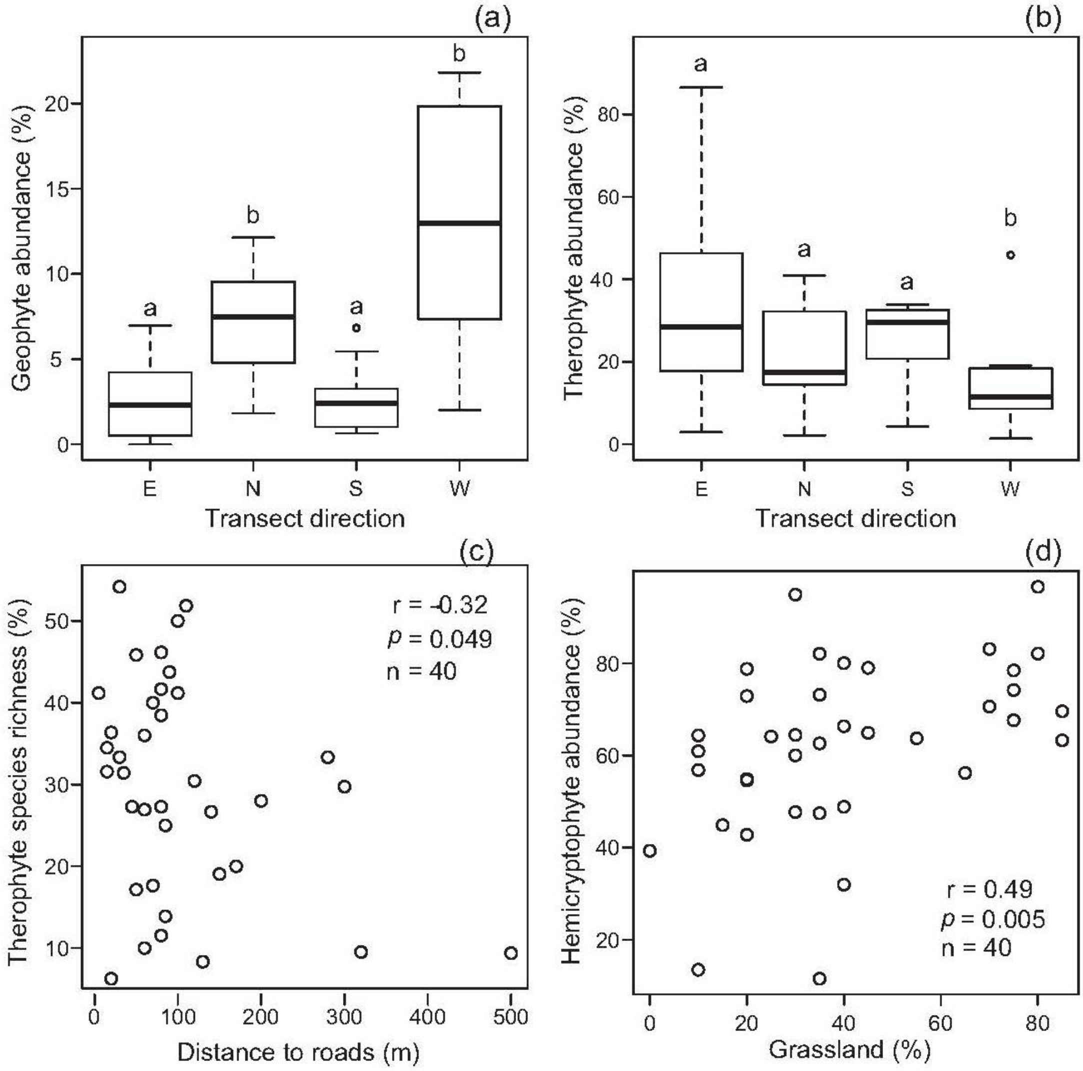

Fig. 6. Abundance of geophytes (a) and therophytes (b) for each transect line, and correlations between therophyte species richness and distance to roads (c), and between hemicryptophyte abundance and percentage of grassland cover in the surroundings (d). Different letters indicate significant differences between transect lines (Tukey's HSD $p < 0.05$).

the remaining directions (Fig. 6b). The percentage of therophyte species was also affected by the distance to the nearest road. Therophyte species richness was higher at sites situated closer to roads than far away (Fig. 6c). Considering exclusively data of three transect lines in the steppe zone, none of the effects on therophytes remained significant (Appendix E).

The percentage of hemicryptophyte species and their abundance were not affected by any of the variables examined, an exception was that the abundance of hemicryptophytes increased with increasing cover of grassland in the surroundings (Fig. 6d). Considering data from the three transect lines in the steppe zone, hemicryptophyte abundance differed between the directions of the transect lines and was affected by density of traffic infrastructure, type of land use and the distances to the nearest road and wooded area (Appendix E). Considering chamaephytes, no significant effect of any explanatory variables was found, with the exception that chamaephyte abundance was influenced by the percentage cropland cover (Appendix E).

85% of the recorded species could be assigned to an evolutionary strategy type (R-strategists 22.5%; C-strategists 39.4%; S-strategists 9.4%; CRS-strategists 13.7%). The percentage of ruderal plant species (R-strategists) was affected by the direction of the transect line and the distance to the nearest road (Appendix F). The abundance of R-strategists was influenced by the type of land use. Considering data of three transect lines, ruderal abundance was affected by the distance to the city centre, the type of land use, the distance to wooded areas and the percentage cover of traffic infrastructure and cropland (Appendix F).

Neither the percentage of competitive species (C-strategists) nor their abundance was affected by any of the variables examined (Appendix F). However, when only data of the three transect lines in the steppe zone were considered, then the abundance of C-strategists was negatively affected by increasing percentages of wasteland and cropland.

The abundance of S-strategists was influenced by the direction of transect lines and type of land use (Appendix F). Considering data of three transect lines, the abundance of S-strategists was affected by the land-use type and the distance to wooded areas.

4. Discussion

The present study showed that plant diversity increased from the city centre to the rural surroundings. This increase was even more pronounced when only native plant species were considered, because the number of alien species decreased from the city centre towards rural surroundings. Plant life forms and evolutionary strategies did not follow any urban–rural gradient, but were affected by various habitat and landscape characteristics in different ways.

4.1. Total species richness, dominant and rare species

The most dominant grass species (*Stipa capillata, S. lessingiana, Festuca valesiaca)* of the formerly undisturbed dry steppe grassland in the Pavlodar region (Lavrenko, 1991) were found only in very low frequencies. Nowadays, *Agropyron pectinatum* and *Elytrigia repens* are the most frequent native grass species. The dominance of *A. pectinatum* might be a result of frequently sowing for pasture improvement in the Soviet period following the Virgin Land Campaign (Kamkin, 2009). *Elytrigia repens* is highly tolerant to anthropogenic disturbance and might have benefited from land modifications.

Seven of the 21 forb species considered as characteristic for the undisturbed dry steppe grassland (Isachenko & Rachkovskaya, 1961; Kalinina, 1961) were found in the present study. Nowadays, two Artemisia species (*Artemisia absinthium,A. dracunculus*) and three forb species (*Convolvulus arvensis*, *Polygonum aviculare* and *Berteroa incana*) occurred in high frequencies in the grasslands. These species are stress-tolerant species and are indicators for the high anthropogenic pressure (Leonova, 2010). Overall, the results of the present study indicate a tremendous change in plant species composition compared to that of the original dry steppe grassland prior to the Virgin Land Campaign.

4.2. Determinants of plant species diversity

The finding that plant diversity increased with increasing distance from the city centre was independent of whether four or three transect lines were considered. Most interestingly, the results of our study contrast previous reports on diversity gradients in cities with increasing plant species richness in urban areas (Burton, Samuelson, & Pan, 2005; Kühn, Brandl, & Klotz, 2004; McKinney, 2006). Habitat heterogeneity, historical development of the centre, large regional species pool (compared to Western Siberia) and intentional and unintentional introduction of many alien plants have been proposed as important factors contributing to the high plant diversity of these cities (Aronson et al., 2014; Zerbe et al., 2004). Pavlodar was founded in 1720 as an Imperial Russian outpost to control the regional salt lakes. Pavlodar's population numbered only about 8000 in 1897. After 1954, the Soviet Government's Virgin Land Campaign prompted the growth and development of Pavlodar. As part of the program, large numbers of young people from throughout the Soviet Union moved to the city. After the failing of the Campaign, rapid industrial (manufacture of aluminium, chemical companies and an oil refinery) and commercial expansion followed. Thus, compared with many European and other cities, Pavlodar has a short historical development. Its strict grid street plan allows little habitat heterogeneity. Furthermore, the species pool (<1500 vascular plant species in the Pavlodar region; Prozorova, 2013) is smaller than in most regions so far studied (Aronson et al., 2014; Niemelä, 2011), mainly due to the harsh environmental conditions (see Section 2.1 Study area) and the originally rather uniform steppe grassland. These factors may explain the relatively simple urban–rural gradient in plant diversity found in Pavlodar city.

In our study, plant diversity was also negatively affected by the percentage cover of built-up area, as was reported in several other studies (reviewed by Aronson et al., 2014; McKinney, 2002). This could be explained by the reduced area suitable for plants in densely built-up areas and the strong trampling of vegetated spots. The type of land use had also a significant effect on plant diversity in our study. Total species richness was higher at agriculturally managed sites than at ornamental sites (Appendix D). Agricultural sites are regularly disturbed by extensive management activities in our investigation area, but are less impacted by waste deposition and point pollution such as polycyclic aromatic hydrocarbons deriving from refinery products than the unmanaged sites. Furthermore, agricultural sites are characterised by a mosaic consisting of irrigated patches, plantations of cultivars and hedges, which increase structural diversity and provide shade and wind shelter for other plant species. Contrasting low plant richness at ornamental sites could be partly explained by both increased disturbance intensity and frequency (trampling, mowing) and leaf litter removal in spring and autumn, which damages the fertile upper soil layer and removes plant seeds and seedlings.

4.3. Alien species

Overall, 38 (23.8%) of the 160 plant species recorded were aliens. The percentage of alien species (about 45% in Pavlodar) is approximately the same as reported in other cities, although the total number of plant species is much lower (Aronson et al., 2014; McKinney, 2008). The western transect line crossing the river Irtysh contained a significantly lower percentage of alien species than the other three transect lines covering former steppe grasslands. Independent of whether data of four or three transect lines were considered, the percentage of alien species was negatively affected by the distance to the city centre, the distance to the nearest road and the percentage cover of grassland. A decrease of alien species from the city centre to rural surroundings has been reported in other cities (Burton et al., 2005; Chocholoušková & Pyšek, 2003; McDonnell et al., 1997; Ranta, 2012). The high percentage of alien species in cities is mainly explained by human introductions and the plants' ability to use new resources in urban habitats (McKinney, 2002). Furthermore, the introduced plants may benefit from thermal radiation emitted from built-up areas (Grimm et al., 2008). Some of the alien species recorded in the present study were planted to improve soil fertility or were cultivated as crops, but most of them were unintentionally introduced. The majority of the alien plants can be characterized as drought-resistant.

Alien species occurred at high frequencies close to roads (Fig. 4a). Similar findings were reported from cities in Japan and Germany (Hayasaka, Akasaka, Miyauchi, Box & Uchida, 2012; von der Lippe & Kowarik, 2008). It is well known that seeds are dispersed by vehicles (von der Lippe & Kowarik, 2008). In the Pavlodar region, shallow 5–10 m wide ditches occur at the verges of most roads. Their primary function is to collect water during snowmelt in spring. These stripes at the roadsides provide suitable habitat for the establishment of new species in the steppe grasslands. Alien species may benefit from these particular conditions despite contamination by exhaust fumes, transport waste and human disturbance.

The percentage of alien species also decreased with increasing cover of grassland in the surroundings (Fig. 4b). In our study, "grassland" includes occasionally grazed pastures, abandoned pastures and remnants of original steppe grasslands. Their plant communities appeared to be relatively resistant to species invasion. The type of land use influenced the percentage of alien species when only the three transect lines in the former steppe grassland were considered. Ornamental sites contained a higher percentage of alien species than agricultural and unmanaged sites. This could be explained by a high propagule pressure (repeated introductions), but also by the biotic acceptance of aliens to ornamental sites (Stohlgren, Jarnevich, Chong, & Evangelista, 2006).

4.4. Community structure

In our study, the species composition of the plant communities was affected by the direction of the transect line, the distance to the nearest built-up area, the distance to the city centre and the percentages of grassland cover, wasteland cover and built-up area. Both the effects of transect line and distance to the nearest built-up area disappeared when data of the western transect line were omitted, indicating that the transect covering the Irtysh valley contained a different plant species composition. Furthermore, there are very few human settlements in the floodplain. The species composition changed from the city centre to the rural surroundings, a pattern recorded in most cities investigated (McDonnell & Hahs, 2008; Pyšek et al., 2004; Vallet, Daniel, Beaujouan, Rozé & Pavione, 2010). This can partly be explained by plant traits (see below). Sites surrounded by wasteland and adjacent to built-up areas contained more species belonging to ruderal plant communities, while sites surrounded by grassland still harboured plant communities similar to those of the original steppe grasslands.

4.5. Plant species characteristics

Plant life forms and evolutionary strategies of species were considered for the first time in a city in Western Siberia. Geophytes were more abundant at sites surrounded by a significant proportion of grassland. This can be explained by the occasional occurrence of ground fire (once per 3–5 years), but also by sheep grazing (Rabotnov, 1984). Therophytes occurred less frequently in the Irtysh valley (western transect). Most therophytes are adapted to dry conditions (Wickens, 1998). The moist soil of the floodplain may provide more suitable habitat for plants with other life forms, which may outcompete therophytes. The abundance of hemicryptophytes was influenced by various factors, particularly when only three transect lines were considered. Other studies reported similar findings and presented different explanations for these effects (Williams, Morgan, McDonnell & McCarthy, 2005). Hemicryptophytes are more adapted to trampling by grazing livestock than geophytes are (Rabotnov, 1984). This may explain the increase of hemicryptophyte abundance with the percentage of grassland cover in the surroundings of the sites. The decrease in chamaephyte abundance in relation to the increasing proportion of cropland in the surroundings might be a result of the repeated removal of weeds (the majority of them were *Artemisia* sp.).

Considering evolutionary strategy types, the abundance of R-strategists was influenced by various habitat and landscape variables. R-strategists respond less sensitively to disturbance than plants with other life strategies. This resistance may explain the higher abundance of R-strategists at both agriculturally managed and ornamental sites compared to less disturbed unmanaged sites. R-strategists (ruderals) are typical for dense built-up areas (Čepelová & Münzbergová, 2012; Godefroid & Koedam, 2007). Considering the three transect lines, the abundance of R-strategists was higher close to the city centre and increased at sites with a high density of traffic infrastructure, but was not influenced by the percentage of built-up area. Thus, R-strategists were only partly influenced by factors of urbanization.

C-strategists were not influenced by any factor of urbanization. However, their abundance was negatively related to both increasing cover of wasteland and cropland. In the present investigation area, C-strategists seem to be resistant to urbanization confirming the findings of other studies (Chocholoušková & Pyšek, 2003; Lososová et al., 2006).

S-strategists were more abundant at ornamental sites than at sites with other land use and at sites far away from wooded areas. These findings contrast the expectation that S-strategists preferentially occur at unmanaged sites (Graae & Sunde, 2000).

5. Conclusions

Our study showed that plant species richness and diversity both increased with increasing distance to the city centre, while the percentage of aliens species decreased. This can be explained by the rapidly expanding urbanization in combination with agricultural land-use changes, which also altered the plant species composition, plant life forms and life strategies in the habitats.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2014.08.014.

References

Aronson, M. F., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., et al. (2014). A global analysis of the impact of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society, Series B*, *281*, 1–8.

Austin, M. P. (2013). Inconsistencies between theory and methodology: A recurrent problem in ordination studies. *Journal of Vegetation Science*, *24*, 251–268.

Bikov, B. A. (1981). *(Red Book of Kazakh SSR. Part 2, Plants)* Красная книга Казахской ССР. Часть 2, Растения. Alma-Ata: Nauka of Kazakh SSR.

Braun-Blanquet, J. (1964). *Pflanzensoziologie: Grundzüge der Vegetationskunde (Plant sociology: Broad Vegetation Science)*. New York 508: Springer.

Burton, M. L., Samuelson, L. J., & Pan, S. (2005). Riparian woody plant diversity and forest structure along an urban–rural gradient. *Urban Ecosystems*, *8*, 93–106.

Burton, M. L., Samuelson, L. J., & McKenzie, M. D. (2009). Riparian wood plant traits across an urban–rural land use gradient and implications for watershed function with urbanization. *Landscape and Urban Planning*, *90*, 42–55.

Čepelová, B., & Münzbergová, Z. (2012). Factors determining the plant species diversity and species composition in a suburban landscape. *Landscape and Urban Planning*, *106*, 336–346.

Chocholoušková, Z., & Pyšek, P. (2003). Changes in composition and structure of urban flora over 120 years: A case study of the city of Plzeň. *Flora*, *198*, 366–376.

Crawley, M. J. (2013). *The R book* (2nd ed.). Chichester, UK: Wiley.

Czerepanov, S. K. (1995). *Plantae Vasculares Rossicae et Civitatum Collimitanearum (in limicis USSR olim) (List of vascular plants of Russia and adjacent states (in the Limits of Former USSR))*. St. Petersburg: Mir I Semia.

De Beurs, K., & Henebry, G. (2004). Land surface phenology, climatic variation, and institutional change: Analysing agricultural land cover change in Kazakhstan. *Remote Sensing of the Environment*, *89*, 497–509.

Du Toit, M. J., & Cilliers, S. S. (2011). Aspects influencing the selection of representative urbanization measures to quantify urban–rural gradients. *Landscape Ecology*, *26*, 169–181.

Godefroid, S., & Koedam, N. (2007). Urban plant species patterns are highly driven by density and function of built-up areas. *Landscape Ecology*, *22*, 1227–1239.

Google Earth. (2013). v.7.1.2.2041, DigitalGlobe, Retrieved from: http://www.earth.google.com

Goloskokov, V. P. (1972). . Иллюстрированный определитель растений Казахстана *(Illustrated Keys to Plants of Kazakhstan)* (1–2) Alma-Ata: Nauka of Kazakh SSR.

Graae, B. J., & Sunde, P. B. (2000). The impact of forest continuity and management on forest floor vegetation evaluated by species traits. *Ecography*, *23*, 720–731.
Grime, J. P. (1979). *Plant strategies and vegetation processes*. New York: John Wiley & Sons.
Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., et al. (2008). Global change and the ecology of cities. *Science*, *319*, 756–760.
Hahs, A. K., & McDonnell, M. J. (2006). Selecting independent measures to quantify Melbourne's urban–rural gradient. *Landscape and Urban Planning*, *78*, 435–448.
Hayasaka, D., Akasaka, M., Miyauchi, D., Box, E. O., & Uchida, T. (2012). Qualitative variation in roadside weed vegetation along an urban–rural road gradient. *Flora*, *207*, 126–132.
Insebaev, T. A., Azerbaev, A. D., Abdrakhmanova, A. D., Randuk, I. V., & Shegenova, Z. K. (2007). Павлодарская область: страницы истории *(1938–2008) (Pavlodar Region: Pages of History (1938–2008))*. Pavlodar: S. Torajgyrov Pavlodar State University.
Isachenko, T. I., & Rachkovskaya, E. I. (1961). Основные зональные типы степей Северного Казахстана *(The Main Regional Types of Steppes of Northern Kazakhstan) (Works of the academy of science of USSR)*. Leningrad: V. L. Komarov Institute of Botany.
Kalinina, A. V. (1961). Песчаные степи Северного Казахстана *(Sandy Steppes of Northern Kazakhstan) (Works of the academy of science of USSR)*. Leningrad: V. L. Komarov Institute of Botany.
Kamkin, V. A. (2009). Закономерности пространственной структуры растительности долины реки Ертыс (в пределах Павлодарской области) *(Patterns of spatial structure of the vegetation of Irtysh Valley (within Pavlodar region)) (Dissertation)*. Almaty: Republic of Kazakhstan.
Klotz, S., Kühn, I., & Durka, W. (2002). BIOFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefässpflanzen in Deutschland. *Schriftenreihe für Vegetationskunde*, *38*, 1–133.
Kühn, I., Brandl, R., & Klotz, S. (2004). The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, *6*, 749–764.
Lavrenko, E. M. (1991). Степи Евразии *(Steppes of Eurasia)*. Leningrad: Nauka.
Leonova, Y. M. (2010). Антропогенная трансформация растительности в зоне влияния промышленных объектов г. Павлодара *(Anthropogenic transformation of flora in the industrial zone of the city of Pavlodar) (Dissertation)*. Almaty: Kazakhstan.
Lososová, Z., Chytrý, M., Kühn, I., Hájek, O., Horáková, V., Pyšek, P., et al. (2006). Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspectives in Plant Ecology, Evolution and Systematics*, *8*, 69–81.
McDonnell, M. J., & Hahs, A. K. (2008). The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: Current status and future directions. *Landscape Ecology*, *23*, 1143–1155.
McDonnell, M. J., Pickett, S. T. A., Groffman, P., Bohlen, P., Pouyat, R. V., Zipperer, W. C., et al. (1997). Ecosystem processes along an urban-to-rural gradient. *Urban Ecosystems*, *1*, 21–36.
McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience*, *52*, 883–890.
McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*, 247–260.
McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*, 161–176.
(2011). *National hydrometeorological service of the Republic of Kazakhstan (Kazhydromet)*. Retrieved from: https://www.kazhydromet.kz
Niemelä, J. (2011). *Urban ecology. Patterns, processes, and applications*. New York: Oxford University Press.
Nurmukhambetova, G. D. (2002). Эколого-геоботаническая характеристика сорной растительности степной зоны (Костанайская область) *(Ecological and geobotanical characteristics of ruderal plant communities in the steppe zone (Kostanay Region)) (Dissertation). Almaty – Kazakhstan*.
Oksanen, J. (2013). *Multivariate analysis of ecological communities in R: Vegan tutorial*. Retrieved from: https://vegan.r-forge.r-project.org
Olden, J. D., & Poff, N. L. (2004). Ecological processes driving biotic homogenization: Testing a mechanistic model using fish faunas. *Ecology*, *85*, 1867–1875.
Pavlov, N. V. (1956–1966). . Флора Казахстана *(Flora of Kazakhstan)* (1–9) Alma-Ata: Academy of Science of Kazakh SSR.
Prozorova, T. A. (2013). Биоразнообразие растительности Павлодарской области *(Biodiversity of flora of Pavlodar region). Investigations of Botanical Diversity of Kazakhstan Nowadays (Materials of the International Conference)*. Almaty: Institute of Botany and Phytointroduction.
Pyšek, P. (1998). Alien and native species in Central European urban floras: A quantitative comparison. *Journal of Biogeography*, *25*, 155–163.
Pyšek, P., Chocholoušková, Z., Pyšek, A., Jarošík, V., Chytry, M., & Tichy, L. (2004). Trends in species diversity and composition of urban vegetation over three decades. *Journal of Vegetation Science*, *15*, 781–788.
Rabotnov, T. A. (1984). Луговедение *(Meadows' Geobotany)* (2nd ed.). Moscow: MGU.
Rachkovskaya, E. I., & Bragina, T. M. (2012). Steppes of Kazakhstan: Diversity and present state. In M. J. I. Werger, & M. A. van Staalduinen (Eds.), *Eurasian steppes. Ecological problems and livelihoods in a changing world. Plant and vegetation* (6) (pp. 104–147).
Ranta, P. (2012). *Urban ecosystems – Response to disturbances, resilience and ecological memory (Dissertation)*. Helsinki: Environmentalica Fennica., 32.
Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography/being the collected papers of C. Raunkiaer*. Oxford: Clarendon Press.
Stohlgren, T. J., Jarnevich, C., Chong, G. W., & Evangelista, P. H. (2006). Scale and plant invasions: A theory of biotic acceptance. *Preslia*, *78*, 405–426.
Vallet, J., Daniel, H., Beaujouan, V., Rozé, F., & Pavione, S. (2010). Using biological traits to assess how urbanization filters plant species of small woodlands. *Applied Vegetation Science*, *13*, 412–424.
Van Heezik, Y., Smyth, A., & Mathieu, R. (2008). Diversity of native and exotic birds across an urban gradient in a New Zealand city. *Landscape and Urban Planning*, *87*, 223–232.
von der Lippe, M., & Kowarik, I. (2008). Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradient. *Diversity and Distributions*, *14*, 18–25.
Weng, Y. (2007). Spatiotemporal changes of landscape pattern in response to urbanization. *Landscape and Urban Planning*, *81*, 341–353.
Wickens, G. E. (1998). *Ecophysiology of economic plants in arid and semi-arid lands*. Berlin – Heidelberg – New York: Springer-Verlag.
Williams, N. S. G., Morgan, J. W., McDonnell, M. J., & McCarthy, M. A. (2005). Plant traits and local extinctions in natural grasslands along an urban–rural gradient. *Journal of Ecology*, *93*, 1203–1213.
Williams, N. S. G., Schwartz, M. W., Vesk, P. A., McCarthy, M. A., Hahs, A. K., Clemants, S. E., et al. (2009). A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology*, *97*, 4–9.
Zerbe, S., Maurer, U., Peschel, T., Schmitz, S., & Sukopp, H. (2004). Diversity of flora and vegetation in European cities as a potential for nature conservation in urban-industrial areas–with examples from Berlin and Potsdam (Germany). In W. W. Shaw, L. K. Harris, & L. VanDruff (Eds.), *Urban wildlife conservation* (pp. 35–49).

