

RESEARCH ARTICLE

Urban plant diversity in Kazakhstan: Effects of habitat type, city size and macroclimate

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Abstract

Questions: Urbanisation has accelerated the spread of alien and apophytic species around the world including the drylands of continental inland Asia. However, few studies have examined the patterns and drivers of urban plant diversity in this region. We ask how habitat type, city size and macroclimate affect species richness and composition of alien, apophytic and non-apophytic indigenous plants in cities of the steppe and forest-steppe zones of Kazakhstan.

Location: Ten cities in central and northeastern Kazakhstan, Middle Asia.

Methods: Using a standardized sampling protocol, we recorded spontaneously occurring vascular plant species in 1-ha plots in seven habitat types (central square, boulevard, residential area, park, early-successional vacant site, mid-successional vacant site and railway station) in five large (>100,000 inhabitants) and five small (<100,000 inhabitants) cities. We used linear mixed-effect models to quantify the effects of habitat type, city size and macroclimate on species richness and the proportion of alien, apophytic and non-apophytic indigenous plants.

Results: Plant species richness differed significantly among habitat types, with the lowest richness in central squares, and the highest in railway stations and residential areas. Apophytic species were most numerous in railway stations and alien species in residential areas. The richness of alien, apophytic and non-apophytic indigenous species varied more among habitats than among cities. The proportion of apophytes increased linearly with annual precipitation. The largest differences in species composition were between disturbed sites in city centres (squares, boulevards and parks) and early-successional, mid-successional and railway station sites. Large and small cities also differed in species composition.

Conclusions: Plant diversity in cities of northern Kazakhstan depends mainly on habitat type and less on macroclimate. Overall, cities in inland continental Asia follow patterns of urban species diversity observed in other Asian and European cities.

KEYWORDS

alien plant, apophyte, biodiversity, biological invasions, Middle Asia, non-native species, species composition, urban ecology, urban habitats, vascular plants, vegetation



1 | INTRODUCTION

Urban ecosystems comprise diverse plant communities, which provide various ecosystem services to citizens (Taylor & Hochuli, 2015; Aronson et al., 2017) and often encompass species-rich assemblages (Kühn et al., 2004; Aronson et al., 2014). Numerous empirical works have examined the environmental factors that determine plant species richness and composition in cities. For example, plant diversity in urban habitats varies depending on the degree and type of disturbance, proportion of hard surfaces, presence of ornamental plantings, and exposure to pollution (Lososová et al., 2011; Melliger et al., 2017; Guarino et al., 2021). Future development of biodiversity-friendly cities requires an understanding of diversity patterns in urban habitats (Oliver et al., 2015; Swan et al., 2021).

In parallel with natural communities, larger cities tend to have higher numbers of plant species (Pyšek, 1998), following the species-area relationship (Rosenzweig, 2003). Moreover, city size and the associated degree of urbanisation can be correlated with plant diversity in particular habitats. For example, residential areas and older successional sites had higher species richness than other habitats in large, but not in small, cities in central Europe (Čeplová et al., 2017). It has also been shown that larger cities tend to have a higher proportion of alien species (Pyšek, 1998; Zerbe et al., 2003; Stešević et al., 2009).

In this context, researchers have started to explore changes in species composition across cities, particularly how alien species influence these patterns (Kühn et al., 2017; Szumańska et al., 2021). The proportion of native to alien species can be used as an indicator of anthropogenic degradation in urban habitats (Lososová et al., 2012a; Rendecková et al., 2019) because alien plant species can degrade natural habitats, deteriorate ecosystem services, impair human health (Nentwig et al., 2017), cause significant economic losses and impose management costs (Diagne et al., 2020), homogenise urban floras (Trentanovi et al., 2013; Zisenis, 2015) and cause local species extinctions (Padullés Cubino et al., 2022).

Another widespread group of urban species are native ruderal plants, which are usually associated with high levels of human disturbance. This group, known as apophytes, occurs mostly in anthropogenic habitats and rarely in natural vegetation. In contrast, vegetation dominated by native species without apophytes prevails in natural areas and rarely occurs in anthropogenic landscapes. The role of apophytes relative to native, non-apophytic species in urban floras has been poorly studied (Sukopp, 2006), although apophytes can rapidly colonise urban habitats because they tolerate a wide range of disturbances (Hill et al., 2002). Therefore, it is essential to know which factors favour the occurrence of native, non-apophytic species (hereafter called 'indigenous species') in urban areas.

Despite the predominant role of anthropogenic factors in determining urban plant diversity, climatic conditions can also influence urban vegetation (Aronson et al., 2014; Kalusová et al., 2019). Previous studies have shown that plant species richness and composition in urban areas are affected by the same climatic factors as the floras of natural habitats (Kalusová et al., 2019; Padullés Cubino et al., 2019). While some studies show that climate is an important determinant of

species composition in urban habitats (Thompson et al., 2004), others demonstrate that anthropogenic factors have the greatest influence on urban plant diversity (La Sorte et al., 2014; Čeplová et al., 2017).

To clarify the importance of climate versus anthropogenic factors, a series of comparative studies using standardized sampling protocols was conducted to quantify plant diversity in different urban habitats across several cities in Europe and North America (Celesti Grapow & Blasi, 1998; Loram et al., 2008; Lososová et al., 2011, 2012a, 2012b, 2018; Čeplová et al., 2017; Kalusová et al., 2017; Glišić et al., 2021). In Asia, urban biodiversity studies have been conducted mainly in the southeast regions of the continent (e.g., Su et al., 2021; Cheng et al., 2022), while studies in continental inland Asia have considered urban plant communities mainly for syntaxonomic classification of ruderal vegetation (Klimeš, 1989), development of phytoremediation techniques for industrial sites (Shilova, 1989), or urban greening and planning (Vakhlamova et al., 2016; Ishankulova et al., 2021). Consequently, very few global reviews have included the urban vegetation of continental Asia (Ruan et al., 2019; Li et al., 2020) or examined the factors that affect plant diversity and composition in cities of this region. Although urban floras in continental inland Asia have been comparatively little studied, we can assume that they differ from urban floras in other regions for several reasons. First, the region's harsh climate could act as a strong environmental filter on species composition. In addition, as landlocked countries in inland Asia were part of the Soviet Union, where trade and human migration were restricted, their urban floras may have faced an invasion debt, with a low proportion of non-native plant species (Lazkov & Sennikov, 2014). However, as these countries lifted many travel and trade restrictions in the early 1990s, this trend may be reversing, as has been reported for eastern Russia (Tret'yakov et al., 2019; Sutkin, 2021).