Supplementary material Chapter I

Appendix A. Table: Classification system to assess ecosystems disturbances

Appendix B. Table: Results for the first three components of the principal component analysis performed on 14 habitat and landscape variables

Appendix C. Figure: Relationships between landscape characteristics and distance to the city centre of sampling sites

Appendix D. Figure: Total species number and plant diversity (Shannon index) affected by the land-use type, the direction of transect line, and the percentage cover of wasteland

Appendix E. Table: Summary of GLM and ANCOVA analyses of the effects of habitat and landscape characteristics on plant life form (Raunkiaer, 1934)

Appendix F. Table: Summary of GLM and ANCOVA analyses of the effects of habitat and landscape characteristics on plant evolutionary strategy types following Graae and Sunde (2000)

Appendix A

Classification system to assess ecosystem disturbances.

Type of disturbance	Intensity of disturbance			
	Absent (0)	Low (1)	Moderate (2)	High (3)
Grazing	–	Traditional grazing by cattle and sheep (free browsing)	Free grazing by medium sized herds of cattle and sheep	Overgrazed by large herds of cattle and sheep
Mowing	–	Haymaking once per second or third year	Haymaking once per year	Mowing more than once per year
Trampling	–	Presence of small footpath	Presence of intensively used footpaths, hardened top layer	Totally trampled spots
Domestic wastes deposits	–	Tiny fractions	Covering ≤ 5% of the plot	Covering > 5% of the plot
Soil disturbance	–	Traces of digging and former building activity	Natural structure is partly destroyed by erosion	Natural structure is heavily destroyed by erosion, signs of desertification
Presence of leaf litter	–	Little reduction of leaf litter	Significant reduction of leaf litter	Complete removal of leaf litter
Disturbance by traffic	–	< 50 m to local roads	< 50 m to roads with high traffic density	< 50 m to highway or railways
Fire	–	Traces of burned spots	Small unorganized fire places with burned spots	Large fire places
Industrial contamination	–	Little from auto services	Periodical pollution from aluminium production, could be smelled. Occasionally polluted spots of PAHs (polycyclic aromatic hydrocarbons)	Constant pollution from petroleum production, could be smelled. Regularly polluted spots of PAHs
Electric power line infrastructure	–	> 50 m	30–50 m	< 30 m

Appendix B

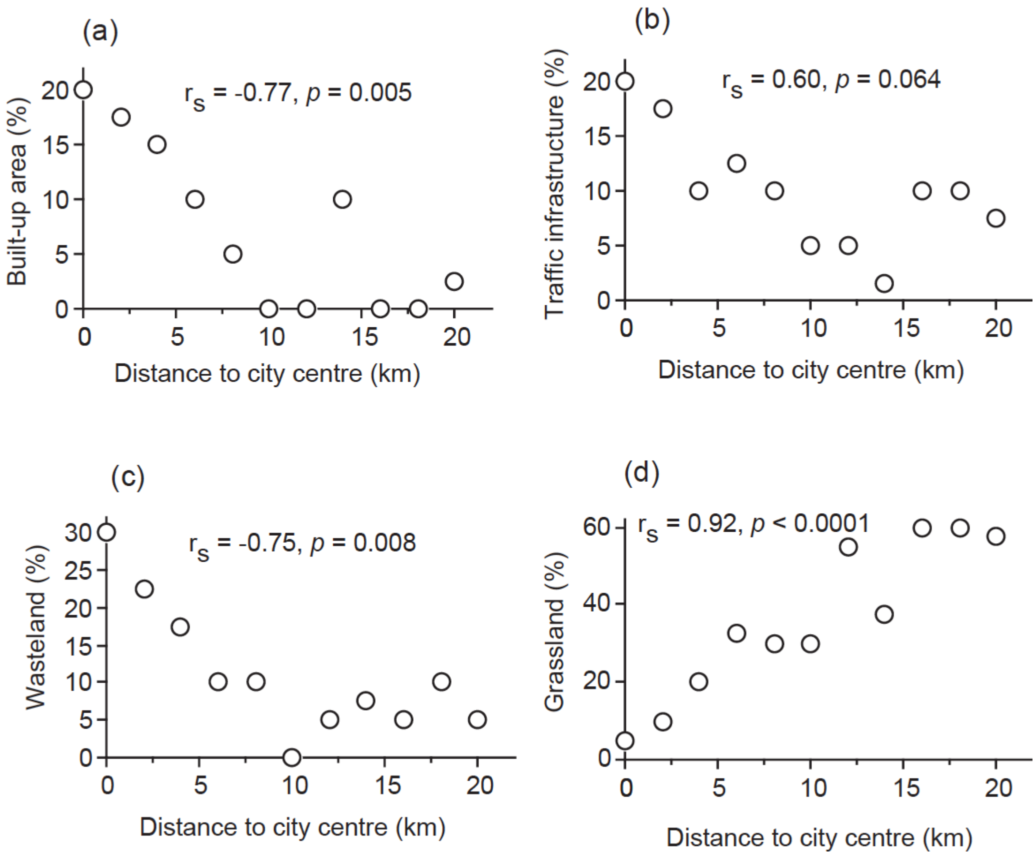
Results for the first three components of the principal component analysis performed on 14 habitat and landscape variables.

	Component I	Component II	Component III
Standard deviation	2.185	1.657	1.294
Explained variance (%)	34.1	19.6	12.0
Eigenvalues			
Direction	0.171	**-0.451**	0.206
Distance to city centre (km)	**0.351**	0.285	0.137
Distance to the nearest built-up area (km)	**0.406**	-0.069	0.014
Distance to the nearest road (km)	0.244	-0.167	-0.261
Distance to the nearest wooded area (km)	0.165	0.146	**0.411**
Distance to the nearest water body (km)	0.049	**0.535**	-0.148
Area of buildings (%)	**-0.391**	0.028	0.010
Area of traffic infrastructure (%)	**-0.336**	0.190	0.223
Area of wasteland (%)	**-0.332**	0.076	0.181
Area of cropland (%)	0.054	**0.304**	-0.219
Area of woodland (%)	-0.162	-0.135	**-0.570**
Area of grassland (%)	**0.329**	0.111	0.253
Area of water body (%)	-0.078	**-0.454**	0.185
Disturbance intensity	-0.273	0.052	**0.355**

Eigenvalues in bold are greater than 0.300 and thus considered to explain a large percentage of the variance.

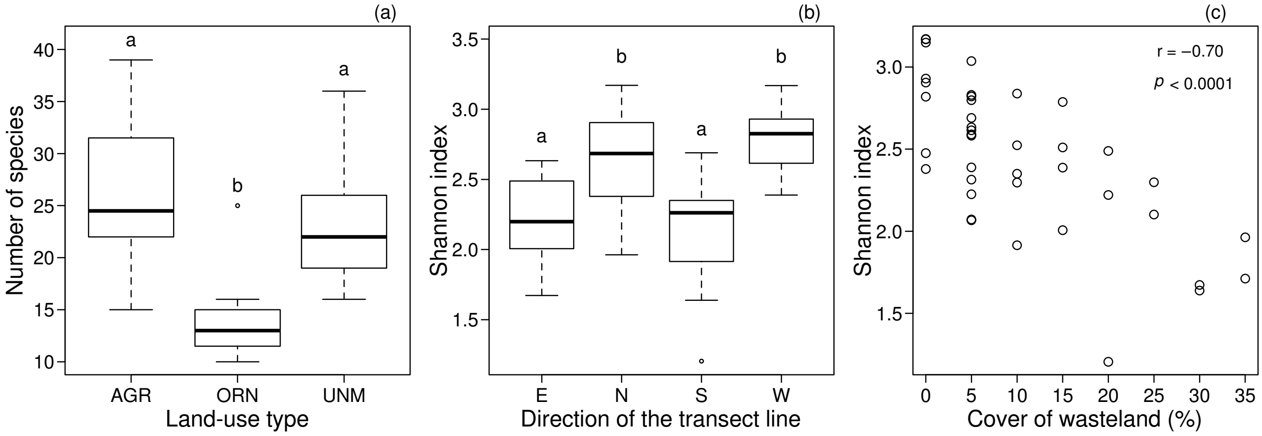
Appendix C

Relationships between landscape characteristics and distance to the city centre of sampling sites: (a) Percentage of build-up area, (b) percentage of traffic infrastructure area, (c) percentage of wasteland area, and (d) percentage of grassland area. Median values of four transect lines at 11 distances to the city centre are shown. Results of Spearman rank correlations are presented.



Appendix D

Total species number and plant diversity (Shannon index) affected by the land-use type (a, AGR – agriculturally managed sites; ORN – ornamental sites; UNM – unmanaged sites), the direction of transect line (b), and the percentage cover of wasteland (c). Different letters indicate significant differences between type of land-use and between direction of the transect lines (Tukey's HSD, $p < 0.05$).



Appendix E

Summary of GLM and ANCOVA analyses of the effects of habitat and landscape characteristics (explanatory variables, listed in Table 1) on plant life form (Raunkiaer, 1934). Percentages of species richness and abundance were used in the analyses.

Dependent variables	Explanatory variables	Four transect lines		Three transect lines	
		Species richness[1]	Abundance[2]	Species richness[1]	Abundance[2]
Geophytes	Direction	$X^2= 6.72$, df=3, $p=0.08$	$F_{3,23} = 14.97$, **$p<0.0001$**	$X^2=1.50$, df=2, $p=0.47$	$F_{2,13} = 16.79$, **$p<0.001$**
	Distance	$X^2= 2.35$, df=9, $p=0.99$	$F_{9,23} = 1.05$, $p=0.43$	$X^2=1.40$, df=9, $p=0.99$	$F_{9,13} = 2.76$, **$p=0.047$**
	Disturbance	–	–	–	–
	Land use	–	–	–	$F_{2,13} = 3.60$, $p=0.06$
	DistRoad^{log}	–	–	–	–
	DistWood^{log}	–	–	–	$F_{1,13} = 3.69$, $p=0.08$
	Build500^{log}	–	$F_{1,23} = 1.69$ $p=0.21$	–	–
	Traf500^{log}	–	–	–	–
	Waste500^{log}	–	–	–	–
	Crop500^{log}	–	–	–	–
	Grass500^{log}	–	$F_{1,23} = 7.26$, **$p=0.013$**	–	$F_{1,13} = 4.99$, **$p=0.044$**
Therophytes	Direction	$X^2=12.29$, df=3, **$p=0.006$**	$F_{3,34}= 3.92$, **$p=0.024$**	$X^2= 0.75$, df=2, $p=0.69$	$F_{2,11} = 2.92$, $p=0.10$
	Distance	$X^2=9.22$, df=9, $p=0.42$	$F_{9,25} = 2.39$, $p=0.05$	$X^2= 7.87$, df=9, $p=0.55$	$F_{9,11} = 2.04$, $p=0.13$
	Disturbance	–	–	$X^2= 1.03$, df=1, $p=0.31$	–
	Land use	–	$F_{2,22}= 2.02$, $p=0.16$	–	$F_{2,11} = 3.81$, $p=0.06$
	DistRoad^{log}	$X^2=5.94$, df=1, **$p=0.015$**	$F_{2,22}= 1.70$, $p=0.21$	$X^2=2.30$, df=1, $p=0.13$	$F_{1,11} = 2.51$, $p=0.14$
	DistWood^{log}	–	$F_{2,22}= 1.26$, $p=0.28$	–	$F_{1,11} = 1.96$, $p=0.18$
	Build500^{log}	$X^2=2.04$, df=1, $p=0.15$	–	–	–
	Waste500^{log}	–	–	–	–
	Traf500^{log}	–	$F_{1,21} = 2.35$, $p=0.14$	–	$F_{1,11} = 4.63$, $p=0.06$
	Crop500^{log}	–	–	–	$F_{1,11} = 1.21$, $p=0.30$
	Grass500^{log}	–	–	–	–
Hemicrypto-phytes	Direction	$X^2=3.08$, df=3, $p=0.38$	$F_{3,18} = 2.43$, $p=0.09$	$X^2= 8.52$, df=2, $p=0.79$	$F_{2,9} = 5.78$, **$p=0.024$**
	Distance	$X^2=2.66$, df=9, $p=0.98$	$F_{9,18} = 1.49$, $p=0.23$	$X^2= 5.65$, df=9, $p=0.97$	$F_{9,9} = 2.50$, $p=0.09$
	Disturbance	–	$F_{1,18} = 2.84$, $p=0.11$	–	$F_{1,9} = 3.65$, $p=0.09$
	Land use	–	$F_{2,18} = 1.52$, $p=0.25$	–	$F_{2,9} = 4.80$, **$p=0.038$**
	DistRoad^{log}	$X^2=2.33$, df=1, $p=0.13$	$F_{1,18} = 2.50$, $p=0.13$	–	$F_{1,9} = 6.60$, **$p=0.030$**
	DistWood^{log}	–	$F_{1,18} = 2.70$, $p=0.12$	–	$F_{1,9} = 13.24$, **$p=0.005$**
	Build500^{log}	–	–	–	$F_{1,9} = 3.28$, $p=0.10$
	Traf500^{log}	–	$F_{1,18} = 1.13$, $p=0.301$	–	$F_{1,9} = 6.62$, **$p=0.030$**
	Waste500^{log}	–	–	–	–
	Crop500^{log}	–	–	–	–
	Grass500^{log}	–	$F_{1,18} = 4.63$, **$p=0.045$**	–	$F_{1,9} = 1.22$, $p=0.23$
Chamaephytes	Direction	$X^2=1.63$, df=3, $p=0.65$	$F_{3,23} = 1.21$, $p=0.33$	$X^2= 0.03$, df=2, $p=0.98$	$F_{2,13} = 0.74$, $p=0.50$
	Distance	$X^2=5.32$, df=9, $p=0.81$	$F_{9,23} = 0.38$, $p=0.93$	$X^2= 3.27$, df=9, $p=0.95$	$F_{9,13} = 0.53$, $p=0.83$
	Disturbance	$X^2=1.59$, df=1, $p=0.21$	$F_{1,23} = 3.19$, $p=0.09$	–	$F_{1,13} = 1.83$, $p=0.20$
	Land use	–	–	–	–
	DistRoad^{log}	–		–	$F_{1,13} = 1.93$, $p=0.19$
	DistWood^{log}	–	–	–	$F_{1,13} = 1.82$, $p=0.20$
	Build500^{log}	–	–	–	–
	Traf500^{log}	–	–	–	–
	Waste500^{log}	–	–	$X^2=2.23$, df=1, $p=0.14$	–
	Crop500^{log}	$X^2=1.07$, df=1, $p=0.30$	$F_{1,23} = 9.76$, **$p=0.005$**	–	$F_{1,13} = 2.68$, $p=0.13$
	Grass500^{log}	–	–	–	–

^{log} log-transformed
[1] percentage data, GLM, binomial distributed errors
[2] ANCOVA, arcsine transformed percentage data
– excluded from the model
Significant results are in bold ($p<0.05$)

Appendix F

Summary of GLM and ANCOVA analyses of the effects of habitat and landscape characteristics (explanatory variables, listed in Table 1) on plant evolutionary strategy types following Graae and Sunde (2000). Percentages of species richness and abundance were used in the analyses.

Dependent variables	Explanatory variables	Four transect lines		Three transect lines	
		Species richness[1]	Abundance[2]	Species richness[1]	Abundance[2]
R+	Direction	X^2=8.55, df=3, **p=0.036**	$F_{3,22}$ = 2.09, p=0.13	X^2=0.69, df=2, p=0.71	$F_{2,9}$ = 3.73, p=0.07
	Distance	X^2=7.44, df=9, p=0.59	$F_{9,22}$ = 1.422 p=0.33	X^2=8.41, df=9, p=0.49	$F_{9,9}$ = 5.21, **p=0.011**
	Disturbance	–	–	–	–
	Land use	X^2=2.72, df=2, p=0.26	$F_{2,22}$ = 3.86, **p=0.037**	–	$F_{2,9}$ = 9.20, **p=0.007**
	DistRoad[log]	X^2=5.71, df=1, **p=0.017**	$F_{1,22}$ = 1.06, p=0.32	X^2=2.34, df=1, p=0.13	$F_{1,9}$ = 2.53, p=0.15
	DistWood[log]	–	–	–	$F_{1,9}$ = 14.64, **p=0.004**
	Build500[log]	–	–	–	$F_{1,9}$ = 1.56, p=0.24
	Traf500[log]	–	–	–	$F_{1,9}$ = 8.70, **p=0.016**
	Waste500[log]	–	–	–	$F_{1,9}$ = 4.53, p=0.06
	Crop500[log]	–	–	–	$F_{1,9}$ = 9.35, **p=0.014**
	Grass500[log]	X^2=1.91, df=1, p=0.17	–	–	–
C+	Direction	X^2=0.59, df=3, p=0.90	$F_{3,25}$ = 0.24, p=0.87	X^2=0.51, df=2, p=0.78	$F_{2,10}$ = 0.36, p=0.71
	Distance	X^2=6.05, df=9, p=0.74	$F_{9,25}$ = 1.89, p=0.11	X^2=6.57, df=9, p=0.68	$F_{9,10}$ = 2.91, p=0.06
	Disturbance	–	–	–	–
	Land use	–	–	–	$F_{2,10}$ = 1.15, p=0.28
	DistRoad[log]	X^2=2.93, df=1, p=0.09	–	X^2=1.66, df=1, p=0.20	–
	DistWood[log]	–	–	–	$F_{1,10}$ = 1.16, p=0.31
	Build500[log]	–	–	–	$F_{1,10}$ = 1.42, p=0.26
	Traf500[log]	–	–	–	$F_{1,10}$ = 3.49, p=0.08
	Waste500[log]	–	–	–	$F_{1,10}$ = 7.10, **p=0.024**
	Crop500[log]	–	–	–	$F_{1,10}$ = 10.25, **p=0.009**
	Grass500[log]	–	–	–	–
S+	Direction	X^2=0.29, df=3, p=0.96	$F_{3,22}$ = 3.15, **p=0.045**	X^2=0.19, df=2, p=0.91	$F_{2,14}$ = 0.98, p=0.40
	Distance	X^2=2.29, df=9, p=0.99	$F_{9,22}$ = 1.70, p=0.15	X^2=0.93, df=9, p=0.99	$F_{9,14}$ = 1.73, p=0.17
	Disturbance	–	–	–	–
	Land use	–	$F_{2,22}$ = 5.45, **p=0.012**	–	$F_{2,14}$ = 6.38, **p=0.012**
	DistRoad[log]	–	–	–	–
	DistWood[log]	–	–	–	$F_{1,14}$ = 4.91, **p=0.044**
	Build500[log]	–	–	–	–
	Traf500[log]	–	–	–	–
	Waste500[log]	–	–	–	–
	Crop500[log]	–	$F_{1,22}$ = 4.10, p=0.06	–	–
	Grass500[log]	–	–	–	–

[log] log-transformed
[1] percentage data, GLM, binomial distributed errors
[2] ANCOVA, arcsine transformed percentage data
– excluded from the model
Significant results are in bold (p<0.05)

Chapter II

Effects of road type and urbanization on the diversity and abundance of alien species in roadside verges in Western Siberia

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Plant ecology (submitted)

Abstract

The spread of alien plant species by vehicles profoundly affects the roadside vegetation. Roads with high traffic densities in urban regions may facilitate the invasion of alien plants. The present study examined the effects of road type and distance to the city centre on native and alien plant species in both the aboveground vegetation and soil seed bank of road verges in originally dry steppe grasslands in the surroundings of Pavlodar, Western Siberia, Kazakhstan. This region is characterized by a recent change of land use and rapidly expanding urbanization. Vegetation surveys were conducted at 12 sites distributed along roads with different traffic densities (national and local roads) and at two distances to the city centre (city edge and rural surroundings). The seedling-emergence method was used to examine the soil seed bank at each site. We found a larger percentage of alien species along national roads (42% in the aboveground vegetation, 57% in the soil seed bank) than along local roads (20% and 44%, respectively), which can be explained by differences in traffic density, location from which the vehicles come and habitat conditions. More alien species were found in road verges at the city edge than in the rural surroundings along both road types, probably due to the spread of propagules from residential areas. Our study demonstrates that national roads are important pathways for the introduction of alien species in this Western Siberian region.

Keywords Grassland diversity • Plant invasion • Plant traits • Soil seed bank • Species composition • Traffic

Introduction

Alien species constitute a major part of plant communities in urban habitats (Pyšek 1998). Road verges are generally considered to be important pathways for the spread of alien plant species (Fowler et al. 2008). As a frequently disturbed habitat, verges provide suitable conditions for the establishment and spread of new species (Christen and Matlack 2006; Arévalo et al. 2010). From roadside verges alien plants may also colonize adjacent habitats (Sharma and Raghubanshi 2009).

Invasion processes are stochastic by their nature and largely unpredictable in the early stages (Sullivan et al. 2009). In grassland habitats, road verges are especially prone to invasion of alien species (Von der Lippe and Kowarik 2012; Menuz and Kettenring 2013). Numerous factors including road type, traffic density, type of road management, disturbance regime and history of the landscape influence plant invasion (Mortensen et al. 2009; Joly et al. 2011). Vehicles are an important vector for plant dispersal (Ansong and Pickering 2013). High traffic densities with vehicles crossing biogeographic borders result in high propagule pressure of alien species in roadside verges (Von der Lippe and Kowarik 2008). However, depending on the adjacent habitats, additional sources for the introduction of alien species may occur in roadside verges. Human-introduced horticultural species may escape from gardens and establish in road verges (Hodkinson and Thompson 1997). Thus, road verges in or close to cities may be exposed to a higher overall propagule pressure of alien species than road verges in rural areas.

Quantifying seed transportation by vehicles (Von der Lippe and Kowarik 2008; Taylor et al. 2012) and surveying the aboveground vegetation in verges (Sharma and Raghubanshi 2009; Arévalo et al. 2010) have so far been the most frequently used approaches. In contrast, consequences of seed transportation by vehicles on the soil seed bank have been largely neglected. Recently introduced alien plant species may not yet be established in the soil seed bank (Holmes and Cowling 1997). Consequently, species composition in the aboveground vegetation and soil seed bank may differ at a given site. This difference might be pronounced at sites with high colonization rate of alien species.

The present study focuses on the role of roads in the dispersal of alien plant species in the dry steppe region of Pavlodar, Kazakhstan. Until 1950, free-roaming grazing livestock, mainly sheep and horses, was the major vector of seed dispersal across these grasslands (Fischer et al. 1996; Manzano and Malo 2006). In 1954–1963, the traditional land-use has been changed dramatically in this region by the USSR's Virgin Land Campaign. Approximately 200,000 people were transferred to the state farms in the Pavlodar region to produce crops. After the failure of the Campaign and farmland abandonment, these people settled in the city of Pavlodar, which increased from a few thousands to 355,000 inhabitants by 2014 (Committee of Statistics of the Republic of Kazakhstan 2015). Nowadays, Pavlodar and its close surroundings constitute a huge industrial agglomerate. As an alternative to agricultural practices, a belt of private gardens was established around the city providing a popular spare-time activity for urban citizens. In the rural surroundings, free-grazing livestock husbandry and crop production continued in smaller areas and at a lower intensity. National roads with high traffic density connect the city of Pavlodar with the industrial areas and other cities, while local roads with low traffic density connect households in the rural surroundings.

In the present study, we examined the effects of traffic density and distance to the city centre on the abundance and composition of alien and native plant species both in the aboveground vegetation and the soil seed bank of roadside verges in Pavlodar and its surroundings. We considered roadside verges along national roads with high traffic density and verges along local roads with relatively low traffic density (hereafter road type effect) both situated at the city edge and at a distance of 14.0–16.1 km from the city centre (distance to city effect). We tested the following hypotheses:

(1) Both the number and percentage of alien species in the aboveground vegetation and soil seed bank are higher in verges along roads with high traffic density (national roads) than along roads with low traffic density (local roads).

(2) Both the number and percentage of alien species in the aboveground vegetation and soil seed bank are higher in road verges situated at the city than in vergers in the rural surroundings.

Disturbances on plant communities are frequently assessed by recording changes in the frequencies of different plant life forms (Cole 1995; Vallet et al. 2010). We therefore also examined changes in the frequencies of plant life forms both in the aboveground vegetation and soil seed bank of roadside verges.

Methods

Study area

The study was conducted in the surroundings of the city of Pavlodar (52°18′N, 76°57′E) at elevations ranging from 125 m to 150 m above sea level in northern-eastern Kazakhstan, Western Siberia. In this region, annual precipitation averages 228 mm and mean annual temperature is 2.1 ^{o}C. A major part of the investigation area was originally dry bunch feather-grass (*Stipa* ssp.) or fescue (*Festuca* ssp.) steppe formed on sandy dark-chestnut soils.

Sampling design

The study was conducted along national and local roads running through dry steppe grasslands. At three pairs of national and local roads, one sampling site per road type was situated at the edge of Pavlodar (6.9–7.6 km to the city centre) and another one in the rural surroundings (14.0–16.1 km to the city centre; Fig. 1).

The paved national roads were 13.4 m wide at the edge of the city and 16.0 m in the rural surroundings and had a traffic density of 25,000–50,000 vehicles per day (Akimat of Pavlodar region, unpublished data). Local roads were unpaved (dirt) and were 4.4 m wide at the edge of the city and 2.8 m in the rural surroundings with a traffic density of approximately 500 vehicles per day. Sand and salt are distributed on national roads under severe winter conditions. With the beginning of summer, the sand is removed from the paved surface. Road repair and mowing of roadside vegetation occur very irregularly, but in general more frequently at the city edge than in the rural surroundings. No similar maintenance work is conducted on local roads.

Pairs of sampling sites situated at a national and a local road were 370–550 m apart. With respect to the prevailing wind directions, which may affect seed dispersal, sampling sites were placed at the eastern or southern side of the roads. At each site, pairs of two subplots, each measuring 2 m x 2 m, were installed at distances of 1, 5 and 10 m to the road edge (Fig. 1). The two subplots were 10 m apart. The twelve sampling sites (six at national and six at local roads) included a total of 72 subplots.

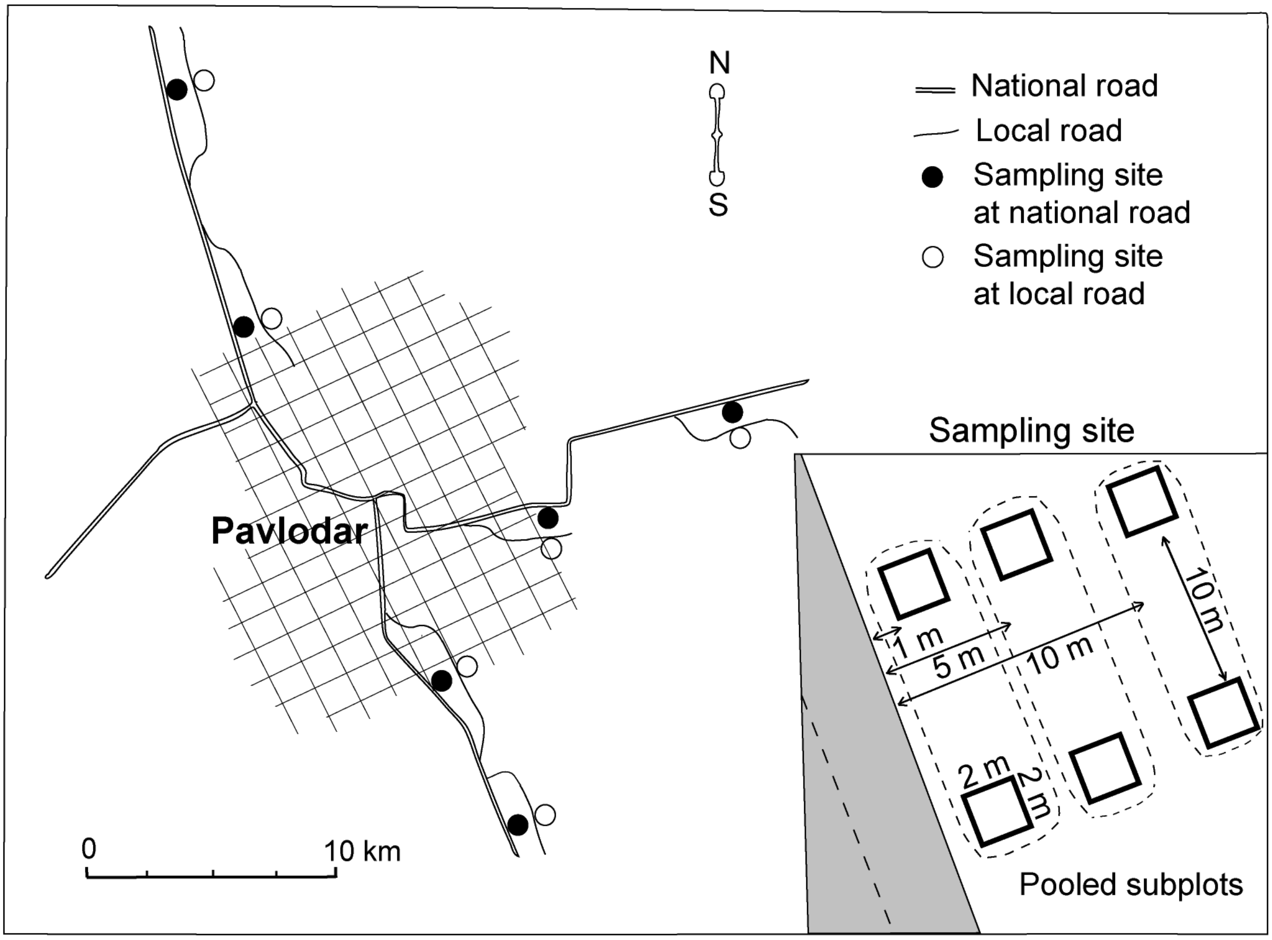

Fig. 1 Location of sampling sites along national and local roads in the surroundings of the city of Pavlodar, Kazakhstan, and the sampling design of a site. The city area is hatched.

Aboveground vegetation

Species richness of vascular plants in the aboveground vegetation (mean height 20 cm, range 1–40 cm) and their abundances were assessed in each 2 m x 2 m subplot in July 2014. The cover of aboveground vegetation was estimated using the Braun-Blanquet scale (1964). Plant species were identified following Pavlov (1956-1966) and Goloskokov (1972) (see Table S1). Nomenclature was adjusted following Czerepanov (1995). Information on non-native (alien) plant species was obtained from Nurmukhambetova (2002).

Soil seed bank

To examine the seed bank, soil samples were taken in each subplot in July 2014. After removing the leaf-litter layer, three to four soil samples were collected in randomly chosen spots from each subplot. Soil samples were taken to a depth of 5 cm using a 10 cm x 10 cm iron frame. Within subplot, the samples were pooled, mixed and sieved using a 4 mm-wide mesh to obtain a volume of 1 L. The soil samples were cold stratified at $0^{o}C$ for one week in darkness to break any dormancy of the seeds.

The seedling-emergence method was used to determine the number of germinable seeds for each species in the soil (Ter Heerdt et al. 1996). The soil samples from each subplot were spread out on a 6 cm-layer of potting soil in two 41.5 cm x 18.5 cm seed trays, resulting in a total area of 1536 cm^2 per subplot (altogether 144 seed trays for the 72 subplots). Another six seed trays filled only with potting soil were used as control for potential contamination of the soil used and for external seed contamination. All trays were randomly arranged on tables and kept shaded under local climatic conditions (range of air temperature 15–$35^{o}C$, natural light conditions of the Pavlodar region) for germinating seeds. The seed trays were regularly watered. To avoid differences in light exposure, the positions of the trays were changed every 5 days. On the same occasions, all trays were checked for seedlings. Newly emerged seedlings were determined (Muller 1978), counted and removed from the tray. Unidentifiable seedlings were transplanted into pots and grown until species identification was possible. The germination test started in July 2014 and lasted 3 months until no further seedlings could be detected.

The aboveground plant species and germinating seedlings were assigned to one of the four life forms (geophytes, therophytes, hemicryptophytes and chamaephytes; Raunkiaer 1934). Furthermore, seeds of emerging seedlings were assigned to different dispersal types using the criteria of Müller-Schneider (1986) and to different types of seed bank according to Thompson and Grime (1979). Data on seed weight and morphology were compiled using an available database (BiolFlor Version 1.1).

Data analyses

Statistical analyses were performed using the software R (R Development Core Team 2011, version 2.14.0). At each site, data from the two subplots at the same distance to the road were combined resulting in 3 pooled subplots (at distances of 1, 5 and 10 m to the road). For pooled subplots, the total number of plant species and number of alien species in the aboveground vegetation were used in the analyses. Similarly, plant diversity in the soil seed bank was expressed as the number of species with emerging seedlings for pooled subplots (observed seed species richness). We also calculated rarefied seed species richness (correcting for different numbers of individual in a sample) and Chao-estimated seed richness (non-parametric statistical estimator of true local species richness reducing the bias of incomplete sampling) using the *vegan* package in R. Furthermore, we calculated total seedling density (number of seedlings per m^2) and density of alien seedlings (number of alien seedlings per m^2).

To examine potential effects of road type, distance to the city centre and distance to the road edge on the observed plant species richness and the number and percentage of alien species in the aboveground vegetation, ANCOVAs or GLMs with quasipoisson distributed errors were applied. Road type, distance to the city centre and distance to the city edge were used as factors and vegetation cover as a cofactor. The same ANCOVAs or GLMs with the cofactor observed aboveground plant species richness were applied to test the effects of road type, distance to the city centre and distance to the road edge on data of soil seed diversity and density (Table S2). Normality of data was assessed using the Shapiro-Wilk test. If necessary, square root-transformations were applied to the variables to fit normal distributions. GLM were used in cases when the data did not fit normal distribution. All models were stepwise reduced according to Crawley (2013).

For each site, Sørensen's similarity indices for the presence/absence of species in the aboveground vegetation and soil seed bank were calculated. To visualize potential differences in plant species composition between sampling sites at national roads and local roads as well as between sites at the city edge and in the rural surroundings, we applied non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measures and

Wisconsin double standardization. The ordinations were fitted using the *metaMDS* function with default options on three dimensions in the *vegan* package in R. PERMANOVA was used to test for statistical differences among the groups' species composition (Anderson 2005).

The same ANCOVAs or GLMs as described above were used to determine effects of road type and distance to the city centre on the percentage of plant species in the soil seed bank with different dispersal types (Table S3). Contingency analysis was applied to examine differences between road type and distance to the city in the percentage of species belonging to the different plant life forms and seed bank type. All trait analyses were based on presence/absence data.

Results

Species richness and percentage of alien plants

A total of 32 alien plant species were recorded in the entire study; 31 (96.9%) of these species were found in the aboveground vegetation and 20 (62.5%) in the soil seed bank. Another 46 species were native. Thus, 41.0% of the species were aliens. In the above-ground vegetation, the alien *Berteroa incana* was common (occurring in 44.4% of all subplots; Table S1). Among the native plants, the most frequently recorded species were *Agropyron pectinatum* (in 91.7% of all subplots), and *Medicago falcata* (61.1%). Considering pooled subplots (8 m^2), 3.4 ± 0.5 (mean ± SE; range 0.0–10.0; N = 36) alien plant species and 3.0 ± 0.5 (1.0–13.0) native species were found in the aboveground vegetation.

A total of 1742 seedlings emerged from the soil samples. Of them, 1674 (96.1%) seedlings could be assigned to the species level. No seedlings were recorded in the control trays filled only with potting soil. The soil samples yielded a mean of 790.2 ± 76.5 seedlings/m^2 (range 176.9–1848.0 seedlings/m^2). Among them, 39.2% (51.9 ± 3.6%, 14.3–100.0%) of the seedlings were aliens. The most frequently occurring species in the soil seed bank were three alien plants: *Atriplex patula* (in 86.1% of pooled subplots), *Berteroa incana* (63.9%) and *Polygonum aviculare* (52.8%; Table S1).

Effects of road type and distance to the city centre

In the aboveground vegetation, both the number and percentage of alien species were affected by road type and distance to the city (Table 1), but not by the distance of the plots to the road. The vegetation along national roads harboured more alien species than that along local roads (Fig. 2a). Furthermore, at both road types more alien plant species were recorded at the city edge than in the rural surroundings (Fig. 2a). Very similar findings were obtained when the percentages of alien species in the aboveground vegetation were examined (Table 1, Fig. 2b). In contrast, the total observed aboveground plant species richness per pooled subplot was not affected by road type, distance to the city centre and distance of the plots to the road (Table 1). However, the extent of vegetation cover influenced the total observed plant species richness (Table 1).

In the soil seed bank, the number of alien seed species, rarefied alien seed species richness and Chao-estimated alien seed species richness were all affected by road type (Table S2a). All three measures of alien seed richness were larger along national roads than along local roads (Table S2a, Fig. S2). Furthermore, independent of road type the number of alien seed species was larger and the percentage of both alien seed species and alien seedlings were higher at the edge of the city than in the rural surroundings (Table S2a, b, Fig. S2).

Table 1 Summary of ANCOVAs or GLMs testing the effects of road type, distance to the city centre, distance of the pooled plots to the road edge and vegetation cover (%) on the number and percentage of alien species and observed total number of plant species in the aboveground vegetation

	Number of alien species[1]	Percentage of alien species[1]	Observed total plant species richness[2]
Road type	**$F_{1,34} = 4.33$, $P = 0.046$**	**$F_{1,34} = 8.35$, $P = 0.007$**	$F_{1,30} = 0.02$, $P = 0.89$
Distance to the city	**$F_{1,33} = 35.21$, $P < 0.0001$**	**$F_{1,33} = 59.09$, $P < 0.0001$**	$F_{1,30} = 1.43$, $P = 0.24$
Distance to the road edge	$F_{2,31} = 2.27$, $P = 0.12$	$F_{2,31} = 2.53$, $P = 0.10$	$F_{2,30} = 0.63$, $P = 0.54$
Vegetation cover	$F_{1,30} = 1.83$, $P = 0.19$	–	**$F_{1,30} = 8.14$, $P = 0.008$**
Road type x distance to the city	$F_{1,29} = 1.03$, $P = 0.29$	–	
Road type x distance to the road edge	–	–	

[1] ANCOVA

[2] GLM, quasipoisson distributed errors

– excluded from the model

Significant results are in bold ($P < 0.05$)

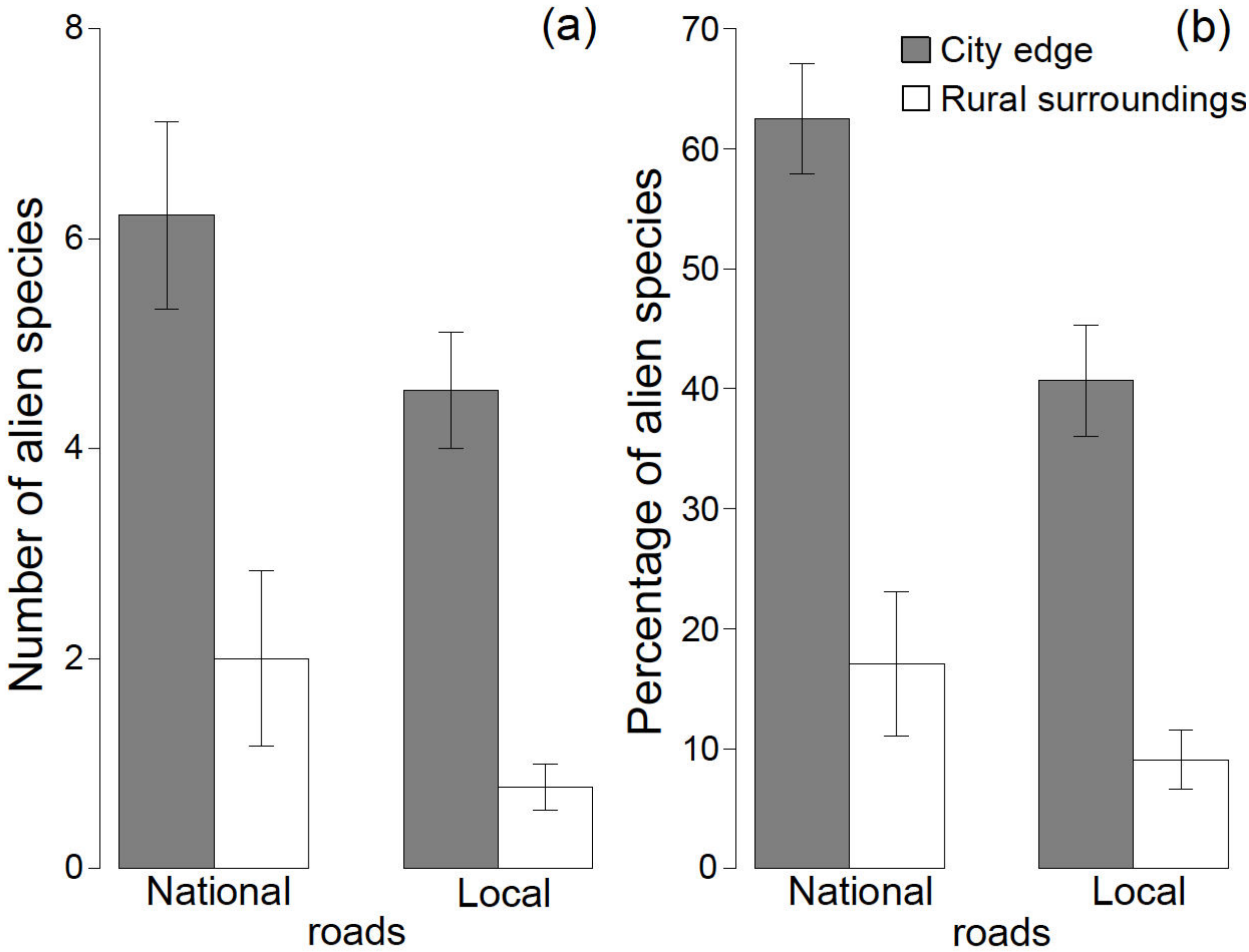

Fig. 2 The number of alien plant species (a), and their percentage (b) in the aboveground vegetation along national and local roads at the edge of the city of Pavlodar and in its rural surroundings. Mean values ± SE are given.

Species composition

NMDS ordination analysis indicated that plant species composition in the aboveground vegetation differed between sites at national and local roads and between sites at the city edge and those in the rural surroundings (Fig. S3). PERMANOVA analysis revealed that road type and distance to the city centre caused significant shifts in the plant species composition of the aboveground vegetation (Table 2). Furthermore, the significant interaction between road type and distance to the city centre indicated that same plant species occurred along roads independent of the distance to the city centre (Table 2). In terms of the soil seed bank, the NMDS ordination showed that plant species composition differed only between sites at the city edge and those in the rural surroundings (Fig. S4). PERMANOVA analysis revealed that plant species composition in the soil seed bank was changed in relation to the distance to the city centre but was not influenced by road type (Table 2). The analysis showed a similar interaction between road type and distance to the city centre as found in the aboveground vegetation. Sørensen's similarity indices in plant species composition between the aboveground vegetation and soil seed bank averaged 0.53 per site (range: 0.33–0.64).

Table 2 Summary of PERMANOVAs testing the effects of road type, distance to city centre and distance of the pooled plots to the road edge on (a) plant species composition in the aboveground vegetation, and (b) plant species composition in the soil seed bank

a) Aboveground vegetation	
Road type	$\boldsymbol{F_{1,30} = 2.13, P = 0.026}$
Distance to the city centre	$\boldsymbol{F_{1,30} = 9.61, P = 0.001}$
Distance to the road edge	$F_{2,30} = 0.68, P = 0.861$
Road type x distance to the city centre	$\boldsymbol{F_{1,30} = 2.98, P = 0.003}$
b) Soil seed bank	
Road type	$F_{1,30} = 1.13, P = 0.301$
Distance to the city centre	$\boldsymbol{F_{1,30} = 3.75, P = 0.001}$
Distance to the road edge	$F_{2,30} = 0.61, P = 0.962$
Road type x distance to the city centre	$\boldsymbol{F_{1,30} = 1.76, P = 0.043}$

Significant *P*-values ($P < 0.05$) are in bold

Plant life form

With respect to plant life forms, hemicryptophytes were most common in both the aboveground vegetation and soil seed bank. In the aboveground vegetation, the percentages of species belonging to the four plant life forms did not differ between the two road types (Chi^2 = 5.30, d.f. = 3, P = 0.15), but between sites at the city edge and those in the rural surroundings (Chi^2 = 45.90, d.f. = 3, P < 0.001; Fig. 3). A larger percentage of therophytes (42.5%) and a smaller percentage of hemicryptophytes (46.0%) were recorded at the edge of the city than in the rural surroundings (therophytes: 5.1%, hemicryptophytes: 88.6%; Fig. 3).

In the seed bank, the percentage of seed species belonging to different plant life forms did not differ between the two road types and between the distances to the city (data not shown; in both cases P > 0.05). However, when the abundance of seedlings that emerged from seed trays were considered, then sites situated at either road type or distance to the city differed in the percentages of seedlings belonging to different plant life forms (Fig. 3). Again a larger percentage of therophytes (45.2%) and a smaller percentage of hemicryptophytes (35.7%) were found at the city edge than in the rural surroundings (24.3% vs. 64.6%; Chi^2 = 19.44, d.f. = 3, P < 0.001; Fig. 3).

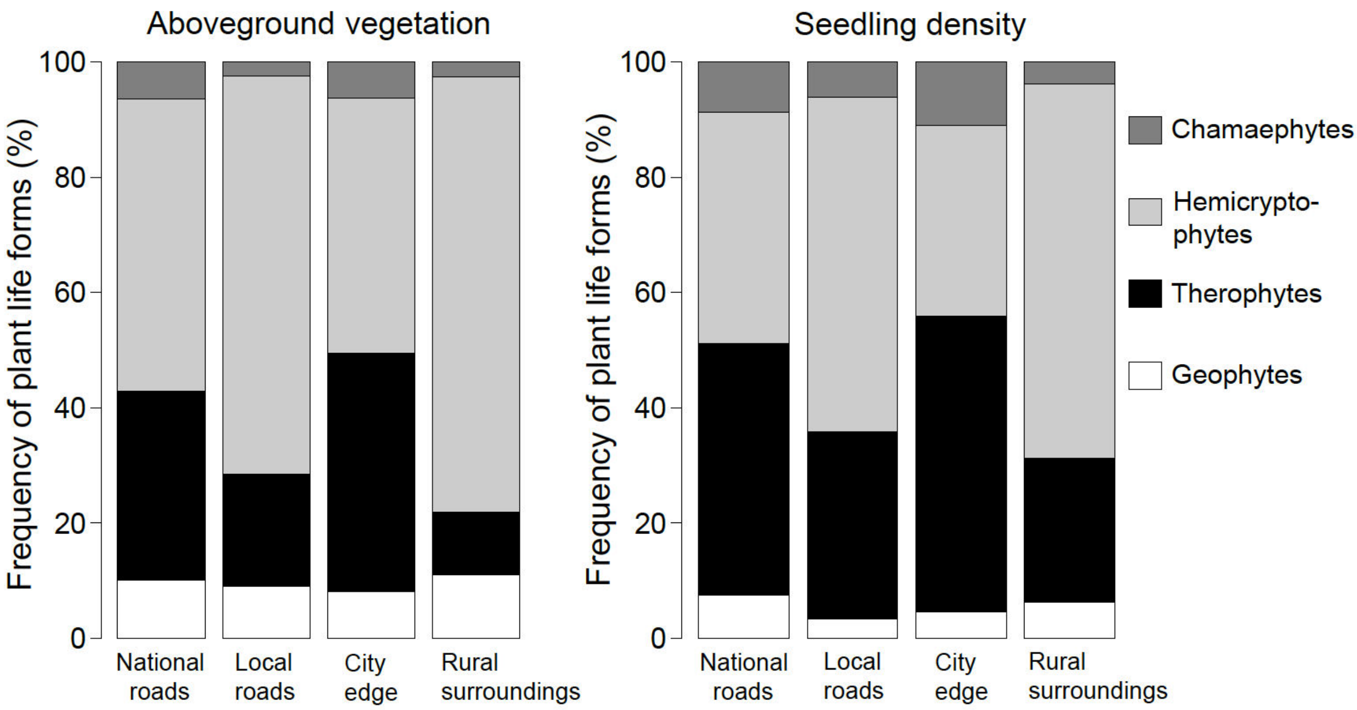

Fig. 3 Percentage (%) of plant species belonging to different life forms in the aboveground vegetation, and percentage of seedlings of different plant life forms in the soil seed bank. Data were recorded along national and local roads at the edge of the city of Pavlodar and in the rural surroundings. Each bar presents data from six sites.