In this study, we aim to fill the knowledge gap on urban floras in continental inland Asia by conducting a field survey based on a standardised sampling protocol. Specifically, we examine the patterns and drivers of species richness and composition of vascular plants in different urban habitats in cities of central and northeastern Kazakhstan. We focus on the effects of habitat type, city size and macroclimate on the richness and composition of alien, apophytic and indigenous species. We expect that: (1) plant species richness and the number and proportion of alien, apophytic and indigenous species vary across urban habitat types, reflecting the degree of disturbance in these habitats; (2) city size and macroclimate contribute to variation in urban plant species richness; and (3) species composition varies in response to habitat type, city size and macroclimate.

2 | METHODS

2.1 | Data collection

We conducted our study in urban habitats of 10 cities in the steppe and forest-steppe zones of central and northeastern Kazakhstan (Figure 1). We considered five large and five small cities (Appendix S1) and chose a threshold of 100,000 inhabitants to distinguish large

from small cities following Čeplová et al. (2017). The study area has a strongly continental climate, with average annual precipitation sums between 250 and 317 mm, a mean annual temperature of 2.5°C, an absolute minimum temperature of −51.6°C and an absolute maximum temperature of 42.5°C across the studied cities (WorldClim data; Fick & Hijmans, 2017). The 10 cities studied in central and northeastern Kazakhstan reflect the typical history of socio-economic development in continental inland Asia. The oldest settlements (Pavlodar and Semey) were founded in the early 18th century as fortresses of the Russian Empire (Appendix S1). Some younger cities (Ekibastuz, Karaganda) were built for coal miners, while other settlements (Nur-Sultan, Osakarovka) initially served as infrastructural points for the needs of the Virgin Land Campaign, a large-scale governmental resettlement programme of the USSR to promote agriculture in the region in 1954–1963. All 10 cities experienced strong population growth since the mid-1960s due to industrial development after the failure of the Campaign. After the collapse of the Soviet Union in 1991, population numbers declined but recovered by the 2000s.

Fieldwork was conducted by the first author from mid-June to late July 2020. We followed the classification of urban habitat types proposed by Lososová et al. (2011, 2012a, 2012b), sampling seven habitat types in each city: (1) central square, (2) boulevard, (3) residential area, (4) central park, (5) early-successional vacant site and (6) mid-successional vacant site. Unlike Lososová et al. (2011, 2012a, 2012b), we did not sample residential areas with a compact building pattern (garden cities) as these were not present in the cities studied. Instead, we additionally sampled (7) railway stations (see Appendix S2 for a detailed description of habitat types).

We used a standardised sampling protocol following Lososová et al. (2011, 2012a, 2012b). The application of a unified methodological and sampling scheme allowed us to compare our results with those obtained by other studies from cities in other countries. We recorded plant species composition in seven square or rectangular 1-ha plots in each city, with each plot representing a single urban habitat. The plot representing each urban habitat was chosen in the inner part of each city based on Google Earth satellite images and subsequent *in-situ* observations. Each plot included all landscape features characteristic of the respective habitat (e.g., buildings, green spaces and paved areas). The share of greenspace and sealed surface was considered as an attribute of a particular urban habitat type. We sampled a total of 70 plots (10 cities × 7 habitats). In each plot, we recorded presence of all spontaneously occurring vascular plant species, including plants growing in cracks of paved areas, escaped garden plants and seedlings of spontaneously regenerating planted trees and shrubs. We did not record deliberately planted individuals. Most mature trees and shrubs within the plots were cultivated and thus excluded from sampling. We performed sampling at the peak of the growing season to avoid seasonal variation within our dataset.

We identified plant species according to Pavlov (1956–1966) and Goloskokov (1972) and used the Catalogue of Life (2021) to unify taxonomy and nomenclature. Alien species were defined as species introduced from outside of Kazakhstan, apophytes as native species preferring human-disturbed sites, and indigenous species as native species that grow predominantly in natural habitats. We assigned 93% of all recorded species to alien, apophyte or indigenous status based on Pavlov (1956–1966). Missing information on species status was completed from the