Seed traits

The percentage and abundance of seed species belonging to different seed bank types were neither affected by the road type nor by the distance to the city of the sampling site (for seed species: road type $Chi^2 = 1.75$, d.f. = 3, $P = 0.63$; distance to the city $Chi^2 = 1.68$, d.f. = 3, $P = 0.64$; for density of seedlings: road type $Chi^2 = 0.84$, d.f. = 3, $P = 0.84$; distance to the city $Chi^2 = 4.22$, d.f. = 3, $P = 0.24$). Similarly, seed weight, percentage of human-dispersed seed species and percentage of seed species with additional appendages were not influenced by road type and distance to the city (Table S3).

Discussion

This study showed that both the aboveground vegetation and soil seed bank of roadside verges contained a large percentage of alien species. The percentage of alien species in the aboveground vegetation was significantly higher (32.3%) than that reported in grassland plots situated 200 m and further away from roads in the same region (15.1%; Vakhlamova et al. 2014). In this study, alien species richness and plant life forms in the aboveground vegetation and soil seed bank were affected by the type of road and the distance to the city centre.

Effect of road type

In both the aboveground vegetation and soil seed bank, the number of alien species was larger and their percentage was higher along national roads than along local roads, confirming our first hypothesis. High traffic density has been reported to favour alien species in roadside verges owing to frequent disturbance and high propagule pressure of exotic plants (Joly et al. 2011). Thus, the establishment of alien plants along roads may be related to the traffic density and the locations from which the vehicles come. National roads in Kazakhstan are used for both passenger and cargo transports over large distances, frequently covering different biogeographical regions, which provides opportunities for the introduction of alien species (Taylor et al. 2012; Menuz and Kettenring 2013). In contrast, local roads connect villages and farms and thus serve a more regionally restricted traffic. By transporting hay, cereals and other plant material, local roads contribute to the spread of various plant species, most of them being native.

Plant growth benefits from run-off water and flushed nutrients in verges (Angold 1997). Along national roads, alien plant species may especially benefit from an increased nutrient level as result of nitrogen oxides, sulphur dioxide and low organic carbon molecules from vehicle exhausted (Menuz and Kettenring 2013).

Effect of distance to city centre

In both the aboveground vegetation and soil seed bank, the number of alien species was larger and their percentage was higher at the edge of the city than in the rural surroundings, confirming our second hypothesis. Cities usually harbour more alien species than their rural surroundings (Roy et al. 1999). Furthermore, in urban areas, the habitats situated close to roads are more heterogeneous and generally harbour more horticultural species than in rural areas (Hodkinson and Thompson 1997). Thus, the native plant community in verges might be enriched by alien plant species from adjacent habitats (Sullivan et al. 2009). It is therefore expected that more alien species colonize road verges at the city edge than in the rural surroundings.

The total species richness in the soil seed bank was lower at the city edge compared with that in the rural surroundings irrespective of road type. Compaction and disturbance of the upper soil layer due to off-road driving and parking may deplete the soil seed bank (Kinugasa and Oda 2014). In the present study, this type of disturbance occurs more frequently at the edge of the city than in the rural surroundings. The probability of seed transportation by vehicles might be similar for native and alien plant species (Auffret and Cousins 2013). However, alien plants germinate better in severely disturbed roadside verges at the city edge than native grassland species, which require more specific habitat conditions (Jutila and Grace 2002). Therefore, the abundance of native plants in the soil seed bank might also be reduced by the conditions of roadside habitat in our study.

Species composition

Several alien plant species recorded along national roads could be a result of cargo routes from other biogeographical regions (see below). This may contributed to the observed difference in plant species composition in the aboveground vegetation between verges along national and local roads. Our finding contrasts other studies reporting homogenization of grassland plant communities across roads (Arévalo et al. 2010; Hayasaka et al. 2012).

Species-specific responses of plants to road management activities may cause changes in plant species composition (Jantunen et al. 2006). In particular, the distance-to-city effect on the species composition found in our study might be a result of disturbance by road maintenance activities at the city edge (road repair and mowing; see Sampling design description). In the rural surroundings, cattle, sheep and horses may also serve as dispersal vectors for seeds and thus influence species composition along roads (Fischer et al. 1996). This may explain the finding that the cover of grassland species (*Artemisia frigida*, *Festuca valesiaca, Stipa capillata*) was higher in sites in the rural surroundings than in sites at the city edge.

Interestingly, plant species composition in the soil seed bank did not differ between national and local roads in our study. In recently invaded areas, changes in diversity and density of native and alien species in the seed bank may be delayed (Robertson and Hickman 2012). In our study region, the traffic density increased significantly in the past two decades. It is therefore expected that total plant species composition in the aboveground vegetation and the soil seed bank in road verges will become more similar in the near future. However, plant species composition in the soil seed bank differed between the city edge and rural surroundings. The establishment of alien species may also influence the abundance of other plants in both the aboveground vegetation and soil seed banks (Fisher et al. 2009). This overlaying effect may contribute to the observed differences in species composition at different distances to the city centre.

Plant life form

In both the aboveground vegetation and soil seed bank, the percentage of therophyte species was increased at sites at the edge of the city. The therophyte life form is reported to be the most frequent for alien species in the roadside flora worldwide (Šerá 2010). Most of these species are weeds or ruderals, such as *Atriplex patula, Lepidium ruderale, Kochia scoparia* in our study. In contrast, a decline of hemicryptophyte species was found along national roads at the edge of the city. The hemicryptophyte life form is reported to be the most common in the grasslands of the study region (48.5–70.2%; Zhumadilov 2012). The decline of typical hemicryptophytes (*Artemisia* ssp., *Stipa capillata*) may indicate a depletion of native plants in the aboveground vegetation and soil seed bank along national roads and at the edge of the city.

Conclusions

Our study demonstrated different effects of road type and distance to the city centre on the percentage of alien plants and plant species composition in the aboveground vegetation and soil seed bank of roadside verges. An increased propagule pressure by transportation through vehicles as well as specific conditions in the roadside verges may determine the establishment of more alien plant species along national than local roads. A further spread of alien plant species and changes in the plant species composition along roads is expected in the study region in the near future. To prevent a further spread of invasive plants from roadside verges to adjoining agricultural land it is recommended to regularly remove all invasive and potentially invasive plants from the roadside verges.

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References

Anderson MJ (2005) PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand

Angold PG (1997) The impact of a road upon adjacent heathland vegetation: effects on plant species composition. J Appl Ecol 34:409–417

Ansong M, Pickering C (2013) Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. PLoS ONE 8(11)e:80275

Arévalo JR, Otto R, Escudero C, Fernández-Lugo S, Arteaga M, Delgado JD, Fernández-Palacios JM (2010) Do anthropogenic corridors homogenize plant communities at a local scale? A case studied in Tenerife (Canary Islands). Plant Ecol 209:23–35

Auffret AG, Cousins SAO (2013) Grassland connectivity by motor vehicles and grazing livestock. Ecography 36:1150–1157

Braun-Blanquet J (1964) Pflanzensoziologie: Grundzüge der Vegetationskunde. Springer, New York

Czerepanov SK (1995) *Plantae Vasculares Rossicae et Civitatum Collimitanearum (in limicis USSR olim) (List of Vascular Plants of Russia and adjacent states (in the limits of former USSR)).* St. Petersburg - Mir I Semia

Christen D, Matlack G (2006) The role of roadsides in plant invasions: a demographic approach. Conserv Biol 20:385–391

Cole DN (1995) Experimental trampling of vegetation. II. Predictors of resistance and resilience. J Appl Ecol 32:215–224

Committee of Statistics of the Republic of Kazakhstan (2015) Pavlodar region. http://www.stat.gov.kz/faces/homePage.htm

Crawley MJ (2013) The R Book. 2nd edition, Wiley, Chichester

Fischer SF, Poschlod P, Beinlich B (1996) Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. J Appl Ecol 33:1206–1222

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ (2009) Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. Biol Conserv 142:256–269

Fowler JF, Sieg CH, Dickson BG, Saab V (2008) Exotic plant species diversity: influence of roads and prescribed fire in Arizona ponderosa pine forests. Rangeland Ecol Manage 61:284–293

Goloskokov VP (1972) *Иллюстрированный определитель растений Казахстана (Illustrated keys to plants of Kazakhstan).* V. 1-2. Alma-Ata - Nauka of Kazakh SSR

Hayasaka D, Akasaka M, Miyauchi D, Box EO, Uchida T (2012) Qualitative variation in roadside weed vegetation along an urban–rural road gradient. Flora 207:126–132

Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. J Appl Ecol 34:1484–1496

Holmes PM, Cowling RM (1997) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. Plant Ecol 133:107–122

Jantunen J, Saarinen K, Valtonen A, Saarnio S (2006) Grassland vegetation along roads differing in size and traffic density. Ann Bot Fennici 43:107–117

Joly M, Bertrand P, Gbangou RY, White M-C, Dubé J, Lavoie C (2011) Paving the way for invasive species: road type and the spread of common ragweed (*Ambrosia artemisiifolia*). Environ Manage 48:514–522

Jutila HM, Grace JB (2002) Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. J Ecol 90:291–302

Kinugasa T, Oda S (2014) Effects of vehicle track formation on soil seed banks in grasslands with different vegetation in the Mongolian steppe. Ecol Eng 67:112–118

Manzano P, Malo JE (2006) Extreme long-distance seed dispersal via sheep. Front Ecol Evol 4: 970–977

Menuz DR, Kettenring KM (2013) The importance of roads, nutrients, and climate for invasive plant establishment in riparian areas in the northwestern United States. Biol Invasions 15:1601–1612

Mortensen DA, Rauschert ESJ, Nord AN, Jones BP (2009) Forest roads facilitate the spread of invasive plants. Invasive Plant Sci Manage 2:191–199

Muller FM (1978) Seedlings of the north-western European flora: a flora of seedlings. Junk, The Hague

Müller-Schneider P (1986) Verbreitungsbiologie der Blütenpflanzen Graubündens. Heft 85. Veröffentl Geobot Inst ETH, Stiftung Rübel, Zürich

Nurmukhambetova GD (2002) *Эколого-геоботаническая характеристика сорной растительности степной зоны (Костанайская область) (Ecological and geobotanical characteristics of ruderal plant communities in the steppe zone (Kostanay region))* (Dissertation). Almaty - Kazakhstan

Pavlov NV (1956-1966) *Флора Казахстана (Flora of Kazakhstan).* V. 1–9. Alma-Ata - Academy of Science of Kazakh SSR

Pyšek P (1998) Alien and native species in Central European urban floras: a quantitative comparison. J Biogeogr 25:155–163

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.Rproject.org

Raunkiaer C (1934) The life forms of plants and statistical plant geography/being the collected papers of C. Raunkiaer. Clarendon Press, Oxford

Robertson SG, Hickman KR (2012) Aboveground plant community and seed bank composition along an invasion gradient. Plant Ecol 213:1461–1475

Roy DB, Hill MO, Rothery P (1999) Effects of urban land cover on the local species pool in Britain. Ecography 22:507–515

Šerá B (2010) Road-side herbaceous vegetation: life history groups and habitat preferences. Pol J Ecol 58:69–79

Sharma GP, Raghubanshi AS (2009) Plant invasions along roads: a case study from central highlands, India. Environ Monit Assess 157:191–198

Sullivan JJ, Williams PA, Timmins SM, Smale MC (2009) Distribution and spread of environmental weeds along New Zealand roadsides. NZ J Ecol 33:190–204

Taylor K, Brummer T, Taper ML, Wing A, Rew LJ (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Diversity Distrib 18:942–951

Ter Heerdt GN, Verweij GL, Bekker RM, Bakker JP (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. Funct Ecol 10:144–151

Thompson K, Grime JP (1979) Seasonal variation in the seed bank of herbaceous species in ten contrasting habitats. J Ecol 67:893–921

Vakhlamova T, Rusterholz H-P, Kanibolotskaya Y, Baur B (2014) Changes in plant diversity along an urban–rural gradient in an expanding city in Kazakhstan, Western Siberia. Landsc Urban Plan 132:111–120

Vallet J, Daniel H, Beaujouan V, Rozé, F, Pavione S (2010) Using biological traits to assess how urbanization filters plant species of small woodlands. Appl Veg Sci 13: 412–424

Von der Lippe M, Kowarik I (2008) Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients. Diversity Distrib 14:18–25

Von der Lippe M, Kowarik I (2012) Interactions between propagule pressure and seed traits shape human-mediated seed dispersal along roads. Perspect Plant Ecol Evol Syst 14:123–130

Zhumadilov BZ (2012) Analysis of flora of Ertysskiy floristic region within Eastern Kazakhstan steppe zone. Dissertation, S. Torajgyrov Pavlodar State University

Supplementary material Chapter II

Table S1. Frequency of occurrence of species recorded in the aboveground vegetation and soil seed bank in verges along national and local roads in the surroundings of Pavlodar, Kazakhstan

Table S2. Summary of ANCOVAs or GLMs testing the effects of road type, distance to the city centre, distance of the pooled plots to the road edge on a) various measures of alien seed diversity; b) total seedling density (per m^2) and density and percentage of alien seedlings in the soil seed bank, and c) various measures of seed diversity

Table S3. Summary of ANCOVAs and GLMs testing the effects of road type and distance to the city on seed traits. The analyses were run at the site level ($n = 12$)

Fig. S1. Observed total seed species richness, total seedling density, rarefied seed species richness and Chao-estimated seed species richness along national and local roads at the edge of the city of Pavlodar and in its rural surroundings (for statistics see Table 2)

Fig. S2. Number of alien seed species, rarefied alien seed species richness, Chao-estimated alien seed species richness, percentage of alien seed species, density of alien seedlings and percentage of alien seedlings along national and local roads at the edge of the city of Pavlodar and in its rural surroundings (for statistics see Table 2)

Fig. S3. NMDS ordination analysis showing plant species composition in the aboveground vegetation. Road type and distance to the city separated plant species into four groups

Fig. S4. NMDS ordination analysis showing seedling species composition emerging from the soil seed bank. Distance to the city (axis 2) slightly separated the species into two groups

Table S1 Frequency of occurrence of species recorded in the aboveground vegetation and soil seed bank in verges along national and local roads in the surroundings of Pavlodar, Kazakhstan.

	Species recorded in the aboveground vegetation and soil seed bank	Frequency of occurrence in the aboveground vegetation (%)[1)]	Frequency of occurrence in the soil seed bank (%)[1)]	Seed density (seeds/m^2)[2)]
1	*Achillea millefolium*	4 (11.1)	–	–
2	*Agropyron pectinatum*	33 (91.7)	15 (41.7)	146.7
3	*Agrostis capillaris*	4 (11.1)	3 (8.3)	188.9
4	*Alopecurus pratensis*	1 (2.8)	1 (2.8)	133.3
5	*Amaranthus retroflexus**	1 (2.8)	–	–
6	*Artemisia absinthium*	18 (50.0)	15 (41.7)	304.4
7	*Artemisia dracunculus*	14 (38.9)	6 (16.7)	72.2
8	*Artemisia frigida*	18 (50.0)	9 (25.0)	359.3
9	*Artemisia gracilensis*	2 (5.6)	–	–
10	*Artemisia scoparia*	10 (27.8)	1 (2.8)	66.7
11	*Artemisia sieversiana*	8 (22.2)	7 (19.4)	252.4
12	*Artemisia vulgaris**	3 (8.3)	1 (2.8)	266.7
13	*Astragalus christianus*	2 (5.6)	–	–
14	*Atriplex patula**	6 (16.7)	31 (86.1)	159.1
15	*Atriplex tatarica**	6 (16.7)	2 (5.6)	133.3
16	*Atriplex sagittata**	3 (8.3)	2 (5.6)	183.3
17	*Berteroa incana**	16 (44.4)	23 (63.9)	300.0
18	*Bromus inermis*	2 (5.6)	3 (8.3)	200.0
19	*Calystegia sepium*	1 (2.8)	–	–
20	*Cannabis sativa**	4 (11.1)	–	–
21	*Capsella bursa-pastoris**	3 (8.3)	–	–
22	*Carex praecox*	2 (5.6)	–	–
23	*Ceratocarpus arenarius*	1 (2.8)	–	–
24	*Chelidonium majus**	1 (2.8)	2 (5.6)	133.3
25	*Chenopodium urbicum**	1 (2.8)	6 (16.7)	105.6
26	*Chenopodium glaucum**	1 (2.8)	–	–
27	*Chenopodium rubrum**	1 (2.8)	1 (2.8)	66.7
28	*Cichorium intybus*	1 (2.8)	–	–
29	*Cirsium arvense**	10 (27.8)	9 (25.0)	188.9
30	*Convolvulus arvensis**	13 (36.1)	5 (13.9)	166.7
31	*Conyza canadensis**	2 (5.6)	–	–
32	*Cyclachaena xanthiifolia**	–	3 (8.3)	77.8
33	*Descurainia sophia**	4 (11.1)	3 (8.3)	77.8
34	*Elytrigia repens*	11 (30.6)	9 (25.0)	329.6
35	*Eragrostis pilosa*	1 (2.8)	–	–
36	*Erysimum cheiranthoides*	1 (2.8)	1 (2.8)	33.3
37	*Festuca valesiaca*	12 (33.3)	9 (25)	763.0
38	*Galium boreale*	5 (13.9)	3 (8.3)	277.8
39	*Glycyrrhisa uralensis*	1 (2.8)	–	–
40	*Gypsophila paniculata*	12 (33.3)	7 (19.4)	100
41	*Helianthus annuus**	–	3 (8.3)	88.9
42	*Hordeum vulgare**	1 (2.8)	–	–
43	*Humulus lupulus*	8 (22.2)	–	–
44	*Kochia prostrata**	1 (2.8)	–	–
45	*Kochia scoparia**	8 (22.2)	4 (11.1)	58.3
46	*Lepidium ruderale**	5 (13.9)	1 (2.8)	33.3
47	*Leymus racemosus*	2 (5.6)	–	–

48	*Lolium perenne*	1 (2.8)	1 (2.8)	166.7
49	*Matricaria perforata*	1 (2.8)	–	–
50	*Medicago falcata*	22 (61.1)	6 (16.7)	188.9
51	*Melilotus albus**	6 (16.6)	–	–
52	*Melilotus officinalis**	7 (19.4)	2 (5.6)	150.0
53	*Phalaroides arundinacea*	1 (2.8)	–	–
54	*Plantago major*	3 (8.3)	–	–
55	*Poa pratensis*	10 (27.8)	6 (16.7)	144.4
56	*Poa trivialis*	6 (16.7)	3 (8.3)	233.3
57	*Polygonum aviculare**	9 (25.0)	19 (52.8)	161.4
58	*Potentilla erecta*	8 (22.2)	3 (8.3)	188.9
59	*Potentilla anserina*	1 (2.8)	5 (13.9)	126.7
60	*Potentilla argentea*	–	7 (19.4)	171.4
61	*Potentilla humifusa*	–	2 (5.6)	250.0
62	*Rumex confertus*	–	1 (2.8)	233.3
63	*Ranunculus repens*	1 (2.8)	3 (8.3)	200.0
64	*Salvia stepposa*	1 (2.8)	–	–
65	*Saponaria officinalis*	5 (13.9)	–	–
66	*Setaria viridis**	1 (2.8)	–	–
67	*Silene wolgensis*	–	1 (2.8)	66.7
68	*Solanum nigrum*	1 (2.8)	6 (16.7)	38.9
69	*Sonchus oleraceus**	2 (5.6)	3 (8.3)	100.0
70	*Sonchus arvensis**	2 (5.6)	11 (30.5)	109.1
71	*Stipa capillata*	7 (19.4)	7 (19.4)	223.8
72	*Taraxacum officinale**	8 (22.2)	2 (5.6)	66.7
73	*Thlaspi arvense**	2 (5.6)	1 (2.8)	133.3
74	*Triticum aestivum**	1 (2.8)	–	–
75	*Vicia cracca*	2 (5.6)	–	–
76	*Rosa pisiformis*⁺	1 (2.8)	–	–
77	*Acer negundo**⁺	1 (2.8)	–	–
78	*Ulmus pumila*⁺	1 (2.8)	–	–

1) Number of occurrence out of 36 pooled subplots. Figures in parentheses indicate percentages.
2) Average seed density of a species, calculated per pooled subplot, in which the species occurred
* Alien species
\+ Woody species in the ground layer

Table S2 Summary of ANCOVAs or GLMs testing the effects of road type, distance to the city centre, distance of the pooled plots to the road edge on a) various measures of alien seed diversity; b) total seedling density (per m^2) and density and percentage of alien seedlings in the soil seed bank, and c) various measures of seed diversity.

a)

Explanatory variables	Number of alien seed species[2]	Rarefied alien seed species richness[2]	Chao-estimated alien seed species richness[2]	Percentage of alien seed species[2]
Road type	$\mathbf{F_{1,34} = 6.47,\ P = 0.017}$	$\mathbf{F_{1,34} = 6.91,\ P = 0.013}$	$\mathbf{F_{1,34} = 11.44,\ P = 0.002}$	$F_{1,34} = 1.04,\ P = 0.32$
Distance to the city	$\mathbf{F_{1,33} = 7.99,\ P = 0.009}$	$F_{1,33} = 0.48,\ P = 0.49$	$F_{1,33} = 3.06, P = 0.09$	$\mathbf{F_{1,33} = 35.68,\ P < 0.001}$
Distance to the road edge	$F_{2,31} = 1.31,\ P = 0.29$	$F_{2,31} = 0.73,\ P = 0.49$	$F_{2,31} = 0.80, P = 0.46$	$\mathbf{F_{2,31} = 5.63,\ P = 0.009}$
Observed aboveground plant species richness	$F_{1,30} = 3.08,\ P = 0.09$	–	$F_{1,30} = 1.24, P = 0.28$	–
Road type x distance to the city	$F_{1,28} = 1.82,\ P = 0.18$	–	–	–
Road type x distance to the road edge	–	–	–	$F_{1,28} = 1.82,\ P = 0.18$

b)

Explanatory variables	Total seedling density[1]	Density of alien seedlings[1]	Percentage of alien seedlings[2]
Road type	$F_{1,28} = 0.15,\ P = 0.70$	$F_{1,29} = 2.59, P = 0.12$	$F_{1,34} = 2.66,\ P = 0.11$
Distance to the city	$\mathbf{F_{1,28} = 6.04,\ P = 0.020}$	$F_{1,29} = 0.61, P = 0.44$	$\mathbf{F_{1,33} = 20.73, P < 0.0001}$
Distance to the road edge	$F_{2,28} = 0.15,\ P = 0.86$	$F_{2,29} = 0.44, P = 0.65$	$F_{2,31} = 0.61,\ P = 0.55$
Observed aboveground plant species richness	$F_{1,28} = 2.16,\ P = 0.15$	–	$\mathbf{F_{1,30} = 6.00,\ P = 0.020}$
Road type x distance to the city	–	–	–
Road type x distance to the road edge	$F_{2,28} = 1.86,\ P = 0.17$	$F_{2,29} = 1.24, P = 0.30$	–

c)

Explanatory variables	Observed total seed species richness[1]	Rarefied seed species richness[2]	Chao-estimated seed species richness[1]
Road type	$F_{1,30} = 2.51,\ P = 0.12$	$F_{1,34} = 3.05,\ P = 0.09$	$F_{1,30} = 2.39,\ P = 0.13$
Distance to the city	$\mathbf{F_{1,30} = 4.64,\ P = 0.040}$	$F_{1,33} = 1.76,\ P = 0.19$	$\mathbf{F_{1,30} = 6.41, P = 0.017}$
Distance to the road edge	$F_{2,30} = 0.25,\ P = 0.78$	$F_{2,31} = 0.80,\ P = 0.46$	$F_{2,30} = 0.02, P = 0.98$
Observed aboveground plant species richness	$F_{1,30} = 3.89,\ P = 0.06$	–	$F_{1,30} = 2.21, P = 0.15$
Road type x distance to the city	–	–	–
Road type x distance to the road edge	–	–	–

[1] ANCOVA
[2] GLM, quasipoisson distributed errors
– excluded from the model
Significant results are in bold ($P < 0.05$)

Table S3 Summary of ANCOVAs and GLMs testing the effects of road type and distance to the city on seed traits. The analyses were run at the site level (n = 12).

a) Number of plant species in the soil seed bank

Explanatory variables	Species seed weight[1]	Percentage of human/wind dispersed seed species [2]	Percentage of seed species with/without additional appendages [2]
Road type	$F_{1,10} = 0.10$, $P = 0.76$	$X^2 = 0.04$, d.f. = 10, $P = 0.85$	$X^2 = 0.43$, d.f. = 10, $P = 0.51$
Distance to the city	$F_{1,9} = 0.73$, $P = 0.41$	$X^2 = 0.29$, d.f. = 9, $P = 0.59$	$X^2 = 1.51$, d.f. = 9, $P = 0.22$
Road type x distance to the city	–	–	$X^2 = 1.78$, d.f. = 8, $P = 0.18$

b) Density of seedlings (per m^2)

Explanatory variables	Total seed mass[3]	Percentage of seedlings with human/wind dispersed seeds [4]	Percentage of seedlings having seeds with/without additional appendages [5]
Road type	$F_{1,10} = 1.38$, $P = 0.27$	$F_{1,9} = 3.49$, $P = 0.09$	$F_{1,10} = 0.18$, $P = 0.68$
Distance to the city	$F_{1,9} = 1.54$, $P = 0.24$	$F_{1,9} = 0.79$, $P = 0.40$	$F_{1,9} = 2.24$, $P = 0.17$
Road type x distance to the city	–	–	–

[1] GLM, quasipoisson distributed errors, mean seed weight per site
[2] GLM, binomial distributed errors
[3] GLM, quasipoisson distributed errors, total seed mass per m^2
[4] ANCOVA
[5] GLM, quasipoisson distributed errors
– excluded from the model

Fig. S1 Observed total seed species richness, total seedling density, rarefied seed species richness and Chao-estimated seed species richness along national and local roads at the edge of the city of Pavlodar and in its rural surroundings (for statistics see Table 2).