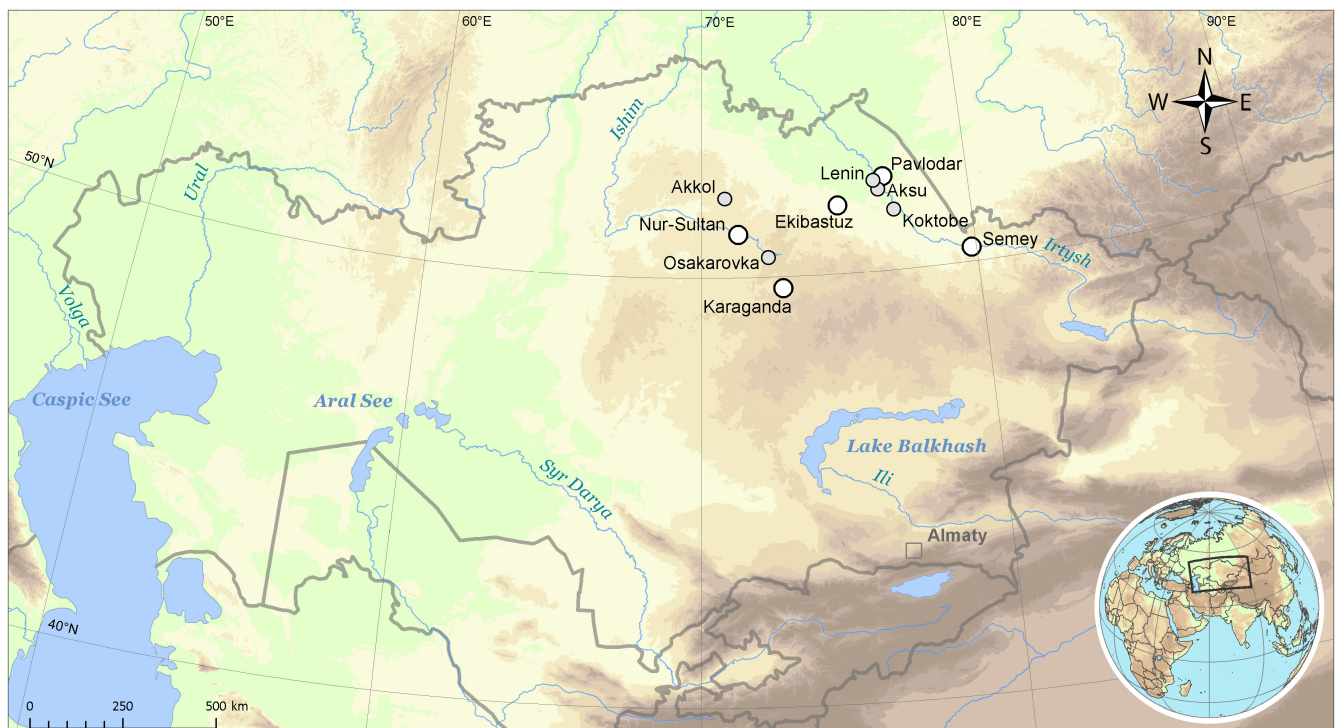


FIGURE 1 Sampled cities in northeastern and central Kazakhstan. Unfilled circles indicate large (Ekibastuz, Karaganda, Nur-Sultan, Pavlodar, Semey) and filled circles indicate small (Akkol, Aksu, Koktobe, Lenin, Osakarovka) cities based on population size



USDA GRIN-Global database (2021; 4% of all species) and from existing databases on native species status (Nurmukhambetova, 2002; Tarasovskaya et al., 2012; the remaining 3% of all species).

We extracted macroclimatic data for each of the 70 plots from the WorldClim dataset (Fick & Hijmans, 2017) using their geographic coordinates. Of the macroclimatic variables, we downloaded annual precipitation, annual mean temperature, and temperature seasonality, which are among the most commonly used variables to explain patterns of plant diversity in macroecological studies.

2.2 | Data analyses

We performed all statistical analyses in R (version 4.0.4; R Core Team, R Foundation for Statistical Computing, Vienna, Austria) and expressed urban vegetation diversity as plant species richness and composition (based on presence/absence data). We calculated plant species richness as the total number of species sampled in each habitat type or city, and also quantified the total number of alien, apophytic and indigenous species and their proportions in each habitat or city.

We used linear mixed-effects models to analyse the effects of habitat type, city size and macroclimatic variables on species richness and the proportion of alien, apophytic and indigenous plants. We defined habitat type as a categorical variable with seven levels and city size as a categorical variable with two levels (large versus small). We used 'city' as a random effect. For each plot, we included the following explanatory variables as fixed effects in the models: (1) habitat type; (2) city size; and (3) three macroclimatic variables. We also included an interaction term between habitat type and city size. These three groups of variables were weakly related and normally distributed. We used Tukey *post-hoc* tests to compare differences in mean total species richness and richness of alien, apophytic and indigenous species among urban habitat types. In addition, we conducted a variance component analysis (Crawley, 2013) using random-effects models for each response variable, with no fixed effects and city size as the only random effect. Because habitat types were the only replicates within cities, this analysis allowed us to compare the amount of explained variation in species richness among cities and within cities (i.e., among habitat types). We conducted these analyses using the R packages *lme4*, *MASS* and *nlme* (Venables & Ripley, 2002; Wood, 2011; Bates et al., 2015).

We used Principal Components Analysis (PCA) to explore the species composition of the sampled plots. The ordination diagram was prepared using the 'rda' function on the Hellinger-transformed matrix of species composition similarity. The explanatory variables were projected as vectors onto the ordination diagram using the 'envfit' function. These calculations were performed using the R package *vegan* (Oksanen et al., 2013).

Differences in species composition among urban habitats and between the two categories of city size were described using diagnostic species. We determined diagnostic species by calculating the *phi* coefficient of association between species occurrence and habitat type or city size category (Chytrý et al., 2002) using the JUICE

program (Tichý, 2002, version 7.1). The statistical significance of the concentration of species occurrences within the target plot categories was assessed using Fisher's exact test ($p < 0.05$) according to Tichý and Chytrý (2006). We considered any species with a statistically significant occurrence concentration and $\varphi > 0.2$ to be diagnostic for the habitat type or the city size category.

3 | RESULTS

3.1 | Most common species in cities

We recorded a total of 174 plant species, including 31 (18%) alien, 76 (44%) apophytes and 67 (38%) indigenous species. Individual 1-ha plots in urban habitats contained on average 21 plant species (range: 10–37). The most common species present in almost all cities were *Agropyron cristatum* var. *pectinatum*, *Artemisia absinthium*, *Atriplex patula*, *Convolvulus arvensis*, *Elytrigia repens*, *Medicago falcata*, *Polygonum aviculare*, *Sonchus arvensis* and *Taraxacum* sect. *Taraxacum*. These species occurred in more than 50% of all sampled plots. Among them, *Convolvulus arvensis*, *Polygonum aviculare* and *Sonchus arvensis* were the most frequent apophytes, while *Agropyron cristatum* var. *pectinatum* and *Medicago falcata* were the most frequent indigenous species. Other indigenous species were recorded with lower frequencies (e.g., *Agrostis capillaris* occurred in <40% of sampled plots). The most frequent alien species were *Amaranthus retroflexus*, *Cannabis sativa* and *Erigeron canadensis* (frequency of occurrence approx. 30%).

3.2 | Differences in species richness across urban habitat types

Species numbers differed significantly among urban habitat types (Table 1). We found the lowest values in central squares, and the highest in railway stations and residential areas ($p < 0.001$; Table 1; Figure 2a). The highest number of alien species was recorded in residential areas (Figure 2b), while apophytes were most abundant in railway stations (Figure 2c). Habitat type explained most of the variation in total plant species richness and richness of aliens, apophytes and indigenous species (variance components of differences in total species richness were 88.7%, for aliens 85.3%, for apophytes 70.6%, and for indigenous species 66.5%).