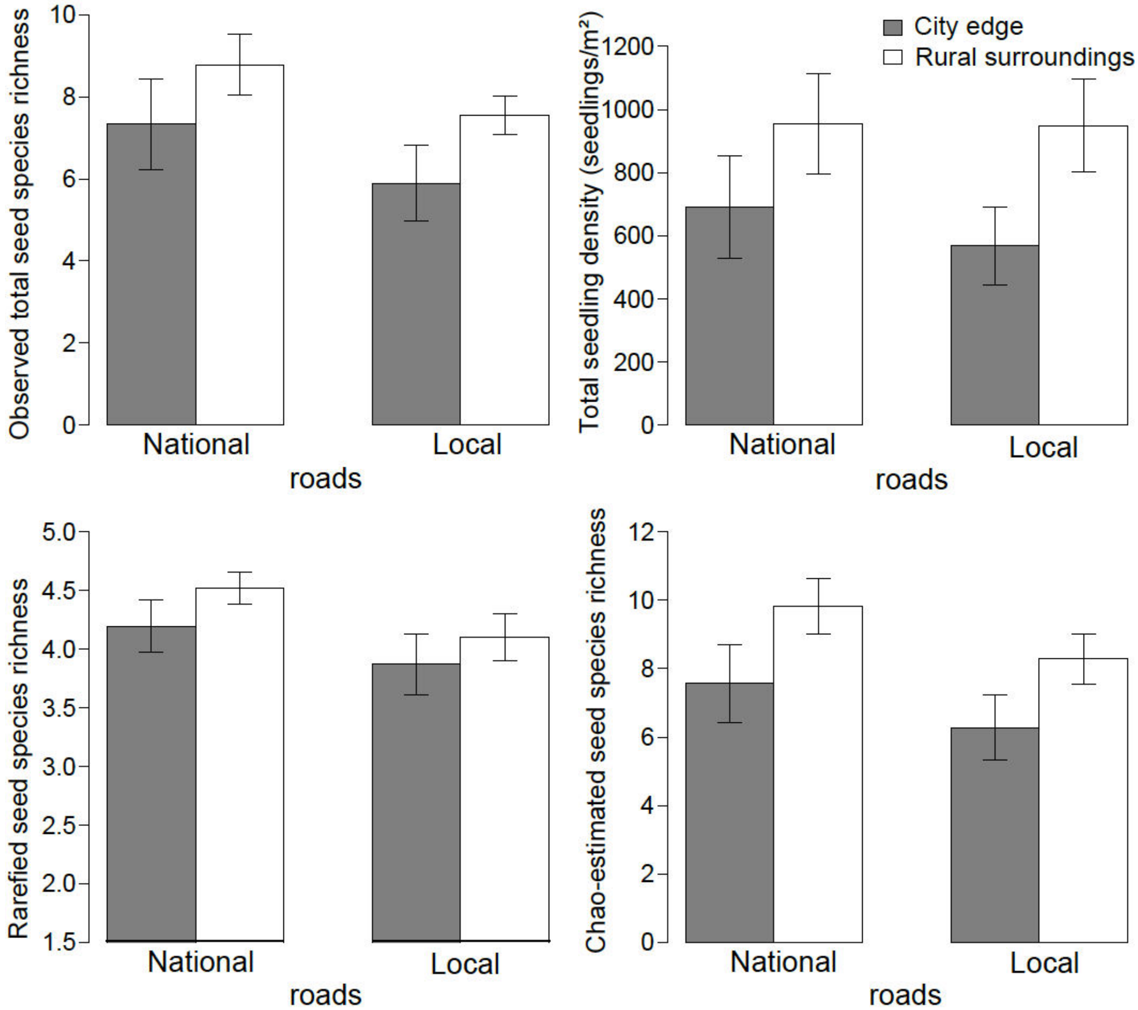


Fig. S2 Number of alien seed species, rarefied alien seed species richness, Chao-estimated alien seed species richness, percentage of alien seed species, density of alien seedlings and percentage of alien seedlings along national and local roads at the edge of the city of Pavlodar and in its rural surroundings (for statistics see Table 2).

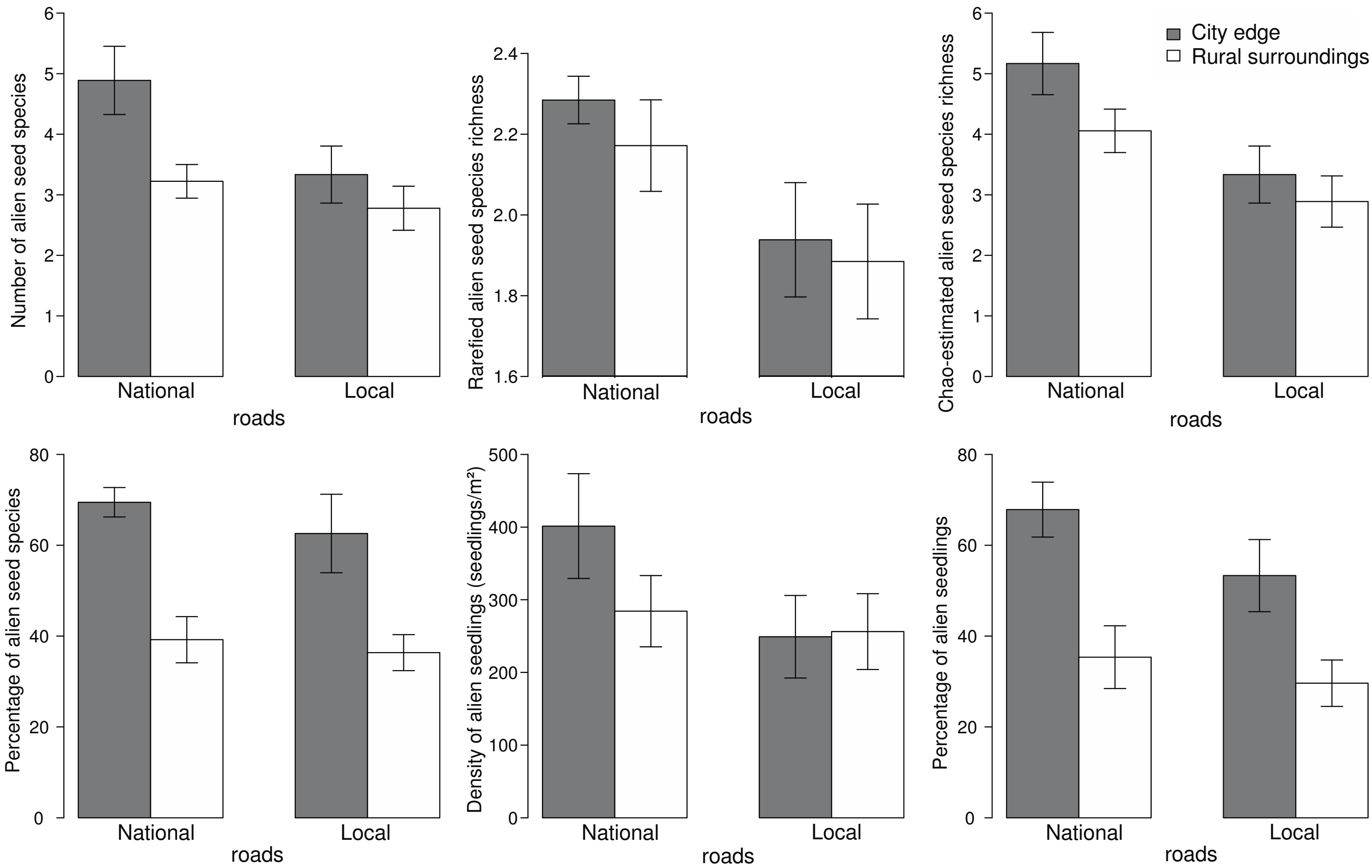


Fig. S3 NMDS ordination analysis showing plant species composition in the aboveground vegetation. Road type and distance to the city separated plant species into four groups.

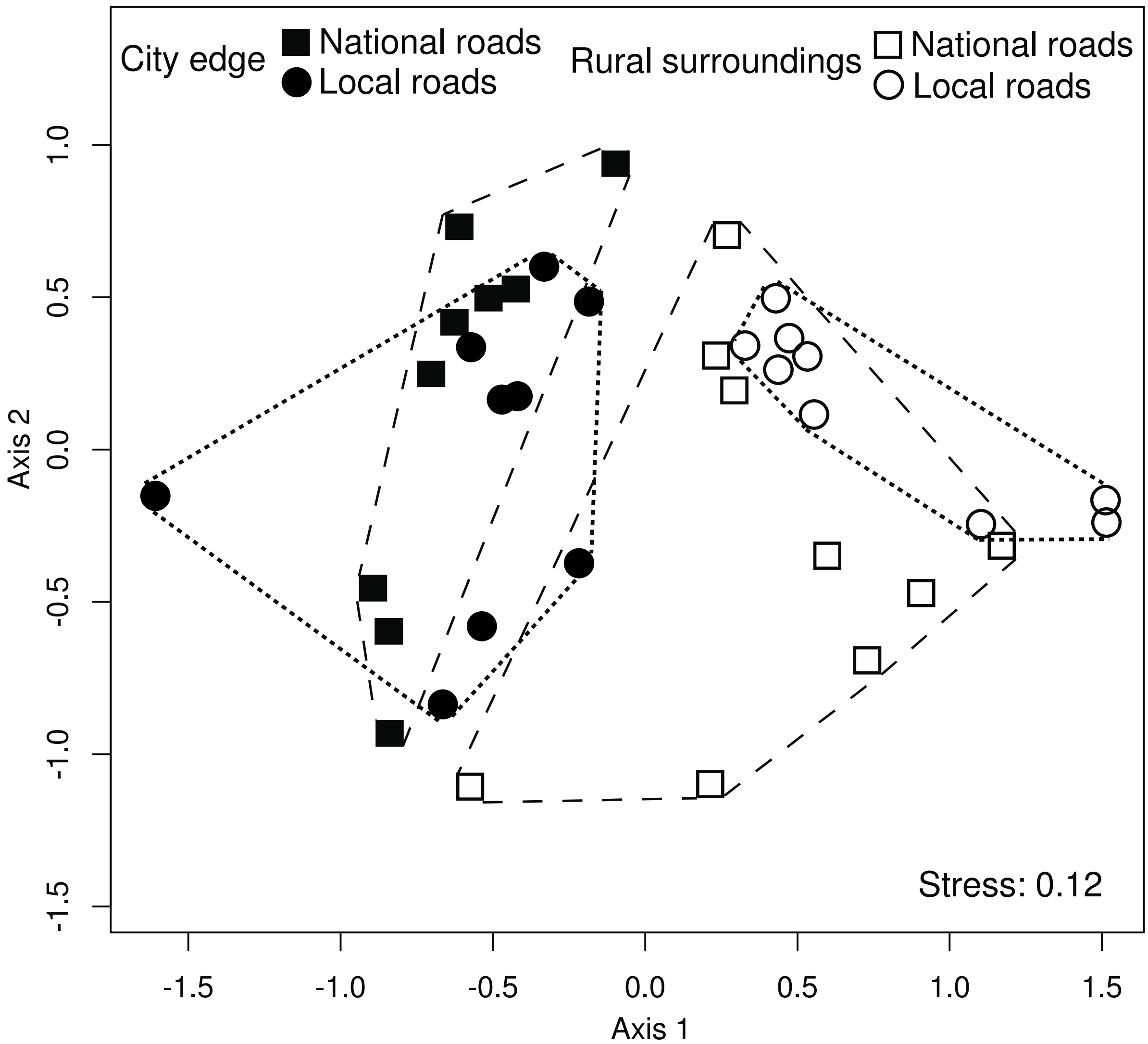
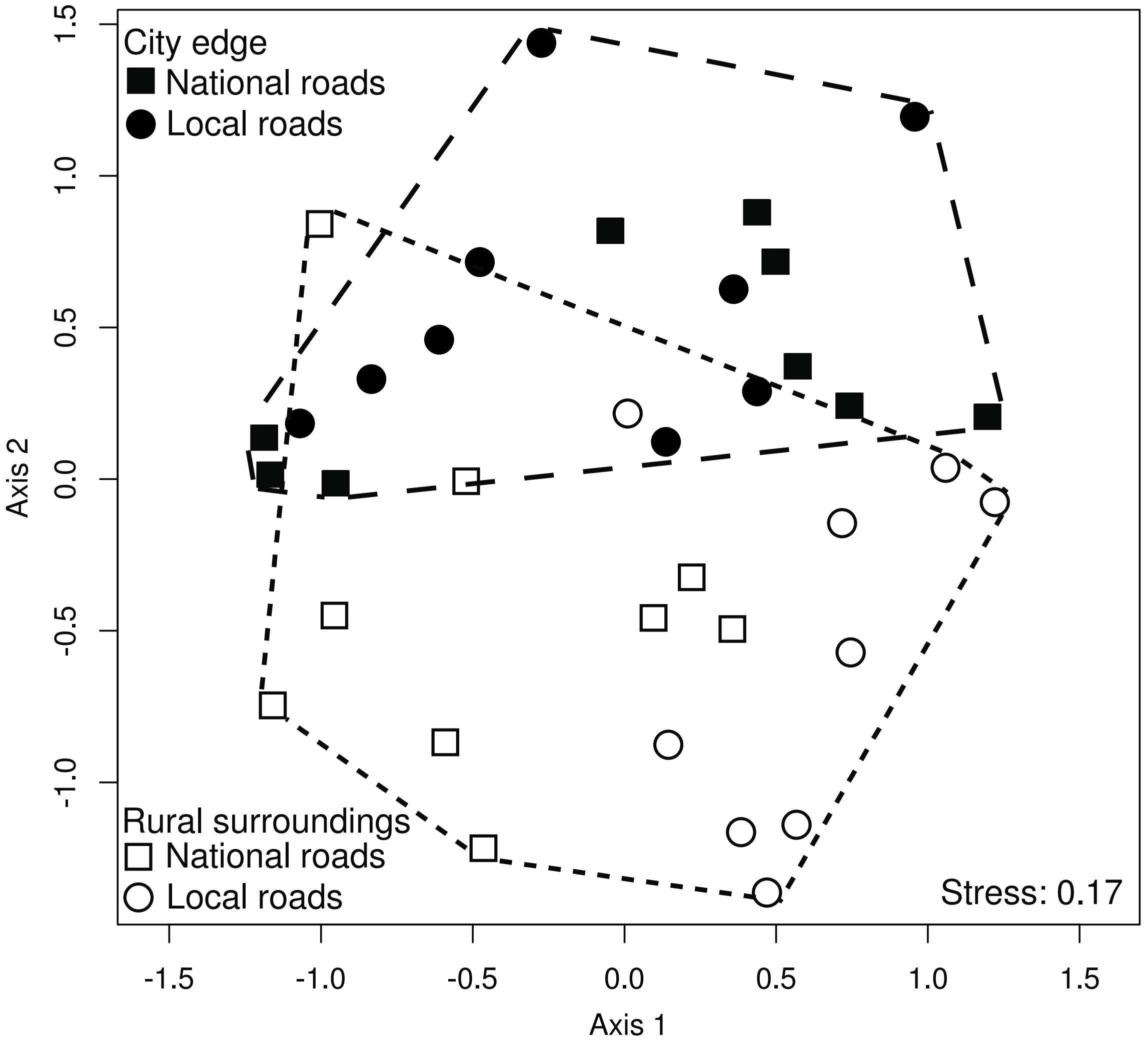


Fig. S4 NMDS ordination analysis showing seedling species composition emerging from the soil seed bank. Distance to the city (axis 2) slightly separated the species into two groups.



Chapter III

Recreational use of urban and suburban forests affects plant diversity in a Western Siberian city

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Urban Forestry and Urban Greening (submitted)

Abstract

The recreational use of urban forests is a highly valued service. However, strong recreational pressure may contribute to the loss of biodiversity in forests. This study assessed the frequency of visitors and their characteristics in 14 urban and 11 suburban forests in the rapidly expanding city of Pavlodar, Kazakhstan, in Western Siberia. Furthermore, the effects of recreation disturbance (trampling, damage to ground vegetation and damage to trees and shrubs) and other human-mediated disturbances (waste deposits, soil disturbance, etc.) on both the vegetation and plant characteristics of urban and suburban forests were quantified. In Pavlodar, urban forests are poorly managed, motivating the people to spend their sparetime in the more distant suburban forests. Urban and suburban forests did not differ in visitor frequency during the summer season (July–September). However, the two forest types differed in the age structure and group size of visitors as well as in the activities of visitors. Urban forests were more frequently visited by younger people for walking, sports, sitting and talking, and playing with children, while suburban forests were often visited by older people for picnicking, fishing and gathering mushrooms. In urban forests, total plant species richness was reduced by recreation disturbance. Urban forests also harboured a large proportion of alien plant species (42.1%; in suburban forests 24.1%). Neither recreation disturbance nor other human-mediated disturbance affected plant species richness in suburban forests, while both disturbance types enhanced the colonization success of alien species. Alterations in plant life forms can be considered as indicator of changes in ecosystem function. In suburban forests, recreation disturbance caused a decline of geophytes and an increase of therophytes. We recommended various management actions to improve the recreation value of degraded urban forests in this Western Siberian city.

Keywords Human-mediated disturbance • Plant diversity • Plant life form • Recreational use

1. Introduction

Urban forests provide a range of important ecosystem services including recreation for residents (Bolund and Hunhammar, 1999), and habitats for plants and animals (Croci et al., 2008). Anthropogenic disturbances are a characteristic of urban forests (Cilliers and Siebert, 2011; Swan et al., 2011). Some of the most obvious types of disturbance include trampling of vegetation and soil compaction (Amrein et al., 2005; Hill and Pickering, 2009), soil pollution, the invasion of alien plants (Sullivan et al., 2005) and green waste deposits (Rusterholz et al., 2012), which all may reduce the quality of ecosystem services. In urban environments the frequency and intensity of disturbances are the major drivers of plant species richness and composition (Hill et al., 2002; Hamberg et al., 2008).

Empirical data on effects of recreation on plant diversity are restricted to urban forests in Europe, North America and Australia (for an overview see Niemelä et al., 2011), but so far no data are available from urban forests in Central Asia, a region, which differs in various aspects from the previously investigated cities. The present study focuses on effects of recreational activities on plant diversity in poorly managed urban forests as well as in increasingly visited suburban riparian forests in Pavlodar, a city in the transition zone from grassland to forest biome in Kazakhstan, Western Siberia. The people of this region experienced very rapid changes in the traditional husbandry system with a dramatic impact on the social and economical development as a result of the Virgin Land Campaign in the former Soviet Union in 1954–1963. In the 1950ies, approximately 200,000 people were transferred to the state farms in the Pavlodar region (Insebaev et al., 2007). After the failure of the Campaign, these people settled in the city of Pavlodar, which increased from a few thousands to 331,000 inhabitants in 2013 (Committee of Statistics of the Republic of Kazakhstan, 2014). Nowadays, Pavlodar and its close surroundings constitute a huge industrial agglomerate. Between 1960 and 1970, considerable resources have been invested into the plantation of new forests within the expanding area of the city. However, after the fall of the Soviet Union (1991), little attention has been directed towards the maintenance of these urban forests. While these forests were originally planted to serve as windbreaks and to improve the urban climate, their importance for recreational use has increased in the past few years. Nowadays most people consider the urban forests no longer attractive and therefore prefer to visit riparian forests for recreational activities (T. Vakhlamova; unpubl.

data). These naturally growing suburban forests are restricted to the floodplain of Irtysh river at the western edge of Pavlodar.

In the present study, we assessed the recreational use of urban and suburban forests and its potential impact on plant diversity. We also examined other human-mediated disturbances that might affect floral diversity of forests. Disturbances may not only alter plant diversity and composition but also the function of the ecosystem (McIntyre et al., 1999). The impact of disturbances on the function of ecosystems is frequently assessed by recording changes in the frequency of different plant life forms (Cole, 1995; Roovers et al., 2004; Vallet et al., 2010). We therefore examined changes in frequency of plant life forms in differently impacted urban and suburban forests. In particular, we addressed the following questions:

(1) Do urban and suburban forests differ in visitor frequency, characteristics of forest visitors and in the extent of both recreation disturbance and other human-mediated disturbances?

(2) Do recreational activities and other human-mediated disturbances affect floral diversity (species richness and number of alien species) and plant life forms to a different extent in urban and suburban forests?

2. Methods

2.1 Study area

The study was conducted in urban and suburban forests in the city of Pavlodar in northern-eastern Kazakhstan (52°18′N, 76°57′E). The city is situated on the eastern embankment of the river Irtysh in the Western Siberian Plateau at the elevation of 125–150 m above sea level. The dry continental climate of the region is harsh for forest vegetation. Annual precipitation averages 228 mm, and mean annual temperature is 2.1 ^{O}C. Mean January temperature is –18.1 ^{O}C (minimum –47 ^{O}C) and mean July temperature 21.3 ^{O}C (maximum 42 ^{O}C; Kazhydromet, 2011). There is usually a constant snow cover (depth 12–14 cm) from beginning of November to beginning of April.

The residential area of Pavlodar covers about 77 km^2 and contains 123 small-sized forest patches ranging in size from 0.05 ha to 16.5 ha (total area: 233 ha [3.02% of residential area]). For our investigation, we chose 14 urban forests planted 34–51 years before the survey (an exception being one forest with an age of 20 years; Fig. 1; Table 1). These urban forests were dominated by the trees *Acer negundo, Betula pendula, Pinus sylvestris, Populus alba, P. nigra* and *Ulmus pumila.* Urban forests with other dominant tree species including parks, roadside plantations, spontaneous green spaces overgrown by shrubs and trees on formerly steppe-like were not considered in this study. Most urban forests are properties of the municipal government (Table 1).

Suburban forests are part of the strip of riparian deciduous forests (70,000 ha in the region) extending along the river Irtysh. Due to alluvial accumulation, the soils of the floodplain contain clay sediments and are more fertile than the other regional soil types. The riparian forests, restricted to uneven micro-relief, are fragmented by hay meadows. The forests serve as recreation zone, and provide habitat for wildlife, but are not managed or used for timber production.

Multivariate ordination analysis revealed that urban and suburban forests differed in the species composition of their ground vegetation (data not shown).

Table 1

Characteristics of urban (n = 14) and suburban forests (n = 11) examined in Pavlodar, Kazakhstan.

Forest type	Forest code	Forest area (ha)	Distance to the city centre (km)	Forest age[+] (years)	Ownership†	Flooding*	Frequency of visitors per hour★
Urban	U1	3.15	8.3	51	mc	0	11.5
	U2	1.27	3.0	34	mc	0	25.3
	U3	1.28	4.4	48	mc	0	21
	U4	0.72	2.5	20	mc	0	8
	U5	0.32	4.7	45	pv	0	5.8
	U6	3.15	0.25	47	mc	0	65.7
	U7	9.88	3.3	34	mc	0	15.2
	U8	1.41	8.5	51	mc	0	10.5
	U9	0.84	2.4	53	mc	0	6.3
	U10	0.61	3.6	42	mc	0	8
	U11	0.77	1.6	47	mc	0	19.3
	U12	0.09	5.2	48	pv	0	9.5
	U13	0.29	9.1	48	mc	0	14.5
	U14	0.23	7.4	51	mc	0	17.8
Suburban	S1	9.88	2.3	–	mc	3	16.8
	S2	6.21	6.8	–	mc	3	7.5
	S3	2.50	6.5	–	mc	3	10.3
	S4	1.13	5.8	–	mc	3	13.6
	S5	1.00	5.0	–	mc	3	14
	S6	1.12	9.6	–	mc	2	4.8
	S7	0.48	6.0	–	mc	3	36.7
	S8	0.42	13.0	–	mc	1	5
	S9	2.56	4.2	–	mc	2	26.4
	S10	0.21	4.4	–	mc	2	14.7
	S11	0.30	4.6	–	mc	2	8

[+] All urban forests were planted. The dominant tree species are *Acer negundo, Betula pendula, Pinus sylvestris, Populus alba, P. nigra, Ulmus pumila.* Suburban forests are naturally growing riparian forests existing since centuries (nowadays in the climax stage).
† mc = municipal government; pv = private
* 0 = absent; 1 = occasional; 2 = several times per decade; 3 = annual
★ Data from this study (between 8:00h and 20:00h in the period July–September 2014)

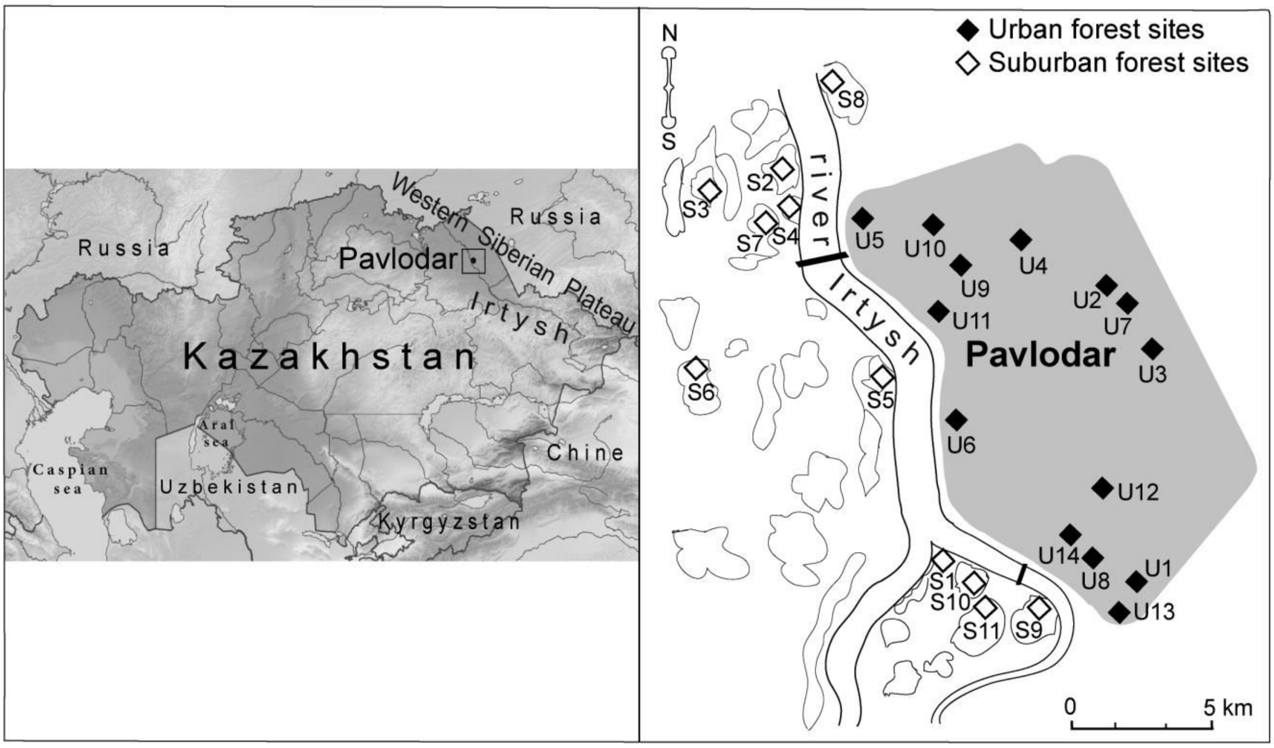

Fig. 1. Location of 14 urban and 11 suburban forests investigated in Pavlodar, Kazakhstan.

2.2 Sampling design and plant survey

Fourteen urban and eleven suburban forests were examined in this study (Table 1). Urban forests were situated at an average distance of 4.015 km (range 0.25–9.1 km; n = 14) from the city centre, suburban forests at a distance of 6.225 km (range 2.3–13.0 km; n = 11). Urban forests measured on average 1.71 ha (range 0.09–9.9 ha; n = 14), suburban forests 2.35 ha (range 0.2–9.9 ha; n = 11). For plant surveys, six plots measuring 4 m x 4 m were installed randomly distributed over the entire area of each forest. The number of vascular plant species in the ground vegetation and cover of single species were assessed in a 2 m x 2 m subplot established in a randomly chosen corner of each 4 m x 4 m plot using the Braun-Blanquet method (1964; *r*: 0.01%; +: 0.1%; 1: 5%; 2: 17.5%, 3: 37.5%; 4: 62.5% and 5: 87.5%). To complete the plant species list in the entire sampling plot, the other three 2 m x 2 m subplots were searched for 20 min each and all new species were recorded. The numbers of shrub and tree species and stem density were assessed in the 4 m x 4 m plots. The total cover of ground vegetation, leaf litter and bare soil were estimated in each plot using the scale of Braun-Blanquet (1964). Plant surveys were carried out between late June and the middle of August 2013. Plant species were identified following the references given in Vakhlamova et al. (2014).

2.3 Forest visitor numbers and their activities

Systematic non-participatory observations were carried out in each urban and suburban forest between 8:00h and 20:00h, both on working days and weekends, between July and September 2014. Following a given transect line, each forest was crossed during a standard scan period of 1 hour, equally distributed over the day. This procedure was repeated 5–6 times for each forest. The scan periods were similarly distributed over both types of forest resulting in a total observation time of 77 h in 14 urban and 58 h in 11 suburban forests. During a scan period, the number of visitors staying or moving in the forest, their gender (male or female), age (children 1–12 years, teens 13–19 years, adults 20–60 years, older adults 60 years or older), the group size (single, pairs, small group [≤ 4 people], large group [> 4 people]) and the activity of the visitors were recorded. Visitor activities were a priori assigned to ten categories: walking, sports (jogging, fighting, gymnastics), biking, picnicking, playing with children, sitting and talking, observing nature, gathering mushrooms or berries, fishing, others (including reading, working, washing cars).

2.4 Habitat and landscape structure characteristics

For each forest, four habitat and seven landscape characteristics were derived from satellite maps (Google Earth, 2013). As habitat characteristics, the minimum distance from the forest edge to the built-up area, the distances from the forest edge to the nearest road, to the nearest other forest and water body were assessed (Appendix A). The percentage cover (estimated to the nearest 5%) of built-up area and traffic infrastructure within a radius of 200 m and 500 m around the most central sampling plot chosen in each forest were determined using the pixel counting function of Adobe Photoshop, version 10.0.1. In the same way, we assessed the percentage cover of wasteland, cropland, forest, grassland and water bodies within radii of 200 m and 500 m. The chosen radii are assumed to represent the relevant scale for landscape effects on vegetation composition.

Compared with suburban forests, the 500-m-surroundings of urban forests were characterised by a higher cover of traffic infrastructure (13% vs. 5%), but lower covers of other forests (18% vs. 33%), grassland (14% vs. 26%) and water surface (6% vs. 22%; Appendix B). The 500-m-surroundings of the two forest types did not differ in cover of built-up area, cropland and wasteland (Appendix B). Some urban forests were partly fenced to prevent car parking between trees along roads. No fencing occurred in suburban forests.

2.5 Assessment of disturbances

For each plot, the degree of recreation disturbance and other human-mediated disturbance were assessed. The degree of recreation disturbance was expressed as a sum of scores (absent (0), low (1), moderate (2) and high (3)) of the three disturbance types “Trampling”, “Damage to ground vegetation” and “Damage to trees and shrubs” (for definitions of damage classes see Appendix C). As a measure of other human-mediated disturbance, we estimated the impact of four different types of disturbances (waste deposits, other soil disturbances, removal of leaf litter layer and traces of ground fire; for definitions of damage classes see Appendix C). For each plot, the sum of scores was determined. At the forest level, the degrees of both recreation disturbance and other human-mediated disturbance were expressed as medians of the corresponding scores per forest. Total human disturbance is the sum of scores of both recreation disturbance and other human-mediated disturbance.

2.6 Plant species characteristics

Based on available data bases (BioFlor Version 1.1; Open atlas of vascular plants of Russia and adjacent areas) and data collected by local botanists, data on plant life form were compiled. The plant species recorded were assigned to one of the four life forms (geophytes, therophytes, hemicryptophytes and chamaephytes; Raunkiaer, 1934).

2.7 Statistical analyses

R software [R Development Core Team, version 2.14.10 (2011); Vienna, Austria] was used for all statistical analyses. Data of landscape characteristics assessed at the scales of 200 and 500 m radii were similar and therefore only results of the 500-m radius are presented. Wilcoxon-rank sum tests were applied to examine whether recreation disturbance, other human-mediated disturbance, and total human disturbance and differ among urban and suburban forests (data at the forest level). Generalized linear models (GLMs) with quasi-Poisson distributed errors and log-link function were used to examine whether urban and suburban forests differ in number of visitors recorded per hour. Contingency tests were applied to examine whether characteristics of visitors differed between the two forest types. Correlations between the number of visitors and the level of recreation disturbance were assessed using Spearman rank correlation.

Based on the numbers of plant species in the six plots we determined total plant species richness of the forests. To examine potential effects of recreation disturbance, other human-mediated disturbance and total human disturbance on total species richness, GLMs with Poisson or quasi-Poisson distributed errors and log-link function were applied. First, the impact of recreation disturbance was included as factor, while total vegetation cover, shrub density and tree density, habitat and landscape variables were used as cofactors (Appendix A). The same model was used for both the degree of other human-mediated disturbance and total human disturbance as factor. Data from urban and suburban forests were analysed separately. Intercorrelated forest characteristics ($P < 0.05$) were not considered in the model. Similar models were used to assess the effects of recreation disturbance and other human-mediated disturbance on the number of alien plant species and their proportion compared to native species. If necessary, log- or square root-transformations were applied to explanatory variables to fit normal distributions.

GLMs with quasi-Poisson distributed errors and log-link function for percentage of plant species with different life forms as well as ANCOVA with arcsine-transformation of data for their abundance were used to determine potential effects of explanatory variables (Table 4). All models were stepwise reduced according to Crawley (2013).

3. Results

3.1 Characteristics of forest visitors

A total of 1,382 visitors were observed in urban forests and 851 visitors in suburban forests (Table 2). The two forest types did not differ in frequency of visitors observed per hour in July–September (urban forests: 17.0 ± 4.1 people/hour; suburban forests: 14.4 ± 2.9 people/hour; $F_{1,23} = 0.27$, $P = 0.61$). The number of visitors observed per hour did not differ between working days and weekends in either forest type (urban: $F_{1,12} = 0.10$, $P = 0.75$; suburban: $F_{1,9} = 3.10$, $P = 0.11$). The gender ratio of visitors was similar in urban and suburban forests (Table 2). However, men were observed more frequently in both forest types than women (Table 2; urban: $Chi^2 = 9.53$, d.f. = 1, $P = 0.002$; suburban: $Chi^2 = 14.61$, d.f. = 1, $P < 0.001$). The two forest types also differed in the age structure of their visitors (Table 2). Urban forests were visited more frequently by young people (< 20 years). Similarly, the two forest types differed in distribution of the group size of visitors. Large groups of visitors were more frequently seen in suburban than in urban forests (Table 2). Furthermore, activities of visitors differed significantly between the two forest types ($Chi^2 = 504.0$, d.f. = 9, $P < 0.001$). The most frequent activities in urban forests were walking, biking, sports, sitting and talking and playing with children (80.2%; Fig. 2). In suburban forests, more visitors were engaged in picnicking and making fires, fishing and gathering mushrooms than in urban forests (36.4% vs. 3.0%; Fig. 2).

Table 2

Number of visitors observed, their gender and demographic data in urban and suburban forests in Pavlodar, Kazakhstan. Data were combined from 14 urban and 11 suburban forests.

Characteristics	Number of visitors (%)		Difference between forest types
	Urban forests	Suburban forests	
Total number	1382	851	
Gender			
female	609 (44.1)	346 (40.7)	
male	773 (55.9)	505 (59.3)	$Chi^2 = 2.36$, d.f. = 1, $P = 0.12$
Age			
1–12 years	186 (13.5)	91 (10.7)	
13–19 years	261 (18.9)	137 (16.1)	
20–60 years	676 (48.9)	470 (55.2)	
> 60 years	259 (18.7)	153 (18.0)	**$Chi^2 = 9.80$, d.f. = 3, $P = 0.020$**
Group size			
single	440 (31.8)	248 (29.1)	
in pairs	376 (27.2)	210 (24.7)	
in small groups (≤ 4 people)	240 (17.4)	114 (13.4)	
in large groups (> 4 people)	326 (23.6)	279 (32.8)	**$Chi^2 = 24.20$, d.f. = 3, $P < 0.001$**

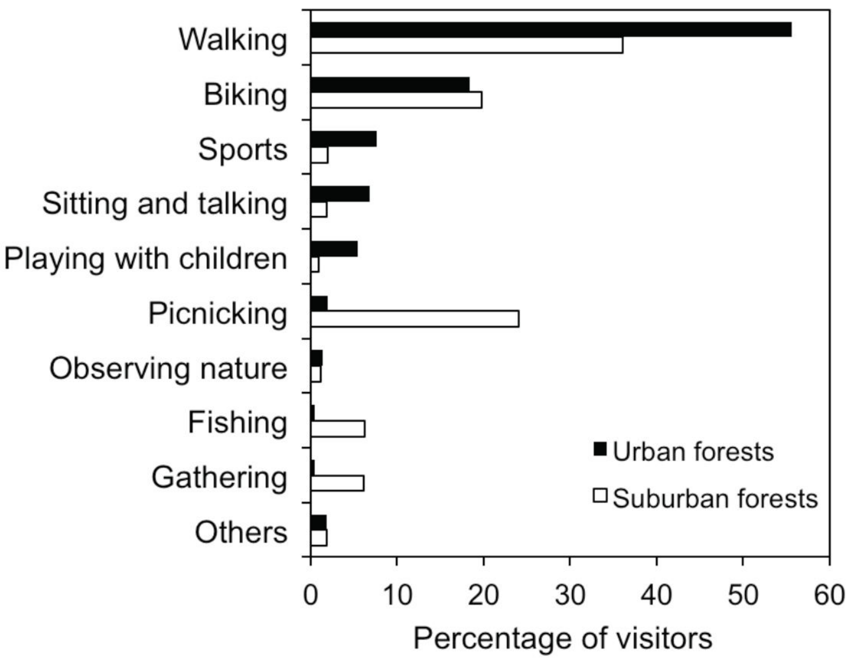

Fig. 2. Activities of the visitors observed in urban and suburban forests in Pavlodar, Kazakhstan. Data were combined from 14 urban and 11 suburban forests.

3.2 Recreation disturbance, other human-mediated disturbance and total human disturbance

At the forest level, the degree of recreation disturbance did not differ between urban and suburban forests (Table 3). However, the extent of other human-mediated disturbances was higher in urban than in suburban forests (Table 3). Considering the extent of total human disturbance, urban and suburban forests did not differ (Table 3).

Table 3

Recreation disturbance, other human-mediated disturbance and total human disturbance in urban and suburban forests in Pavlodar, Kazakhstan.

	Urban forests (n = 14)		Suburban forests (n = 11)		Wilcoxon-rank sum test
	Median	Range	Median	Range	
Recreation disturbance	1.5	0–4	1.5	0–4	*W* = 93.0, *P* = 0.39
Other human-mediated disturbance	4.3	1–6.5	2.5	0.5–4	***W* = 27.0, *P* = 0.006**
Total human disturbance	5.0	1–10	3.5	1.5–8	*W* = 35.0, *P* = 0.24

Median values and ranges based on the medians of each of six plots per forest are presented

3.3 Correlation between recreation disturbance and frequency of forest visitors

In urban forests, median recreation disturbance assessed at the plot level (see Methods) was not correlated with the number of visitors observed in the corresponding forest (Spearman rank correlation: $r_s = 0.43$, n = 14, $P = 0.12$). However, median recreation disturbance was positively correlated with the number of picnicking visitors observed per hour ($r_s = 0.58$, n = 14, $P = 0.028$). In contrast, in suburban forests no correlations were found between recreation disturbance and either the number of visitors observed per hour ($r_s = 0.08$, n = 11, $P = 0.81$) or the number of picnicking people observed per hour ($r_s = 0.30$, n = 11, $P = 0.36$).

3.4 Plant species diversity in urban and suburban forests

In the 14 urban forests, 115 vascular plant species belonging to the ground vegetation and 16 shrub and tree species were found. In the 11 suburban forests, 117 plant species and 12 shrub and tree species were recorded. Plant species number per 16 m^2 plot averaged 6.9 species in urban forests and 9.7 species in suburban forests (Appendix D). At the forest level, species richness of the ground vegetation averaged 29.3 species in urban forests and 42.7 species in suburban forests.

In the layer of ground vegetation, 39 out of the 167 plant species recorded (23.4%) were aliens. Urban forests harboured 42.1% of alien species, suburban forests 21.4% (Appendix D).

The ground vegetation cover averaged 67.8% in urban and 81.0% in suburban forests. Corresponding figures for leaf litter were 26.8% and 13.0% and those for the cover of bare ground 26.8% and 13.0%.

3.5 Effects of recreation disturbance, other human-mediated disturbance and total human disturbance on total plant species richness and alien species

Results of GLM analyses revealed that total species richness of ground vegetation in urban forests was affected by recreation disturbance and forest area (Table 4a). Total plant species richness tended to decrease with increasing recreation disturbance and tended to increase with increasing forest area (Fig. 3). However, total plant species richness was not influenced by other human-mediated disturbance (Table 4b). Considering suburban forests, neither recreation disturbance nor other human-mediated disturbance or any habitat or landscape characteristics affected total plant species richness (Table 4a and b).

In urban forests, the number of alien species was neither affected by recreation disturbance nor by other human-mediated disturbance or any other variables (Table 4a and b). However, the proportion of alien species was influenced by the degree of total human disturbance (Table 4c). The proportion of alien species tended to decrease with increasing forest area (Fig. 3).

In suburban forests, the number of alien species was influenced by recreation disturbance and ground vegetation cover (Table 4a). Species richness of aliens decreased with increasing cover of the ground vegetation (Fig. 3). Furthermore, the number of alien species was affected by the degree of other human-mediated disturbance (Table 4b). The proportion of alien species was influenced by both recreation disturbance and other human-mediated disturbance, as well as by vegetation cover and distance to the nearest road (Table 4a and b). The proportion of alien species increased with increasing extent of other human-mediated disturbance.

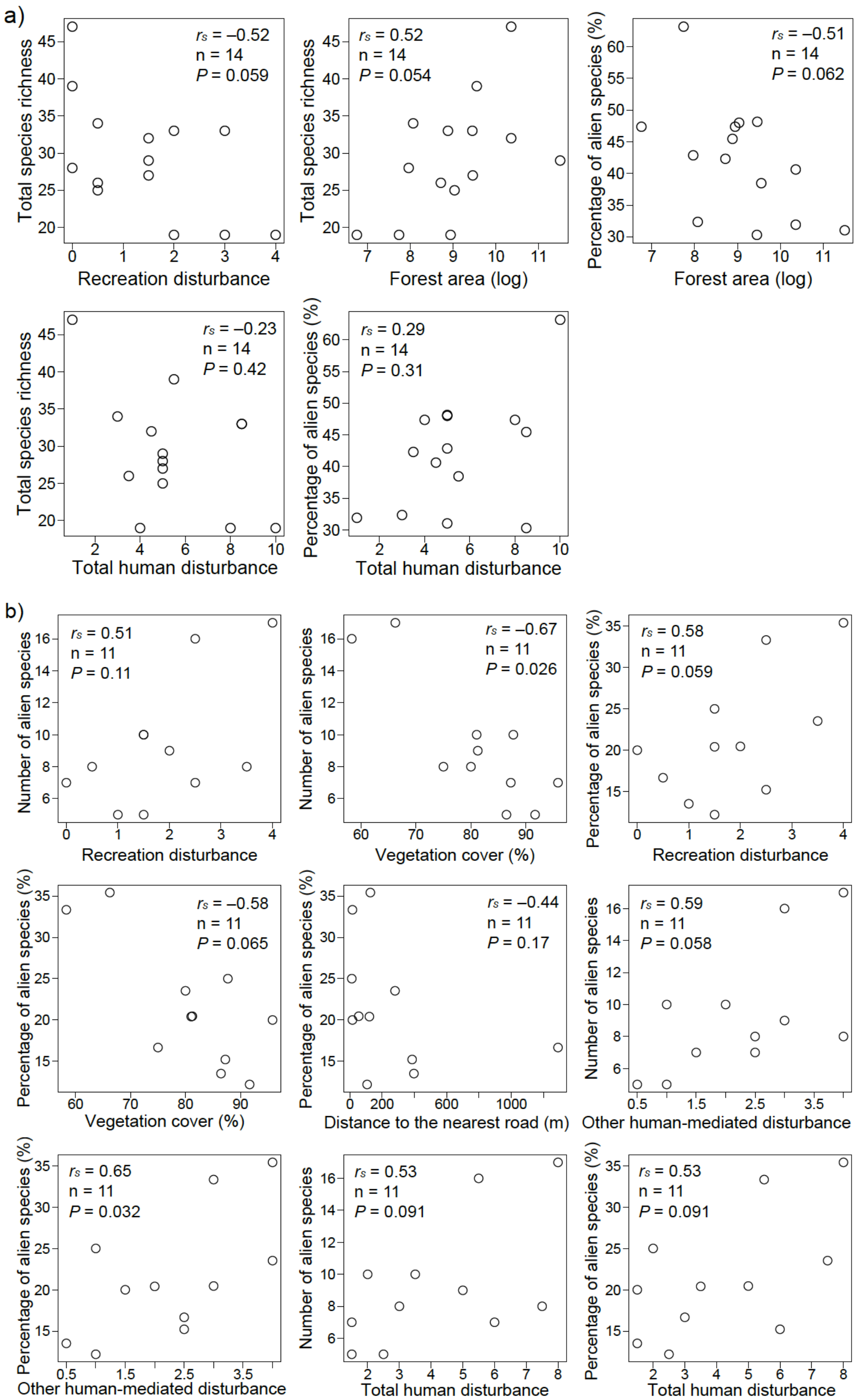

Fig. 3. Total number of plant species, number of alien species and their percentages in relation to recreation disturbance, other human-mediated disturbance and total human disturbance as well as other characteristics of urban (a) and suburban (b) forests in Pavlodar, Kazakhstan. Scatterplots are given for all significant effects of the GLM analyses shown in Table 4.

Table 4
Summary of GLM analyses of the effects of recreation disturbance (a), other human-mediated disturbance (b), and total human disturbance (c) as well as habitat and landscape characteristics (explanatory variables, listed in Appendix A) on the total plant species richness of the ground vegetation, and number and percentage of alien species in urban (n = 14) and suburban forests (n = 11).