3.3 | Effects of city size and macroclimate on urban species richness

We found that the total number of species and the proportion of alien, apophytic and indigenous species did not differ between large and small cities (all $p > 0.05$; Table 1).

The total number of species was significantly positively related to annual precipitation ($p = 0.03$; Table 1). This relationship was caused by the increased proportion of apophytes in cities with higher

TABLE 1 Summary of linear mixed-effects models testing the effects of habitat type, city size and macroclimatic factors on species richness and proportions of alien, apophytic and indigenous species. Cell content shows *F*-test results and marginal and conditional R^2 .

Explanatory variables	Species richness	Proportion of alien species	Proportion of apophytic species	Proportion of indigenous species
Habitat type	$F = 6.08, p < 0.001$	$F = 2.59, p = 0.03$	$F = 0.97, p = 0.46$	$F = 0.76, p = 0.60$
City size	$F = 0.09, p = 0.77$	$F = 0.11, p = 0.75$	$F = 1.38, p = 0.27$	$F = 0.45, p = 0.52$
Annual mean temperature	$F = 3.96, p = 0.06$	$F = 0.005, p = 0.98$	$F = 2.51, p = 0.12$	$F = 0.97, p = 0.33$
Temperature seasonality	$F = 3.72, p = 0.06$	$F = 0.01, p = 0.91$	$F = 2.78, p = 0.10$	$F = 0.90, p = 0.35$
Annual precipitation	$F = 5.02, p = 0.03$	$F = 0.28, p = 0.60$	$F = 5.29, p = 0.03$	$F = 3.37, p = 0.07$
Habitat type \times City size	$F = 1.46, p = 0.22$	$F = 0.70, p = 0.65$	$F = 1.12, p = 0.37$	$F = 0.35, p = 0.91$
Marginal R^2	0.43	0.32	0.32	0.32
Conditional R^2	0.59	0.45	0.35	0.40

Significant results are in bold ($p < 0.05$).

precipitation ($p = 0.03$; Table 1; Figure 3). We found no other significant effect of macroclimatic variables on urban species richness.

3.4 | Effects of habitat type and city size on urban plant composition

Species composition varied by habitat type and with city size (Figure 4). The ordination diagram contrasted the species composition of disturbed plots in city centres (squares, boulevards and parks) and the species composition of early-successional, mid-successional and railway station sites. The greatest difference in species composition was observed between central squares at one end of the second PCA axis and early-successional sites at the opposite end. In contrast, parks and boulevards were poorly discriminated along the ordination axes. These habitats shared several indigenous grasses, including *Poa pratensis*, as well as some widespread apophytic species (e.g., *Elytrigia repens*, *Sonchus arvensis* and *Taraxacum* sect. *Taraxacum*). However, we found a substantial difference among these two habitats and residential areas. Railway stations differed in species composition from all other urban habitats, but shared some weedy species (*Amaranthus retroflexus*, *Sedobassia sedoides*) with residential areas.

We also found a different species composition between large and small cities (Figure 4). The separation of plots along the first ordination axis was largely due to the presence of species escaping cultivation in larger cities (*Agropyron cristatum* var. *pectinatum*, and seedlings of widely planted *Acer negundo* and *Ulmus pumila*). Weedy assemblages in these cities included the apophytes *Atriplex patula*, *Lepidium ruderae* and *Polygonum aviculare*. The ordination showed no significant effects of macroclimatic parameters on plant species composition.

3.5 | Diagnostic species of urban habitats

Central squares contained a single diagnostic species — the apophyte *Stellaria media* (Table 2). All the other habitat types were characterised

by the presence of both apophytic and indigenous diagnostic species. The railway stations harboured the largest number of diagnostic species, including the indigenous *Corispermum orientale* and *Gypsophila paniculata*. Successional sites also contained several diagnostic species. Early-successional sites were mainly characterised by apophytes (e.g., *Descurainia sophia* and *Urtica dioica*), whereas mid-successional sites were characterised by annual weedy apophytes (*Oxybasis urticae*, *Sisymbrium loeselii*) and indigenous grassland species (*Bromus inermis*, *Stipa capillata*). Both types of successional habitats were favourable for the alien *Cannabis sativa*. Early-successional and railway station sites shared some diagnostic species such as *Artemisia absinthium* and *Sedobassia sedoides* (both apophytes). Among diagnostic species of boulevards and parks, the trampling-tolerant *Sibbaldianthe bifurca* was common in both habitat types. Alien species were also diagnostic for particular urban habitats. The alien species *Amaranthus retroflexus* and *Portulaca oleracea* were diagnostic for residential areas, *Cyclachaena xanthiifolia* for mid-successional sites and *Ambrosia artemisiifolia* for railway stations.

Large cities had a larger group of diagnostic plant species (Table 3), most of which were apophytes, but also hosted other species associated with human-dependent unintentional introductions (the alien *Erigeron canadensis*) or ornamental planting (spontaneously established seedlings of *Ulmus pumila*). In contrast, small cities were characterised by indigenous steppe species (*Artemisia gracilescens*, *Artemisia pontica* and *Potentilla humifusa*). However, small cities were also positively associated with some apophyte species (e.g., *Artemisia abrotanum* and *Carduus nutans*) or the alien weed *Chenopodium album*.

4 | DISCUSSION

Our study is the first to explore the patterns of urban plant diversity among habitat types and cities in continental inland Asia. Our results show that the species composition of urban vegetation in this region is influenced by both habitat type and city size, with macroclimate having only a limited effect. Overall, our results are comparable to those reported in similar studies worldwide (e.g., Loram et al., 2008;