	Response variable	Explanatory variables[3]	Urban forests	Suburban forests
a)	Total species richness[1]	Recreation disturbance	**X^2 = 9.51, d.f. = 12, P = 0.002**	X^2 = 0.31, d.f. = 9, P = 0.57
		Forest area^{log}	**X^2 = 5.74, d.f. = 11, P = 0.019**	–
		Vegetation cover	–	X^2 = 2.42, d.f. = 8, P = 0.11
		Shrub density	–	–
		Tree density	–	–
		Build500^{log}	–	–
		Waste500^{log}	–	–
		Grass500^{log}	–	–
	Number of alien species[1]	Recreation disturbance	X^2 = 0.87, d.f. = 12, P = 0.35	**X^2 = 5.67, d.f. = 9, P = 0.017**
		Forest area^{log}	–	–
		Vegetation cover	–	**X^2 = 6.11, d.f. = 8, P = 0.013**
		DistRoad^{log}	–	X^2 = 1.52, d.f. = 7, P = 0.26
		Build500^{log}	–	–
		Traf500^{log}	–	–
		Waste500^{log}	–	–
	Percentage of alien species[2]	Recreation disturbance	F = 4.28, d.f. = 1,12, P = 0.07	**F = 15.62, d.f. = 1,9, P = 0.006**
		Forest area^{log}	F = 4.21, d.f. = 1,11, P = 0.07	–
		Vegetation cover	–	**F = 9.27, d.f. = 1,8, P = 0.013**
		DistRoad^{log}	–	**F = 4.43, d.f. = 1,7, P = 0.026**
		Build500^{log}	–	–
		Traf500^{log}	–	–
		Waste500^{log}	–	–
b)	Total species richness[1]	Other human-mediated disturbance	X^2 = 1.90, d.f. = 12, P = 0.17	X^2 = 0.14, d.f. = 9, P = 0.67
		Forest area^{log}	**X^2 = 7.07, d.f. = 11, P = 0.008**	–
		Vegetation cover	–	–
		Shrub density	–	–
		Tree density	–	–
		Build500^{log}	X^2 = 3.25, d.f. = 10, P = 0.07	–
		Waste500^{log}	–	–
		Grass500^{log}	–	–
	Number of alien species[1]	Other human-mediated disturbance	X^2 = 0.02, d.f. = 12, P = 0.94	**X^2 = 6.27 d.f. = 9, P = 0.012**
		Forest area^{log}	–	–
		Vegetation cover	–	**X^2 = 5.31, d.f. = 8, P = 0.021**

		DistRoad^{log}	–	X^2 = 2.44, d.f. = 7, P = 0.21
		Build500^{log}	–	–
		Traf500^{log}	–	–
		Waste500^{log}	–	–
	Percentage of alien species[2]	Other human-mediated disturbance	F = 2.18, d.f. = 1,12, P = 0.17	**F = 21.34, d.f. = 1,9, P = 0.004**
		Forest area^{log}	**F =7.05, d.f. = 1,11, P = 0.026**	F = 1.52, d.f. = 1,8, P = 0.26
		Vegetation cover	–	**F = 9.66, d.f. = 1,7, P = 0.021**
		DistRoad^{log}	–	**F = 6.77, d.f. = 1,6, P = 0.010**
		Build500^{log}	–	–
		Traf500^{log}	F = 1.49, d.f. = 1,10, P = 0.25	–
		Waste500^{log}	F = 4.37, d.f. = 1,9, P = 0.07	–
c)	Total species richness[1]	Total human disturbance	**X^2 = 5.88, d.f. = 12, P = 0.015**	X^2 = 0.64, d.f. = 9, P = 0.44
		Forest area^{log}	**X^2 = 6.71, d.f. = 11, P = 0.009**	–
		Vegetation cover	–	–
		Shrub density	–	–
		Tree density	–	–
		Build500^{log}	–	–
		Waste500^{log}	–	–
		Grass500^{log}	–	–
	Number of alien species[1]	Total human disturbance	X^2 = 0.09, d.f. = 12, P = 0.64	**X^2 = 8.29, d.f. = 9, P = 0.004**
		Forest area^{log}	–	–
		Vegetation cover	–	X^2 = 2.99, d.f. = 8, P = 0.08
		DistRoad^{log}	–	X^2 = 1.31, d.f. = 7, P = 0.25
		Build500^{log}	–	–
		Traf500^{log}	–	–
		Waste500^{log}	–	–
	Percentage of alien species[2]	Total human disturbance	**F = 9.51, d.f. = 1,12, P = 0.002**	**F = 14.83, d.f. = 1,9, P = 0.006**
		Forest area^{log}	**F =5.74, d.f. = 1,11, P = 0.019**	–
		Vegetation cover	–	–
		DistRoad^{log}	–	F = 4.22, d.f. = 1,8, P = 0.07
		Build500^{log}	–	F = 1.67, d.f. = 1,7, P = 0.24
		Traf500^{log}	–	–
		Waste500^{log}	–	–

[1] GLM with poisson distributed errors
[2] GLM with quasipoisson distributed errors
[3] For a description of the variables see Appendix A
– excluded from the model
Significant results are in bold (P < 0.05)

3.6 Effects of recreation disturbance and other human-mediated disturbances on plant life forms

Results of GLM and ANCOVA revealed that the proportions of species with different plant life form were not affected by recreation disturbance in urban forests (Appendix E). However, the relative abundance of geophyte species was affected by forest area, as was the proportion of therophyte species (Appendix E).

In suburban forests, the relative abundance of geophytes was influenced by the degree of recreation disturbance (Appendix E). Relative abundance of geophytes decreased with increasing recreation disturbance (Fig. 4a). Both the percentages of therophyte species and their relative abundance were influenced by recreation disturbance and the distance to the nearest neighbour forest (Appendix E). The relative abundance of therophytes increased with increasing extent of recreation disturbance (Fig. 4b). Similarly, the percentage of hemicryptophyte species was affected by recreation disturbance and distance to the nearest neighbour forest (Appendix E).

Other human-mediated disturbance influenced the relative abundance of geophytes in urban forests (Appendix F). Furthermore, the relative abundance of geophytes, the percentage of therophyte species and their relative abundance as well the relative abundance of chamaephytes were all influenced by the forest area (Appendix F). The relative abundance of geophytes increased while the percentage of therophyte species decreased with increasing forests area (Fig. 4c and d). In suburban forests, very similar effects of other human-mediated disturbance on geophytes and therophytes were found (Appendix F).

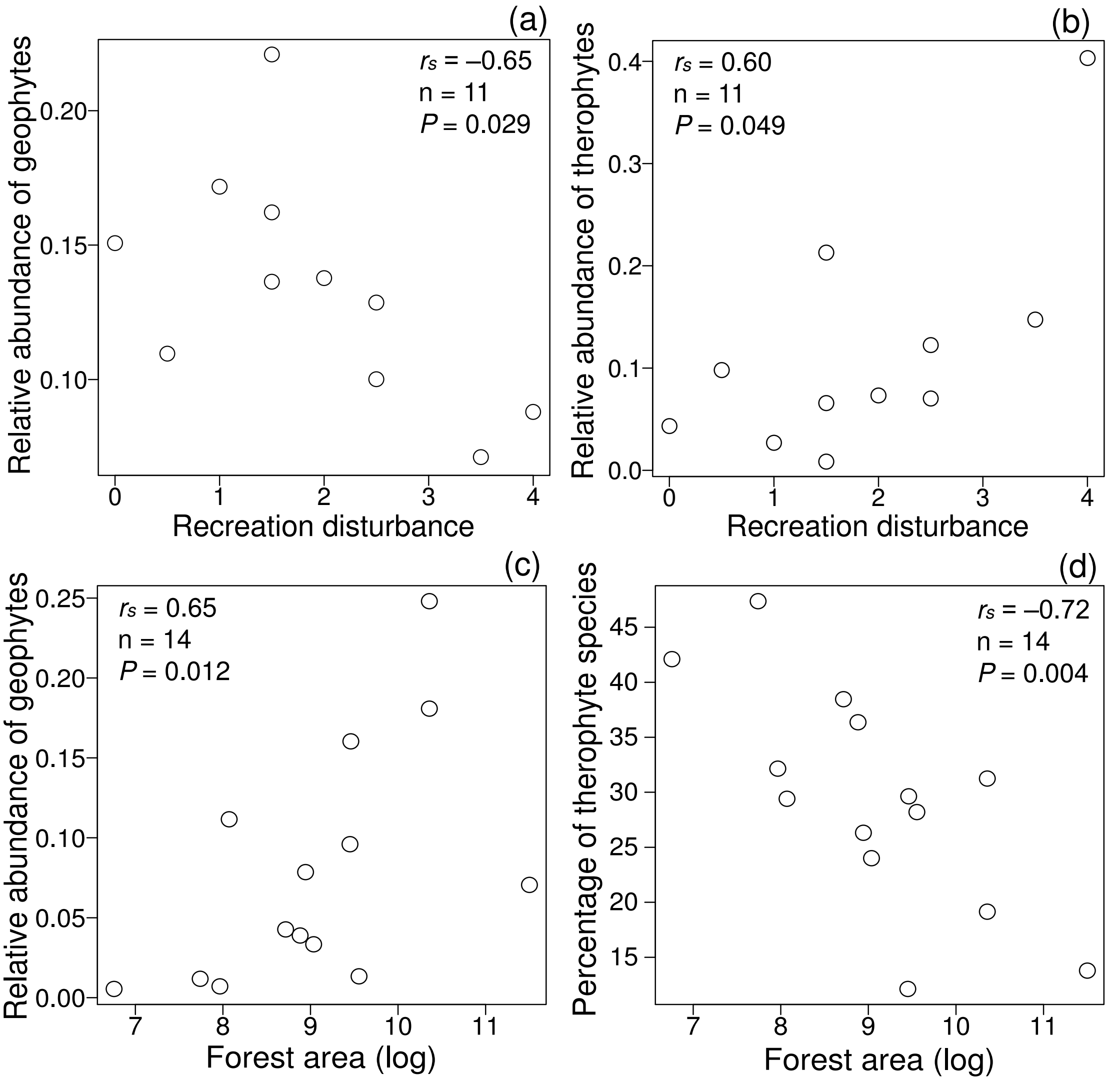

Fig. 4. The relative abundance and percentage of species with different plant life forms in relation to recreation disturbance and forest area: geophytes (a) and therophytes (b) in relation to recreation disturbance in suburban forests; geophytes (c) and therophytes (d) in relation to forest area in urban forests.

4. Discussion

Our study showed that both urban and suburban forests in Pavlodar have important but different functions for recreation. Visitors of the two forest types differed in demographic characteristics and activity, although urban and suburban forests were visited in similar frequencies. Plant species richness and number of alien species were both affected to a different extent by recreation disturbance and other human-mediated disturbance in either forest type, while plant life forms (geophytes and therophytes) were only slightly influenced.

4.1 Frequency and characteristics of visitors

In the residential part of Pavlodar, the urban forest area accounts to 7.0 m^2 per inhabitant. In addition, there is other open green space of 16.5 m^2 per resident available, which corresponds to the rules and normatives of Kazakhstan (12–21 m^2; SNiP RK, 2011). Thus, the area of urban forests per inhabitant is much smaller in Pavlodar than in most European, North American and Australian cities (Dwyer et al., 2000; Konijnendijk et al., 2005; City of Melbourne, 2012). For example, in Berlin there is an average forest area of 45.5 m^2 per resident (SenStadt, 2008). In Pavlodar, scarce green space may partly explain the high recreational pressure on urban forests and the increased use of suburban forest areas.

The differences in demographic characteristics and activities of forest visitors are most probably caused by personal preferences and difference in educational level and cultural and socio-economic background of the urban residents (Heer et al., 2003; Seeland et al., 2009; Edwards et al., 2012). Furthermore, a number of attributes of urban forests including proximity, safety, amenities, aesthetics and features of the vegetation may explain differences in recreational use (Jorgensen et al., 2002; Tyrväinen, 2003; Eriksson et al., 2012). In our study, women visited forests less frequently than men. Women are usually accompanied by children and other adults, which might be a security reason. The majority of visitors crossed the urban forests on their way to work or just spent some time for relaxation, while suburban forests were mainly visited for fishing, picking berries or picnicking (T. Vakhlamova; unpubl. data). Good accessibility was the main motive of forest choice in urban forests and naturalness in suburban forests (T. Vakhlamova; unpubl. data).

In the present study, recreation disturbance at the plot level was positively correlated with the number of picnicking visitors observed per hour in the corresponding urban forests, but not in suburban forests. This could be a result of reduced accessibility to suburban forests, which are flooded for 1–2 months in spring and early summer. Thus, considering the entire year, the total number of forest visitors might be higher in urban than in suburban forests, although we observed similar numbers of visitors per hour in both types of forest between July and September. In contrast, other human-mediated disturbance at the plot level was not correlated with the number of forest visitors observed per hour in either forest type. This can be explained by the way other human-mediated disturbance was measured. Human-mediated disturbance includes types of disturbance (waste deposits, removal of leaf litter) that are not related to the number of forest visitors.

4.2 Effects on plant species richness and alien species

We found that recreation disturbance reduced total plant species richness in urban forests. Similar negative effects on ground vegetation caused by recreation have been reported in other forests (Hobbs, 1988; Malmivaara et al., 2002). Trampling is considered as a major impact leading to soil compaction, altered soil characteristics, reduced plant diversity and changed species composition (Littlemore and Barker, 2001; Amrein et al., 2005; Hamberg et al., 2008; Kissling et al., 2009). In suburban forests, neither recreation disturbance nor other human-mediated disturbance seem to affect plant species richness. In Pavlodar, suburban forests are mainly visited for picnicking, fishing and gathering mushrooms. These activities are restricted to periods of dry soil conditions because of seasonal flooding (see above). In general, the vegetation of floodplain forests is sensitive to trampling (Liddle, 1997; Roovers et al., 2004a). In our study, the impact of recreational activities might be less severe because the suburban forests are mainly visited during dry conditions.

Among the habitat and landscape characteristics examined, only forest area positively influenced plant species richness in urban forests. The species-area relationships found in urban forests has often be an explained by the increased habitat diversity in large forest areas (Guirado et al., 2006; Rosati et al., 2010).

The percentage of alien species found in urban forests in Pavlodar (42.1% of the ground vegetation) was very similar to the one reported in European cities (42.6%; Nielsen et al., 2014). The large number of alien species has been explained by urban-rural gradients in cities (Hansen et al., 2005; Brunzel et al., 2009), in which alien species could occupy new niches owing to their high tolerance towards various stress situations (Lake and Leishman, 2004). It is important to mention that the urban forests examined were not yet mature, and colonization of alien species may still be going on.

In suburban forests, the percentage of alien species was only half compared to that of urban forests, most of the species being annuals. This finding is surprising because riparian forests are usually highly invaded by various alien species (Loewenstein and Loewenstein, 2005; Stoll et al., 2012). However, the propagule pressure of alien species into riparian forests is relatively low in this region due to lack of cargo shipping on the Irtysh river in Kazakhstan and further upstream. The proportion of alien species increased with the degree of other human-mediated disturbance and tended to increase with the degree of recreation disturbance. Species richness of alien plants decreased with increasing vegetation cover in suburban forests. A dense vegetation cover is usually more resistant to the colonization of alien species (Von Holle, 2005; Saccone et al., 2013).

4.3 Effects on plant life forms

Our study showed that urban and suburban forests did not differ in the proportions of plants with different life forms. In urban forests, neither the proportions nor the abundances of the various plant life forms were influenced by recreation disturbance. However, the proportion of therophyte species and the relative abundances of geophytes, therophytes and chamaephytes were all affected by the size of the forest. So far, contrasting findings concerning human impact on plant life forms have been reported, which make any interpretation difficult (McIntyre et al., 1999; Douda, 2010).

In suburban forests, the relative abundance of geophytes decreased and that of therophytes increased with both increasing recreation disturbance and other human-mediated disturbance. Geophyte species are generally resistant to human trampling (Cole, 1995; Liddle, 1997; Hegetschweiler et al., 2009). However, after periods of prolonged trampling, a decline of geophytes has been observed in forests (Roovers et al., 2004b). In our study, severe soil compaction most probably reduced the performance of geophytes. Similar changes in the proportion of therophytes in response to human disturbance have been reported in other studies (Hill et al., 2002; Golivets, 2014). Therophytes may benefit from increasing disturbance in urbanized areas owing to their short life span, high seed production and long-distance dispersal of seeds (Knapp et al., 2009).

Conclusions

Our study showed that the impact of recreation disturbance and other human-mediated disturbances affected the vegetation in urban and suburban forests in a Western Siberian city in a different way. Suburban forests were preferred for longer stays including picnicking. Urban forests were frequently visited on the way to daily work, for doing sport and playing with children. However, degraded urban forest sites might be less attractive. We therefore recommend that city and state authorities should improve management actions in favour of recreation and implement them in urban forests. Regular removal of waste, the construction of some recreation infrastructure (picnic places, playgrounds, off-road trails, benches) as well as the planting of new shrubs and trees are most important. This may reduce negative effects of recreation on the biodiversity of urban forests. In suburban forests, regular waste removal and fire protection are recommended.

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Appendices A–F. Supplementary data

References

Amrein, R., Rusterholz, H.-P., Baur, B., 2005. Disturbance of suburban *Fagus* forests by recreational activities: Effects on soil characteristics, above-ground vegetation and seed bank. Applied Vegetation Science 8, 175–182.

Bolund, P., Hunhammar, S., 1999. Ecosystem services in urban areas. Ecological Economics 29, 293–301.

Braun-Blanquet, J., 1964. Pflanzensoziologie: Grundzüge der Vegetationskunde (Plant Sociology: Broad Vegetation Science). Springer, New York.

Brunzel, S., Fischer, S.F., Schneider, J., Jetzkowitz, J., Brandl, R., 2009. Neo- and archaeophytes respond more strongly than natives to socio-economic mobility and disturbance patterns along an urban–rural gradient. Journal of Biogeography 36, 835–844.

Cilliers, S.S., Siebert, S.J., 2011. Urban flora and vegetation: patterns and processes. In: Niemelä, J., Breuste, J., Elmqvist, T., Guntenspergen, G., James, P., McIntyre, N. (Eds.), Urban Ecology: Patterns, Processes and Applications. Oxford University Press, Oxford, pp. 148–158.

City of Melbourne, 2012. Urban Forest Strategy: Making a Great City Greener 2012–2032. City of Melbourne.

Cole, D.N., 1995. Experimental trampling of vegetation. II. Predictors of resistance and resilience. Journal of Applied Ecology 32, 215–224.

Committee of Statistics of the Republic of Kazakhstan, 2014. Pavlodar region. The official statistical information. Retrieved from http://www.stat.gov.kz/faces/homePage.htm.

Crawley, M.J., 2013. The R Book. 2nd edition, Wiley, Chichester.

Croci, S., Butet, A., George, A., Aguejdad, R., Clergeau, P., 2008. Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. Landscape Ecology 23, 1171–1186.

Douda, J., 2010. The role of landscape configuration in plant composition of floodplain forests across different physiographic areas. Journal of Vegetation Science 21, 1110–1124.

Dwyer, J.F., Nowak, D.J., Noble, M.H., Sisinni, S.M., 2000. Connecting people with ecosystems in the 21st century: an assessment of our nation's urban forests. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland.

Edwards, D., Jay, M., Jensen, F.S., Lucas, B., Marzano, M., Montagné, C., Peace, A., Weiss, G., 2012. Public preferences for structural attributes of forests: Towards a pan-European perspective. Forest Policy and Economics 19, 12–19.

Eriksson, L., Nordlund, A., Olsson, O., Westin, K., 2012. Beliefs about urban fringe forests among urban residents in Sweden. Urban Forestry and Urban Greening 11, 321–328.

Golivets, M., 2014. Ecological and biological determination of invasion success of non-native plant species in urban woodlands with special regard to short-lived monocarps. Urban Ecosystems 17, 291–303.

Guirado, M., Pino, J., Rodà, F., 2006. Understorey plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. Global Ecology and Biogeography 15, 50–62.

Hamberg, L., Lehvävirta, S., Malmivaara-Lämsä, M., Rita, H., Kotze, D.J., 2008. The effects of habitat edges and trampling on understorey vegetation in urban forests in Helsinki, Finland. Applied Vegetation Science 11, 83–98.

Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., Jones, K. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15, 1893–1905.

Heer, C., Rusterholz, H.-P., Baur, B., 2003. Forest perception and knowledge of hikers and mountain bikers in two different areas in Northwestern Switzerland. Environmental Management 31, 709–723.

Hegetschweiler, K.T., van Loon, N., Ryser, A., Rusterholz, H.-P., Baur, B., 2009. Effects of fireplace use on forest vegetation and amount of woody debris in suburban forests in Northwestern Switzerland. Environmental Management 43, 299–310.

Hill, M.O., Roy, D.B., Thompson, K., 2002. Hemeroby, urbanity and ruderality: bioindicators of disturbance and human impact. Journal of Applied Ecology 39, 708–720.

Hill, R., Pickering, C., 2009. Differences in resistance of three subtropical vegetation types to experimental trampling. Journal of Environmental Management 29, 1305–1312.

Hobbs, E.R., 1988. Species richness of urban forest patches and implications for urban landscape diversity. Landscape Ecology 1, 141–152.

Insebaev, T.A., Azerbaev, A.D., Abdrakhmanova, A.D., Randuk, I.V., Shegenova, Z.K., 2007. Павлодарская область: страницы истории (1938–2008) (Pavlodar region: pages of history (1938–2008)). S. Torajgyrov Pavlodar State University, Pavlodar. (In Kazakh and Russian)

Jorgensen, A., Hitchmough, J., Calvert, T., 2002. Woodland spaces and edges: their impact on perception of safety and preference. Landscape and Urban Planning 60, 135–150.

Kazhydromet [National Hydrometeorological Service of the Republic of Kazakhstan], 2011. Retrieved from http://www.kazhydromet.kz.

Kissling, M., Hegetschweiler, K.T., Rusterholz, H.-P., Baur, B., 2009. Short-term and long-term effects of human trampling on above-ground vegetation, soil density, soil organic matter and soil microbial processes in suburban beech forests. Applied Soil Ecology 42, 303–314.

Konijnendijk, C.C., Nilsson, K., Randrup, T.B., Schipperijn, J. (Eds.), 2005. Urban Forests and Trees. Springer, Heidelberg.

Knapp, S., Kühn, I., Bakker, J.P., Kleyer, M., Klotz, S., Ozinga W.A., Poschlod, P., Thompson, K., Thuiller, W., Römermann, C., 2009. How species traits and affinity to urban land use control large-scale species frequency. Diversity and Distributions 15, 533–546.

Lake, J.C., Leishman, M.R., 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation 117, 215–226.

Liddle, M., 1997. Recreation Ecology. The Ecological Impact of Outdoor Recreation and Ecotourism. Chapman & Hall, London.

Littlemore, J., Barker, S., 2001. The ecological response of forest ground flora and soils to experimental trampling in British urban woodlands. Urban Ecosystems 5, 257–276.

Loewenstein, N.J., Loewenstein, E.F., 2005. Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. Urban Ecosystems 8, 79–91.

Malmivaara, M., Löfström, I., Vanha-Majamaa, I., 2002. Anthropogenic effects on understorey vegetation in *Myrtillus* type urban forests in southern Finland. Silva Fennica 36, 367–381.

McIntyre, S., Lavorel, S., Landsberg, J., Forbes, T.D.A., 1999. Disturbance response in vegetation – towards a global perspective on functional traits. Journal of Vegetation Science 10, 621–630.

Nielsen, A.B., van den Bosch, M., Maruthaveeran, S., van den Bosch, K.C., 2014. Species richness in urban parks and its drivers: A review of empirical evidence. Urban Ecosystems 17, 305–327.

Niemelä, J., Breuste, J., Elmqvist, T., Guntenspergen, G., James, P., McIntyre, N. (Eds.), 2011. Urban Ecology: Patterns, Processes and Applications. Oxford University Press, Oxford.

Raunkiaer, C., 1934. The life forms of plants and statistical plant geography/being the collected papers of C. Raunkiaer. Clarendon Press, Oxford.

Roovers, P., Verheyen, K., Hermy, M., Gulinck, H., 2004a. Experimental trampling and vegetation recovery in some forest and heathland communities. Applied Vegetation Science 7, 111–118.

Roovers, P., Baeten, S., Hermy, M., 2004b. Plant species variation across path ecotones in a variety of common vegetation types. Plant Ecology 170, 107–119.

Rosati, L., Fipaldini, M., Marignani, M., Blasi, C., 2010. Effects of fragmentation on vascular plant diversity in a Mediterranean forest archipelago, Plant Biosystems 144, 38–46.

Rusterholz, H.-P., Wirz, D., Baur, B., 2012. Garden waste deposits as a source for non–native plants in mixed deciduous forests. Applied Vegetation Science 15, 329–337.

Saccone, P., Girel, J., Pages J.-P., Brun, J.-J., Michalet, R., 2013. Ecological resistance to *Acer negundo* invasion in a European riparian forest: relative importance of environmental and biotic drivers. Applied Vegetation Science 16, 184–192.

Seeland, K., Dübendorfer, S., Hansmann, R., 2009. Making friends in Zurich's urban forests and parks: The role of public green space for social inclusion of youths from different cultures. Forest Policy and Economics 11, 10–17.

SenStadt [Senate Department for Urban Development], 2008. Berlin Digital Environmental Atlas. Land Use. Retrieved from http://www.stadtentwicklung.berlin.de/umwelt/umweltatlas/eic601.htm.

SNiP RK, 2011. СНиП РК 3.01-01-2008. Градостроительство. Планировка и застройка городских и сельских населенных пунктов (Urban planning. Layout and development of urban and rural communities). (In Russian). Retrieved from http://www.zakon.kz.

Stoll, P., Gatzsch, K., Rusterholz, H.-P., Baur, B., 2012. Response of plant and gastropod species to knotweed invasion. Basic and Applied Ecology 13, 232–240.

Sullivan, J.J., Timmins, S.M., Williams, P.A., 2005. Movement of exotic plants into coastal native forests from gardens in northern New Zealand. New Zealand Journal of Ecology, 29, 1–10.

Swan, C.M., Pickett, S.T.A., Szlavecz, K., Warren, P., Willey, K.T., 2011. Biodiversity and community composition in urban ecosystems: coupled human, spatial, and metacommunity processes. In: Niemelä, J., Breuste, J., Elmqvist, T., Guntenspergen, G., James, P., McIntyre, N. (Eds.), Urban Ecology: Patterns, Processes and Applications. Oxford University Press, Oxford, pp. 179–188.

Tyrväinen, L., Silvennoinen, H., Kolehmainen, O., 2003. Ecological and aesthetic values in urban forest management. Urban Forestry and Urban Greening 1, 135–149.

Vakhlamova, T., Rusterholz, H.-P., Kanibolotskaya, Y., Baur, B., 2014. Changes in plant diversity along an urban–rural gradient in an expanding city in Kazakhstan, Western Siberia. Landscape and Urban Planning 132, 111–120.

Vallet, J., Daniel, H., Beaujouan, V., Rozé, F., Pavione, S., 2010. Using biological traits to assess how urbanization filters plant species of small woodlands. Applied Vegetation Science 13, 412–424.

Von Holle, B., 2005. Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. Journal of Ecology 93, 16–26.

Supplementary material Chapter III

Appendix A. Table: List of habitat and landscape variables used in GLM and ANCOVA analyses

Appendix B. Table: Habitat and landscape characteristics of urban and suburban forests in Pavlodar, Kazakhstan

Appendix C. Table: Classification system to assess recreation disturbance and other human-mediated disturbance

Appendix D. Table: Vegetation parameters of urban and suburban forests in Pavlodar, Kazakhstan

Appendix E. Table: Summary of GLM analyses of the effects of recreation disturbance and habitat and landscape characteristics (explanatory variables, listed in Appendix A) on plant life form (Raunkiaer, 1934)

Appendix F. Table: Summary of GLM and ANCOVA analyses of the effects of other human-mediated disturbance (OHMD) and habitat and landscape characteristics (explanatory variables, listed in Appendix A) on plant life form (Raunkiaer, 1934)

Appendix A

List of habitat and landscape variables used in GLM and ANCOVA analyses.

Variables codes	Definition
Habitat characteristics:	
DistForest	Distance from forest edge to nearest other forest (m)
DistBuild	Distance from forest edge to nearest built-up area (m)
DistRoad	Distance from forest edge to nearest road (m)
DistWater	Distance from forest edge to nearest water body (river, stream; in m)
Landscape characteristics:	Cover (in %) of different landscape elements within a radius of 200 m and 500 m around the most central sampling plot
Build200/Build500	built-up area – including residential areas and industrial buildings
Traf200/Traf500	traffic infrastructure – roads, railway trails, parking areas and pedestrian paths
Waste200/Waste500	wasteland – trampled spots, industrial land, landfills and waste deposits, salted and eroded patches and other spots with bare soil
Crop200/Crop500	cropland – arable fields and private gardens
Forest200/Forest500	forest area – planted and natural occurrences of trees and bushes
Grass200/Grass500	grassland – unwooded natural remnants (occasionally grazed pastures and abandoned pastures), floodplains, lawns
Water200/Water500	water surface area – river Irtysh and small channels and ditches

Accuracy of distance measures are 10 m, that of cover variables 5%

Appendix B

Habitat and landscape characteristics of urban and suburban forests in Pavlodar, Kazakhstan.

Variables	Urban forests (n = 14)		Suburban forests (n = 11)		Wilcoxon rank-sum test
	Mean	Range	Mean	Range	
Distance to the nearest built-up area (m)	163	15–1,110	382	28–1,220	***W* = 35.0, *P* = 0.023**
Distance to the nearest road (m)	11	2–35	255	12–1,290	***W* = 9.5, *P* < 0.001**
Distance to the nearest water body (m)	1,508	0.5–3,533	169	1–693	***W* = 126.0, *P* = 0.008**
Distance to the nearest neighbour forest (m)	1,162	90–3,590	516	8–5,420	***W* = 139.0, *P* < 0.001**
Cover of built-up area (in %) [1]	18	0–40	9	0–40	*W* = 96.5, *P* = 0.29
Cover of traffic infrastructure (in %) [1]	13	5–25	5	0–10	***W* = 132.0, *P* = 0.001**
Wasteland cover (in %) [1]	6	0–25	1	0–10	*W* = 100.5, P = 0.13
Cropland cover (in %) [1]	24	0–65	4	0–35	*W* = 107.5, *P* = 0.055
Forest cover (in %) [1]	18	10–25	33	15–45	***W* = 15.0, *P* < 0.001**
Grassland cover (in %) [1]	14	5–40	26	5–50	***W* = 34.0, *P* = 0.018**
Water surface area (in %) [1]	6	0–40	22	0–50	***W* = 33.0, *P* = 0.011**

[1] within a radius of 500 m around the most central sampling plot

Appendix C

Classification system to assess recreation disturbance and other human-mediated disturbance.

	Type of disturbance	Degree of disturbance			
		Absent (0)	Low (1)	Moderate (2)	High (3)
Recreation disturbance	Trampling (cover of footpaths in %)	0	< 5%	5–25%	> 25%
	Damage to ground vegetation (area of picnic places in %)	0	< 5%	5–25%	> 25%
	Damage to trees and shrubs (yellowing and fall of leaves in % of branches[1])	0	< 5% (no dead branches)	5–25% (no dead branches)	> 25% (dead branches)
Other human-mediated disturbance	Domestic/ building waste deposits (cover of the plot in %)	0	< 1%	1–5%	> 5%
	Soil disturbance (traces of digging and former building activity)	0	< 1%	1–5%	> 5%
	Removal of leaf litter layer (reduction of leaf litter in the plot in %)	0	< 5%	5–25%	> 25%
	Ground fire	0	Traces of burned spots	Small burned spots	Large burned areas

Data were collected in six plots in each forest

[1] Seasonal changes in leaf colour usually occurred after our assessment

Appendix D

Vegetation parameters of urban and suburban forests in Pavlodar, Kazakhstan.

Forest type	Total species richness of ground vegetation	Total number of alien species	Percentage of alien species (%)	DBH of trees (cm)
Urban forests (n = 14)	29.3 ± 2.1 (19–47)	11.9 ± 0.6 (9–15)	42.1 ± 2.4 (30.3–63.2)	29.9 ± 2.1 (22.6–52.6)
Suburban forests (n = 11)	42.7 ± 1.7 (34–49)	9.3 ± 1.2 (5–17)	21.4 ± 2.3 (12.2–35.4)	39.9 ± 3.4 (26.5–61.8)

Mean values ± S.E. are given with ranges in parentheses.

Appendix E

Summary of GLM analyses of the effects of recreation disturbance and habitat and landscape characteristics (explanatory variables, listed in Appendix A) on plant life form (Raunkiaer, 1934).

Response variables	Explanatory variables[1]	Urban forests		Suburban forests	
		Proportion of species[2]	Relative abundance[2]	Proportion of species[2]	Relative abundance[2]
Geophytes	Recreation disturbance	$F_{1,12}$ = 0.97, P = 0.37	$F_{1,12}$ = 0.51, P = 0.49	$F_{1,9}$ = 0.26, P = 0.62	**$F_{1,9}$ = 6.87, P = 0.034**
	Forest area	$F_{1,11}$ = 3.66, P = 0.09	**$F_{1,11}$ = 5.53, P = 0.040**	–	–
	DistForest	–	–	–	–
	Build500	–	–	$F_{1,8}$= 2.62, P = 0.14	$F_{1,8}$ = 1.47, P = 0.26
	Traf500	$F_{1,10}$ = 4.34, P = 0.07	$F_{1,10}$ = 1.58, P = 0.24	–	$F_{1,7}$= 4.20, P = 0.08
	Forest500	–	–	–	–
Therophytes	Recreation disturbance	$F_{1,12}$ = 0.91, P = 0.36	$F_{1,12}$ = 4.09 P = 0.08	**$F_{1,9}$ = 24.60, P = 0.004**	**$F_{1,9}$ = 23.41, P = 0.003**
	Forest area	**$F_{1,11}$ = 11.39, P = 0.007**	$F_{1,11}$ = 3.81, P = 0.09	–	$F_{1,8}$ = 1.80, P = 0.37
	DistForest	–	$F_{1,10}$ = 1.49, P = 0.26	**$F_{1,8}$ = 15.45, P = 0.011**	**$F_{1,7}$ = 10.83, P = 0.017**
	Build500	$F_{1,10}$ = 1.33, P = 0.28	$F_{1,9}$ = 3.21, P = 0.11	$F_{1,7}$ = 5.79, P = 0.06	–
	Traf500	–	$F_{1,8}$ = 2.77, P = 0.13	$F_{1,6}$ = 1.34, P = 0.30	$F_{1,6}$ = 2.26, P = 0.19
	Forest500	–	–	$F_{1,5}$ = 1.57, P = 0.24	–
Hemicrypto-phytes	Recreation disturbance	$F_{1,12}$ = 1.15, P = 0.31	$F_{1,12}$ = 2.39, P = 0.16	**$F_{1,9}$ = 12.87, P = 0.007**	$F_{1,9}$ = 4.21, P = 0.08
	Forest area	$F_{1,11}$ = 2.98, P = 0.11	–		$F_{1,8}$ = 2.65, P = 0.15
	DistForest	–	$F_{1,11}$ = 1.50, P = 0.25	**$F_{1,8}$ = 5.78, P = 0.042**	$F_{1,7}$ = 1.47, P = 0.27
	Build500	–	$F_{1,10}$ = 2.19, P = 0.17	–	–
	Traf500	–	$F_{1,9}$ = 2.28, P = 0.17	–	$F_{1,6}$ = 2.55, P = 0.16
	Forest500	–	–	–	–
Chamaephytes	Recreation disturbance	$F_{1,12}$ = 0.65, P = 0.44	$F_{1,12}$ = 0.32, P = 0.59	$F_{1,9}$ = 1.27, P = 0.28	$F_{1,9}$ = 0.02, P = 0.90
	Forest area	$F_{1,11}$ = 1.02, P = 0.34	$F_{1,11}$ = 4.07, P =0.07	–	$F_{1,8}$ = 1.70, P = 0.24
	DistForest	$F_{1,10}$ = 4.65, P = 0.06	$F_{1,10}$ = 2.99, P = 0.11	–	$F_{1,7}$= 3.45, P = 0.10
	Build500	$F_{1,9}$ = 1.68, P = 0.24	–	–	–
	Traf500	–	$F_{1,9}$ = 2.84, P = 0.13	–	$F_{1,6}$= 3.77, P = 0.10
	Forest500	$F_{1,8}$ = 1.89, P = 0.21	–	–	–

[1] For a description of the variables see Appendix A
The variables Forest area, DistForest, Build500, Traf500 and Forest500 were all log-transformed
[2] GLM, quasipoisson distributed errors
– excluded from the model
Significant results are in bold (P < 0.05)

Appendix F

Summary of GLM and ANCOVA analyses of the effects of other human-mediated disturbance (OHMD) and habitat and landscape characteristics (explanatory variables, listed in Appendix A) on plant life form (Raunkiaer, 1934).

Response variables	Explanatory variables[1]	Urban forests		Suburban forests	
		Proportion of species[2]	Relative abundance[2]	Proportion of species[2]	Relative abundance[3]
Geophytes	OHMD	$F_{1,12} = 0.73$, $P = 0.41$	**$F_{1,12} = 12.55$, $P = 0.004$**	$F_{1,9} = 0.37$, $P = 0.56$	**$F_{1,9} = 32.52$, $P < 0.001$**
	Forest area	–	**$F_{1,11} = 8.22$, $P = 0.015$**	–	–
	DistForest	–	–	–	–
	Build500	–	–	$F_{1,8} = 2.47$, $P = 0.15$	–
	Traf500	–	–	–	–
	Forest500	–	–	–	–
Therophytes	OHMD	$F_{1,12} = 0.09$, $P = 0.77$	$F_{1,12} = 2.05$, $P = 0.19$	$F_{1,9} = 4.52$, $P = 0.08$	**$F_{1,6} = 17.09$, $P = 0.006$**
	Forest area	**$F_{1,11} = 119.5$, $P = 0.005$**	**$F_{1,11} = 5.19$, $P = 0.049$**	$F_{1,8} = 3.08$, $P = 0.12$	**$F_{1,6} = 9.23$, $P = 0.022$**
	DistForest	–	$F_{1,10} = 2.44$, $P = 0.15$	**$F_{1,7} = 9.79$, $P = 0.020$**	**$F_{1,6} = 19.33$, $P = 0.005$**
	Build500	–	–	$F_{1,6} = 2.85$, $P = 0.14$	–
	Traf500	–	$F_{1,9} = 3.13$, $P = 0.11$	–	$F_{1,6} = 1.89$, $P = 0.22$
	Forest500	–	–	–	–
Hemicrypto-phytes	OHMD	$F_{1,12} = 1.82$, $P = 0.22$	$F_{1,12} = 0.36$, $P = 0.55$	$F_{1,9} = 2.82$, $P = 0.14$	$F_{1,7} = 0.74$, $P = 0.42$
	Forest area	$F_{1,11} = 2.31$, $P = 0.17$	–	$F_{1,8} = 1.55$, $P = 0.25$	$F_{1,7} = 5.21$, $P = 0.06$
	DistForest	$F_{1,10} = 2.31$, $P = 0.17$	$F_{1,11} = 1.38$, $P = 0.27$	$F_{1,7} = 4.54$, $P = 0.07$	$F_{1,7} = 1.31$ $P = 0.28$
	Build500	–	$F_{1,10} = 2.22$, $P = 0.16$	–	–
	Traf500	–	–	–	–
	Forest500	–	–	–	–
Chamaephytes	OHMD	$F_{1,12} = 1.51$, $P = 0.24$	$F_{1,12} = 2.63$, $P = 0.13$	$F_{1,9} = 1.19$, $P = 0.30$	$F_{1,5} = 0.01$, $P = 0.97$
	Forest area	–	**$F_{1,11} = 5.70$, $P = 0.041$**	–	$F_{1,5} = 1.30$, $P = 0.31$
	DistForest	–	$F_{1,10} = 1.88$, $P = 0.20$	–	$F_{1,5} = 3.47$, $P = 0.12$
	Build500	$F_{1,11} = 3.13$, $P = 0.10$	–	–	–
	Traf500	–	$F_{1,9} = 3.74$, $P = 0.09$	–	$F_{1,5} = 4.64$, $P = 0.08$
	Forest500	–	–	–	$F_{1,5} = 1.80$, $P = 0.24$

[1] For a description of the variables see Appendix A
The variables Forest area, DistForest, Build500, Traf500 and Forest500 were all log-transformed
[2] GLM, quasipoisson distributed errors
[3] ANCOVA
– excluded from the model
Significant results are in bold ($P < 0.05$)

GENERAL DISCUSSION

The present thesis examined the impacts of urban growth on original ecosystems in a Western Siberian city. As it was assumed in the research questions and hypotheses, the recent degradation of landscape due to land-use change and enforced urban growth influenced significantly local plant diversity in the city of Pavlodar and its surroundings. In particular, the consequences of urban expansion affected plant species richness and their abundances, the number and proportion of alien species and plant species characteristics in this region. The findings presented in this thesis showed that the components of urbanization are threatening native biodiversity. Harsh climatic conditions contributed to the specific character of changes in plant communities under the urban impact.

In **Chapter I**, I investigated whether plant diversity was altered along an urban–rural gradient under the impacts of land use change, disturbance and landscape and habitat features. I found a significant increase of local plant diversity (expressed as species richness and Shannon diversity index) with increasing distance from the city centre. Contrasting findings of a high species richness in cities were reported in other studies (Kühn et al., 2004; Zerbe et al., 2004; Knapp, 2010). I explained my results by the lack of habitat heterogeneity, short historical development of the city centre and the small species pool in the study region. Similarly, the results in **Chapter II** showed a lower soil seed species diversity in roadside verges in the city area than in the rural surroundings. Furthermore, in **Chapter III** I reported the degradation of urban forests, situated close to the city centre. Considering urban forests, the results showed that the decrease of plant species richness in these ecosystems was caused by recreation disturbance. The results presented in the **Chapter III** underlined the negative effect of tramping as a component of recreation disturbance on plant diversity. I conclude that the fact of the reduction in plant species richness in the city core may indicate the high sensibility of local plant communities to urban changes in this region as well as the wrong management of urban ecosystems.

I found an increased number of alien species close the centre of the city (**Chapters I, II and III**). The effect of urbanity enhancing the proportion of alien species was closely related to the influence of traffic infrastructure. The proximity of roads (**Chapter I and Chapter III**) and road type (**Chapter II**) influenced the colonization success of alien plants. We demonstrated national roads with high traffic density to be important pathways for the introduction of alien species. Similar findings from other studies underlined the key role of traffic density in the establishment of alien species in roadside verges (see for example Joly et al., 2011). Furthermore, the dispersal of alien species over large distances by vehicles was recently approved (Taylor et al., 2012). In this Western Siberian region, passenger and cargo transports from remote biogeographical regions through national roads provide opportunities for the introduction of alien plants.

Among the other factors promoted the high density of alien species in the study area, human disturbance and recreational use enhanced the number and proportion of alien species in suburban forests in Pavlodar (**Chapter III**). Owing to frequent disturbance from picnicking visitors, trampling, damage to ground vegetation, shrubs and trees, the change in species composition is going on in these forests. Similar negative effects on plant diversity caused by recreation pressure have been reported in other forests (Amrein et al., 2005; Hamberg et al., 2008). Being tolerant to various stress situations, alien species occupy new niches in disturbed habitats (Lake and Leishman, 2004). Furthermore, in urban areas numerous horticultural species contribute to the abundance of alien flora (Hodkinson and Thompson, 1997). Therefore, land-use type influenced the proportion of alien species in my study presented in **Chapter I**.

The factors that positively affected diversity of native plant species in my studies included the extent of vegetation cover and the area of the investigated forest patch **(Chapter III)**. In **Chapter III**, species richness of alien plants decreased with increasing vegetation cover. An intact urban vegetation cover was reported to support natural diversity in the communities (Aronson et al., 2014). Moreover, a dense vegetation cover is usually more resistant to the colonization of alien species (for example Von Holle, 2005). Furthermore, I found an increase of total plant species richness and a decrease of the proportion of alien species with increasing forest area. The positive effect of patch size on biodiversity has been frequently reported in other studies (Hobbs, 1988; Beninde et al., 2015).

Distribution of plant species along the gradient of urbanization might be connected with characteristics of species. Plants' life forms and evolutionary strategies may determine their ability to persist under urban conditions (Lososová et al., 2006; Knapp et al., 2009). In my study, the therophyte life form was found to enable plant species to cope with the city's environment (**Chapters I**, **II and III**). Therophyte plant species seemed to benefit from human disturbance, land-use change and even specific roadside conditions. Short life span, high seed production and long-distance dispersal of seeds of therophytes may lead to further spread of these species in the study area. In contrast, the geophyte life form was negatively influenced by urban expansion (**Chapter I, Chapter III**). This finding contradicts the assumption of general resistance of geophytes to human disturbance (Liddle, 1997). The vulnerability of geophyte species may lead to the local extinction of these plants in the future in urban settings of the study region.

Implications and Outlook

As urbanization is unlikely to stop, recently many efforts are applied to develop a strategy for protecting biodiversity within urbanized areas (Knapp, 2010). Based on my principal findings, I formulate recommendations to prevent further anthropogenic degradation of original ecosystems in the urban areas of the region:

– reduce the disturbance of the vegetation cover, which could prevent the invasion of alien plants;

– conserve the leaf litter layer containing viable seeds of plants;

– improve the management of urban forests, providing some recreation infrastructure such as picnic places, playgrounds, benches and removing waste;

– protect soil against trampling (enclosure, off-road trails);

– restore degraded forests patches by planting new trees and shrubs.

These actions could pave the way towards further sustainable development of urban ecosystems in the study region. The principal message of this thesis is that there is an urgent need to reduce the impact of the growing city on biodiversity. Despite the negative effects of urbanization processes on ecosystem functioning, “ecologically sustainable urbanization” might become real, providing benefit for people.

References

Amrein, R., Rusterholz, H.-P., Baur, B., 2005. Disturbance of suburban *Fagus* forests by recreational activities: Effects on soil characteristics, above-ground vegetation and seed bank. Appl Veg Sci 8, 175–182.

Aronson, M. F., La Sorte, F. A. Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S. G., Cilliers, S., Clarkson, B. et al., 2014. A global analysis of the impact of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proc R Soc B 281, 1–8.

Beninde, J., Veith, M., Hochkirch, A., 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. Ecol Lett 18, 581–592.

Hamberg, L., Lehvävirta, S., Malmivaara-Lämsä, M., Rita, H., Kotze, D. J., 2008. The effects of habitat edges and trampling on understorey vegetation in urban forests in Helsinki, Finland. Appl Veg Sci 11, 83–98.

Hobbs, E. R., 1988. Species richness of urban forest patches and implications for urban landscape diversity. Landsc Ecol 1, 141–152.

Hodkinson, D. J., Thompson, K., 1997. Plant dispersal: the role of man. J Appl Ecol 34, 1484–1496.

Joly, M., Bertrand, P., Gbangou, R. Y., White, M.-C., Dubé, J., Lavoie, C., 2011. Paving the way for invasive species: road type and the spread of common ragweed (*Ambrosia artemisiifolia*). Environ Manage 48, 514–522.

Lake, J. C., Leishman, M. R., 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biol Conserv 117, 215–226.

Liddle, M., 1997. Recreation Ecology. The Ecological Impact of Outdoor Recreation and Ecotourism. Chapman & Hall, London.

Lososová, Z., Chytrý, M., Kühn, I., Hájek, O., Horáková, V., Pyšek, P., Tichý, L., 2006. Patterns of plant traits in annual vegetation of man-made habitats in central Europe. Perspect Plant Ecol Evol Syst 8, 69–81.

Knapp, S., Kühn, I., Bakker, J. P., Kleyer, M., Klotz, S., Ozinga W. A., Poschlod, P., Thompson, K., Thuiller, W., Römermann, C., 2009. How species traits and affinity to urban land use control large-scale species frequency. Divers Distrib 15, 533–546.

Knapp, S., 2010. Plant Biodiversity in Urbanized Areas. VIEWEG + TEUBNER, GWV

Fachverlage GmbH, Wiesbaden.

Kühn, I., Brandl, R., Klotz S., 2004. The flora of German cities is naturally species rich. Evol Ecol Res 6, 749–764.

Taylor, K., Brummer, T., Taper, M. L., Wing, A., Rew, L. J., 2012. Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Diversity Distrib 18, 942–951.

Von Holle, B., 2005. Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. J Ecol 93, 16–26.

Zerbe, S., Maurer, U., Peschel, T., Schmitz, S., Sukopp, H., 2004. Diversity of flora and vegetation in European cities as a potential for nature conservation in urban-industrial areas – with examples from Berlin and Potsdam (Germany). In Shaw, W. W., Harris, L. K., VanDruff, L. Urban Wildlife Conservation, 35–49.

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Scientific publications (peer-reviewed)

Vakhlamova T, Rusterholz H-P, Kanibolotskaya Y, Baur B (2014) Changes in plant diversity along an urban–rural gradient in an expanding city in Kazakhstan, Western Siberia. *Landscape and Urban Planning* 132:111–120

Vakhlamova T, Rusterholz H-P, Kamkin V, Baur B (2015) Recreational activities in urban and suburban forests in a Western Siberian city alter the local plant diversity. *Urban Forestry and Urban Greening* (submitted)

Vakhlamova T, Rusterholz H-P, Kanibolotskaya Y, Baur B (2015) Effects of road type and urbanization on the diversity and abundance of alien species in roadside verges in Western Siberia. *Plant ecology* (submitted)

Scientific publications in local journals

Vakhlamova T, Almishev U (2007) Application of rotational grazing of horses in Kazakhstan and Mongolia. Materials of International scientific practical conference *Kazakhstan and the World Languages*, PSU after S. Toraigyrov, Pavlodar, 106–111 (in English)

Vakhlamova TA, Almishev UX (2007) Ecology of horse breeding in Central Asia. Nikonov's readings-2007. Russian University of agricultural problem named after Nikonov, Moscow, 47–49 (in Russian)

Vakhlamova TA (2007) Horse breeding in the steppe zone of Mongolia. 3rd International scientific practical conference *Actual problems of veterinary medicine and agricultural biotechnology*, Innovat. Euras. Uni, Pavlodar, 89–93 (in English)

Vakhlamova TA, Sherbakova MA (2005) Influence of «Baykal EM-1» on the recovery of soil contaminated by hydrocarbons. Materials of *Satpaev's readings V*. PSU after S. Torajgyrov, Pavlodar, 31–35 (in Russian)

Kulbezekova DV, Vakhlamova TA (2004) Reaction of plants on the contamination of soil by hydrocarbons. Materials of *Satpaev's readings IV*. PSU after S. Torajgyrov, Pavlodar, 79–84 (in Russian)

Vakhlamova TA (2004) Stimulation of restoration processes in soil contaminated by hydrocarbons. Materials of 9th international ecological conference "Ecology of Russia and adjacent areas". Novosibirsk State University, Russia, 169–171 (in Russian)

Talks at conferences

Vakhlamova T, Baur B, Rusterholz H-P, "Changes in plant diversity along urban-rural land-use gradients in Kazakhstan, Western Siberia", at *PACE 14*, Geneva, February 2014

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