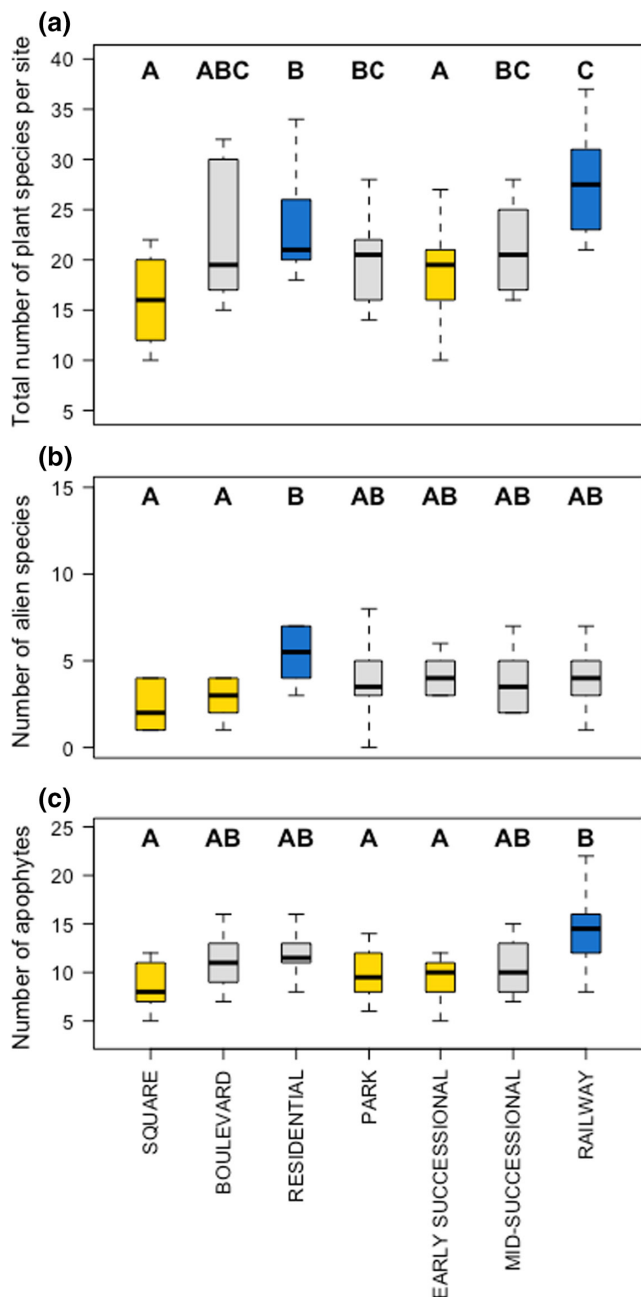


FIGURE 2 Total species richness (a), and richness of alien (b) and apophytic (c) species in plots of urban habitat types. Different letters indicate significant differences between habitat types (Tukey *post-hoc* tests at $p < 0.05$). Blue colour corresponds to habitat types with the highest species richness, while yellow colour corresponds to habitat types with the lowest species richness within each species group.

Lososová et al., 2011, 2012a, 2012b; Kalusová et al., 2017; Glišić et al., 2021).

4.1 | Species richness in urban habitats

Our study showed that urban habitats in Kazakhstan appear to have, on average, a much lower absolute number of species (21 species

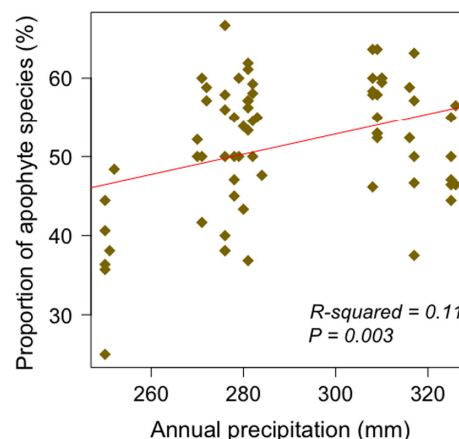


FIGURE 3 Relationship between the proportion of apophytic species and annual precipitation. The R^2 coefficient was derived from linear regression.

per hectare) than those in European cities (101 species; Lososová et al., 2012a, 2012b). We can explain this discrepancy by the harsh climatic conditions in the study area, which could act as a strong environmental filter preventing the establishment of alien and apophytic species. In contrast, native steppe species are adapted to drought stress but not to disturbance regimes in the urban environment. In the steppe zone of central Kazakhstan, natural vegetation contains ~30 species per 100-m² plot (Chytrý et al., unpublished data) and is thus more species-rich than urban vegetation. Similar results are reported from northeastern Kazakhstan (Vakhloмова et al., 2014). This supports the idea that the conversion of steppe to urban area leads to a decline in steppe species and that the diversity of urban vegetation is not compensated by the establishment of apophytic or alien plants. In addition, most of the studied cities are relatively young compared to the previously studied European cities, which were founded in the 5th–13th centuries AD. Probably, the short history of cities in Kazakhstan did not allow the accumulation of many alien and apophytic species. The invasion debt is generally greater in younger cities than in older ones because species need more time to become established (Hahs et al., 2009). Moreover, frequent severe disturbances, such as road grading and paving or constructions, may prevent some species from colonizing new urban habitats (Faeth et al., 2011).

We found a similar proportion of alien species (18%) as in studies from urban habitats in Europe that used the same standardised sampling protocol [24.9% in 60 European cities according to Lososová et al. (2018); 14.1%–15.3% in Mediterranean cities according to Celesti Grapow and Blasi (1998) and Stešević et al. (2009)]. The proportion of alien species in urban floras varies widely across geographical areas and environmental gradients. Aronson et al. (2014) found that on average 20.8% of urban plant species in 110 cities across the globe were exotic. This proportion was consistently lower in eight cities in Israel (10.9%; Keren et al., 2022) under extreme environmental conditions, but consistently higher in 54 cities in Europe (40.3%; Pyšek, 1998) and in Shanghai (57.8%; Wang et al., 2020), with milder and wetter climates. However, these studies and reviews

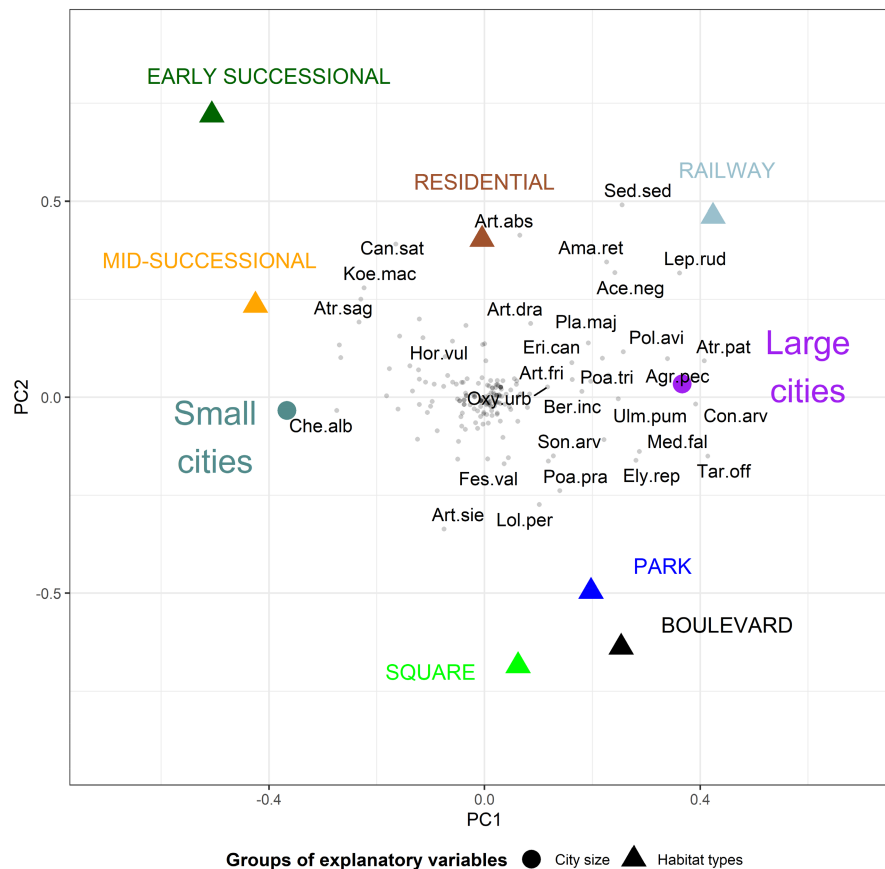


FIGURE 4 Principal Components Analysis (PCA) showing the effects of habitat type and city size on plant species composition. Species with the highest scores on the first two axes are coded as follows: Ace.neg = *Acer negundo*, Agr.pec = *Agropyron cristatum* var. *pectinatum*, Agr.cap = *Agrostis capillaris*, Ama.ret = *Amaranthus retroflexus*, Art.abs = *Artemisia absinthium*, Art.fri = *Artemisia frigida*, Art.dra = *Artemisia dracunculus*, Art.sie = *Artemisia sieversiana*, Atr.pat = *Atriplex patula*, Atr.sag = *Atriplex sagittata*, Ber.inc = *Berteroa incana*, Can.sat = *Cannabis sativa*, Che. alb = *Chenopodium album*, Con.arv = *Convolvulus arvensis*, Ely.rep = *Elytrigia repens*, Eri.can = *Erigeron canadensis*, Fes.val = *Festuca valesiaca*, Hor.vul = *Hordeum vulgare*, Koe.mac = *Koeleria macrantha*, Lep.rud = *Lepidium rudale*, Lol.per = *Lolium perenne*, Med.fal = *Medicago falcata*, Oxy.urb = *Oxybasis urbica*, Pla.maj = *Plantago major*, Pol.avi = *Polygonum aviculare*, Poa.pra = *Poa pratensis*, Poa.tri = *Poa trivialis*, Sed.sed = *Sedobassia sedoides*, Son.arv = *Sonchus arvensis*, Tar. off = *Taraxacum* sect. *Taraxacum*, Ulm.pum = *Ulmus pumila*.

were based on data collected using different protocols and often included the entire city flora rather than the flora of smaller plots in specific habitats.

Although apophytes are a characteristic group of urban species worldwide (Celesti Grapow & Blasi, 1998; Sukopp, 2006), we could not compare their proportion with analogous studies in other regions because different studies used different terminology for them. The same species group is often referred to as weeds, generalists, hemerobic, urban specialists, species 'with high urbanity', ruderals, cosmopolites, or urbanophiles (e.g., Hill et al., 2002; Rat et al., 2017).

4.2 | Effects of habitat type on plant richness and the proportion of alien, apophytic and indigenous species

Our study confirmed that habitat type is more important than city size or macroclimate in explaining plant diversity. This result is consistent with analogous studies in European cities (Čeplová

et al., 2017; Piano et al., 2017; Glišić et al., 2021). Similarly, the lowest species richness being found in highly disturbed central squares and the highest in less disturbed residential areas has also been reported across several cities (Lososová et al., 2011, 2012a, 2012b; Čeplová et al., 2017). As a negative factor, high proportions of sealed surfaces may limit plant species' establishment in the central squares and other paved habitats (Malkinson et al., 2018). In addition, we found the highest species richness at railway stations, a pattern also observed in other urban studies (Galera et al., 2014; Toffolo et al., 2021). This finding could be attributed to the high availability of microhabitats in these locations and the limited mowing and fertilisation, which allow the establishment of various species. Thus, our results confirm the role of railways as potential hotspots of urban species diversity (Toffolo et al., 2021).

Although railways are considered ecological corridors for alien species dispersal and establishment (Wrzesień & Denisow, 2017), we found that railway stations have the highest number of apophytes, but not alien plants. Because of their adaptation to a stressed



TABLE 2 Diagnostic plant species of urban habitat types in Kazakhstan; numbers are percentage occurrence frequencies in individual habitat types; species are listed by decreasing values of ϕ in each habitat type

Species	Species status	Habitat types						
		Square	Boulevard	Residential	Park	Early successional	Mid-successional	Railway
<i>Stellaria media</i>	Apophyte	20**	–	–	–	–	–	–
<i>Camphorosma monspeliaca</i>	Indigenous	–	40**	–	–	–	–	–
<i>Lotus corniculatus</i>	Indigenous	–	50**	–	–	–	–	–
<i>Achillea millefolium</i>	Apophyte	–	40*	–	–	–	–	–
<i>Taraxacum</i> sect. <i>Taraxacum</i>	Apophyte	–	90*	–	–	–	–	–
<i>Portulaca oleracea</i>	Alien	–	–	40***	–	–	–	–
<i>Oxybasis glauca</i>	Apophyte	–	–	20**	–	–	–	–
<i>Potentilla anserina</i>	Indigenous	–	–	30*	–	–	–	–
<i>Atriplex sagittata</i>	Apophyte	–	–	70*	–	–	–	–
<i>Amaranthus retroflexus</i>	Alien	–	–	70*	–	–	–	–
<i>Gaillardia aristata</i>	Alien	–	–	–	40***	–	–	–
<i>Stachys palustris</i>	Indigenous	–	–	–	20**	–	–	–
<i>Ceratocarpus arenarius</i>	Apophyte	–	–	–	30*	–	–	–
<i>Trifolium repens</i>	Apophyte	–	–	–	40*	–	–	–
<i>Poa pratensis</i>	Indigenous	–	–	–	60*	–	–	–
<i>Verbascum phoeniceum</i>	Indigenous	–	–	–	–	40***	–	–
<i>Sonchus oleraceus</i>	Apophyte	–	–	–	–	30**	–	–
<i>Urtica cannabina</i>	Apophyte	–	–	–	–	20**	–	–
<i>Descurainia sophia</i>	Apophyte	–	–	–	–	50**	–	–
<i>Puccinellia distans</i>	Apophyte	–	–	–	–	50*	–	–
<i>Urtica dioica</i>	Apophyte	–	–	–	–	30*	–	–
<i>Sisymbrium loeselii</i>	Apophyte	–	–	–	–	–	70***	–
<i>Stipa capillata</i>	Indigenous	–	–	–	–	–	30**	–
<i>Veronica longifolia</i>	Indigenous	–	–	–	–	–	30**	–
<i>Phragmites australis</i>	Indigenous	–	–	–	–	–	40*	–
<i>Cyclachaena xanthiifolia</i>	Alien	–	–	–	–	–	50*	–
<i>Bromus inermis</i>	Indigenous	–	–	–	–	–	50*	–
<i>Oxybasis urbica</i>	Apophyte	–	–	–	–	–	50*	–
<i>Gypsophila paniculata</i>	Indigenous	–	–	–	–	–	–	60***
<i>Corispermum orientale</i>	Indigenous	–	–	–	–	–	–	40***
<i>Lactuca tatarica</i>	Apophyte	–	–	–	–	–	–	30***
<i>Artemisia dracunculus</i>	Apophyte	–	–	–	–	–	–	80**
<i>Ambrosia artemisiifolia</i>	Alien	–	–	–	–	–	–	30**
<i>Artemisia scoparia</i>	Apophyte	–	–	–	–	–	–	40**
<i>Lepidium ruderae</i>	Apophyte	–	–	–	–	–	–	80*
<i>Calamagrostis epigejos</i>	Indigenous	–	–	–	–	–	–	40*
<i>Sibbaldianthe bifurca</i>	Indigenous	–	40*	–	40*	–	–	–
<i>Cannabis sativa</i>	Alien	–	–	–	–	70*	70*	–
<i>Sedobassia sedoides</i>	Apophyte	–	–	–	–	90*	–	100**
<i>Artemisia absinthium</i>	Apophyte	–	–	–	–	80*	–	100**

*, $\phi > 0.2$; **, $\phi > 0.4$; ***, $\phi > 0.5$.

TABLE 3 Diagnostic plant species of large and small cities in Kazakhstan based on pooled species data from the seven habitat types; numbers are percentage occurrence frequencies in individual habitat types; species are listed by decreasing values of ϕ in large and small cities

Species	Species status	Size of the city	
		Large	Small
<i>Convolvulus arvensis</i>	Apophyte	91.4**	–
<i>Medicago falcata</i>	Indigenous	82.8*	–
<i>Erigeron canadensis</i>	Alien	42.9*	–
<i>Trifolium repens</i>	Apophyte	28.6*	–
<i>Oxybasis urtica</i>	Apophyte	34.9*	–
<i>Poa trivialis</i>	Apophyte	33.3*	–
<i>Lepidium ruderalis</i>	Apophyte	51.4*	–
<i>Artemisia vulgaris</i>	Apophyte	14.3*	–
<i>Lolium perenne</i>	Alien	37.1*	–
<i>Atriplex patula</i>	Apophyte	65.7*	–
<i>Capsella bursa-pastoris</i>	Apophyte	28.6*	–
<i>Cirsium arvense</i>	Apophyte	22.9*	–
<i>Artemisia frigida</i>	Apophyte	31.4*	–
<i>Ulmus pumila</i>	Indigenous	68.5*	–
<i>Chenopodium album</i>	Alien	–	51.4**
<i>Carduus nutans</i>	Apophyte	–	34.3**
<i>Artemisia abrotanum</i>	Apophyte	–	22.8*
<i>Potentilla humifusa</i>	Indigenous	–	20.0*
<i>Artemisia gracilescens</i>	Indigenous	–	17.1*
<i>Atriplex sagittata</i>	Apophyte	–	40.0*
<i>Rumex confertus</i>	Apophyte	–	31.4*
<i>Artemisia pontica</i>	Indigenous	–	14.3*
<i>Ceratocarpus arenarius</i>	Apophyte	–	14.3*

*, $\phi > 0.2$; **, $\phi > 0.4$; ***, $\phi > 0.5$.

environment, apophytic plants may particularly benefit from the intermediate disturbance regime, gravel surfaces and increased soil nutrient levels along railway tracks. The relatively low proportion of alien species in railway stations in this region might be due to the fact that the space between railway tracks is characterised by conditions that are too dry and hot for common alien species. Moreover, the alien species in the studied cities include many species escaped from cultivation, such as *Cannabis sativa*, which grows exclusively near sources of introduction (i.e., residential areas). More detailed studies are needed to reveal factors controlling the growth and survival of alien plants in this region.

In contrast to previously reported patterns, we did not find high species diversities at successional sites or in parks. In addition, early and mid-successional sites were often dominated by several competitive weeds, which could reduce species diversity in these habitats. In many cities, parks represent remnants of natural forests that harbour forest species (Zerbe et al., 2003;

Lapaix & Freedman, 2010; Chang et al., 2021). However, in the study area, forests are almost absent due to climatic constraints (Rachkovskaya & Bragina, 2012), so parks likely do not represent forest remnants.

Although alien species appeared to be relatively evenly distributed across the different city habitats, their numbers were highest in residential areas. In most of the areas surveyed, housing development started in the 1960s, following intensive industrial development, resulting in recent introductions of alien plants through direct human activities, such as exotic ornamentals and escapes from gardens (Kent et al., 1999). In addition, alien plants germinate better in severely disturbed, compacted soils than native grassland species, which require more specific habitat conditions (Jutila & Grace, 2002). Although residential areas are less frequently disturbed than other habitat types, their flora is disturbed by compaction and disturbance of the upper soil layer due to trampling by pedestrians, off-road driving and off-street parking. Given that residential areas have a higher share of alien plant species than other habitats and that invasion debt is high in our studied cities, we hypothesise that alien plants would expand further in this habitat type in the future.

4.3 | Contribution of city size and macroclimate to species richness

Contrary to our expectations, neither city size nor climate had a significant effect on plant species richness. In particular, we could not confirm that total species richness was higher in larger cities than in smaller cities, as reported by Čeplová et al. (2017) in an analogous study of 45 cities or by Pyšek (1998) for total floras in 54 cities. Our results contradict the expected increase in alien species richness associated with urbanisation in large cities, as observed in many studies (Pyšek, 1998; Kent et al., 1999; Zerbe et al., 2003; Rat et al., 2017). The lack of a significant relationship between city size and species richness in our study area could again be due to the short historical development of the studied cities compared to European settlements.

Considering macroclimate, we found that the proportion of apophytes increased with annual precipitation. This result can be partly explained by the fact that most apophytes have a wide distribution and prefer areas with high precipitation (Trzcińska-Tacik & Wasylukowa, 1982). Therefore, they were more common in humid parts of the study area and less abundant in the drier cities. Similar findings of more diverse spontaneous weed vegetation in areas with higher precipitation have been reported in urban yards in the USA (Wheeler et al., 2017; Padullés Cubino et al., 2019) and on arable urban land in the Czech Republic (Tyšer & Kolářová, 2021).

In general, the much weaker effect of climate than habitat type on urban vegetation diversity may be due to a stronger filtering effect of urbanisation than climate. Alternatively, it is possible that the spatial distribution of our studied cities may have not been sufficiently large to detect a significant effect of climate on plant

diversity. Instead, the lack of significant effects of macroclimate on diversity might be compensated by the effect of microclimatic conditions associated with different urban habitats. Future studies of urban diversity in continental Asia should consider broader climatic gradients to further explore this relationship, for example in mountainous continental Asia, where climate is milder and cities often older.

4.4 | Effects of habitat type and city size on species composition

Our results show a strong influence of habitat type on plant species composition. Analogous studies from European cities reported similar trends (Lososová et al., 2011, 2012a, 2012b, 2018; Čeplová et al., 2017; Glišić et al., 2021). As in these studies, we demonstrated contrasting species composition between central squares and successional sites, floristic similarity between parks and boulevards, and different species composition in residential areas.

Despite the relatively low plant diversity in urban habitats compared to adjacent natural areas, our study showed that indigenous steppe plant species survive in most urban habitats. In particular, railway stations and mid-successional sites hosted many indigenous steppe species, indicating that these species are adapted to open and disturbed spaces and thus can thrive in these urban habitats (Tikka et al., 2001). Other urban studies reported that plant diversity in cities depends on the similarity of urban habitats and species' native habitats (reviewed by Norton et al., 2016). At the same time, railway stations and early-successional sites shared several apophytes. Abiotic factors strongly constrain urban plant species in harsh environments (e.g., in Egypt — Abd El-Ghani et al., 2015). Boulevards, squares and parks may overlap in abiotic conditions and share the same diagnostic species. Considering the dry climate in the study area, irrigation in these habitats may have also contributed to the floristic similarities between these three urban habitats. However, forest species normally found in woody urban environments were poorly represented in our study area due to the lack of forest remnants in cities (Rachkovskaya & Bragina, 2012).

Our study shows that large and small cities have different species compositions, which is confirmed by the analysis of diagnostic species. The diagnostic plants of large cities included typical urban specialists (Hill et al., 2002). Among the diagnostic species of large cities, we found many taxa that also occur in urban floras in other regions, such as *Capsella bursa-pastoris*, *Convolvulus arvensis*, and *Cirsium arvense* (Tabašević et al., 2021). The alien *Erigeron canadensis*, one of the most successful urban invaders (Szumańska et al., 2021), also appeared among the diagnostic species of large cities. These results suggest that the probability of biotic homogenisation is greater in larger cities than in smaller ones. In small cities the number of apophytic diagnostic species was lower than in large cities. Moreover, the presence of indigenous steppe plants in the urban habitats of small cities suggests a greater similarity

in abiotic conditions between natural landscapes and small cities than large cities. Furthermore, the differences in species composition between cities of different sizes could be explained by the industrial or arable land-use history of the cities. The small cities in our study were mostly located in arable areas and have a higher probability of receiving species that have dispersed from arable fields (e.g., *Hordeum vulgare*), a pattern also reported by Angold et al. (2006).

5 | CONCLUSION

Our study found a stronger filtering effect of urbanisation than climate on the diversity of urban vegetation. Findings were consistent with results of several similar studies in Europe but showed important differences in species richness of individual habitats (i.e., successional sites and parks). In general, indigenous plant species thrived in urban habitats, but the conversion of steppe to urban areas has likely led to a decline in indigenous species richness. Meanwhile, the establishment of alien and apophytic species may be constrained by macroclimatic filters and invasion debt in young cities. Native steppe species in cities preferred habitats with open, disturbed areas such as railway stations and mid-successional sites. This study advances our knowledge of the poorly sampled urban floras in continental inland Asia. Further research should compare our results with those from other Asian cities with contrasting climatic conditions and historical background.

AUTHOR CONTRIBUTIONS

Zdeňka Lososová, Tatyana Vakhlamova and Viktoria Wagner conceived the research idea and developed the study design. Tatyana Vakhlamova carried out the field surveys, analysed the data and took the lead in writing the manuscript. Zdeňka Lososová supervised the study. Josep Padullés Cubino verified the statistical methods, and Milan Chytrý contributed to the interpretation of the results. All authors discussed the results, provided critical feedback on the analysis and helped write the manuscript.

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DATA AVAILABILITY STATEMENT

Original data are provided in Appendix S3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1 Cities sampled in central and northeastern Kazakhstan.

Appendix S2 An overview of the seven sampled habitat types.

Appendix S3 Original data sets 1 and 2.

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