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Invasive alien plants of Russia: insights from regional inventories

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Abstract Recent research on plant invasions indicates that some parts of the world are understudied with temperate Asia among them. To contribute towards closing this gap, we provide a standardized list of invasive alien plant species with their distributions in 45 Russian regions, and relate the variation in their richness to climate, socioeconomic parameters and human influence. In total, we report 354 invasive alien species. There are, on average, 27 ± 17 (mean ± SD) invasive plants per region, and the invasive species richness varies from zero in Karelia to 71 in Kaluga. In the European part of Russia, there are 277 invasive species in total, in Siberia 70, and in the Far East 79. The most widespread invaders are, in terms of the number of regions from which they are reported, *Acer negundo*, *Echinocystis lobata* (recorded in 34 regions), *Erigeron canadensis* and *Elodea canadensis* (recorded in 30 regions). Most invasive species in Russia originate from other parts of temperate Asia and Europe. There were significant differences in the representation of life forms between the European, Siberian and Far East biogeographical regions, with perennials being over-represented in the Far East, and shrubs in the European part of Russia. The richness of invasive species can be explained by climatic factors, human population density and the percentage of urban population in a region. This publication and the associated dataset is the first comprehensive treatment of the invasive flora of Russia using standardized

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criteria and covering 83% of the territory of this country.

Keywords Climate · Exotic plants · Invasive flora · Life-form · Russia · Socioeconomic factors

Introduction

In recent years there has been considerable progress in developing regional inventories of alien plant species (see Pyšek et al. 2017 for an overview). Such inventories represent key inputs for continental and global databases (Lambdon et al. 2008; van Kleunen et al. 2015) that provide data for testing general hypotheses on biological invasions (e.g. Dellinger et al. 2016; Maurel et al. 2016; Razanajatovo et al. 2016; Dawson et al. 2017), identifying long-term trends in species introductions (Seebens et al. 2017) as well as drivers associated with invasions (Pyšek et al. 2015; Seebens et al. 2015; Dawson et al. 2017). As there are clearly documented impacts of alien plants on the environment and human livelihoods by a subset of alien species (Vilà et al. 2010, 2015; Pyšek et al. 2012; Kumschick et al. 2015; Rumlerová et al. 2016), biological invasions have become a focus of national (Essl et al. 2011; Pergl et al. 2016b) and international policies (Hulme et al. 2009; Genovesi et al. 2015; Pergl et al. 2016a).

Comprehensive and rather complete lists of naturalized alien plants in regions (countries, islands, federal states or provinces of large countries) using a standardized classification of invasion status, mostly following the one proposed by Richardson et al. (2000), started to appear in the 2000s. For example, in Europe, the first national alien plant species checklists were published in 2002 for Austria (Essl and Rabitsch 2002) and the Czech Republic (Pyšek et al. 2002). The European Union-funded DAISIE project (DAISIE 2009) led to the compilation and update of alien plant species inventories for many countries in this continent (e.g. Medvecká et al. 2012; Pyšek et al. 2012). Similar activities were also done e.g. in temperate Asia, and elsewhere (e.g. Liu et al. 2006; Wu et al. 2010; Jiang et al. 2011; Xu et al. 2012; Shrestha 2016; Uludag et al. 2017; Inderjit et al. 2018). However, despite this substantial progress, recent publications that provide the most comprehensive overviews of naturalized plant species inventories worldwide (van Kleunen et al. 2015; Pyšek et al. 2017) show that there are still some major data gaps in global coverage, the biggest one being large parts of temperate Asia (see van Kleunen et al. 2015, their Fig. 1). Global knowledge of the distribution of invasive plants, i.e. the subset of naturalized plants that rapidly spread over large distances from focal populations (Richardson et al. 2000; Blackburn et al. 2011), is even more limited than is the case with naturalized plants and up to date information on numbers of invasive plant species in world regions has only been summarized recently (Pyšek et al. 2017).

Improving the knowledge of distributions and richness of alien plant species, both naturalized and invasive, in poorly studied regions is important for many reasons including better understanding of factors determining local invasions, but also for obtaining a more complete picture of global alien species richness (Pyšek et al. 2008, 2017; van Kleunen et al. 2015). Only thoroughly compiled inventories that aim at obtaining complete lists of alien species for individual regions, provide a robust basis for analyses of regional levels of invasions and underlying drivers (Pyšek et al. 2018). Even if such inventories do not record all alien species, specifically casuals or less widely distributed naturalized species that are difficult to capture in countries with a poorer tradition of floristic research, it is important to aim at completeness for the category chosen for the study, be it naturalized or invasive species (Latombe et al. 2017).

With regard to coverage of administrative regions, the largest current gap refers to Russia. The European region of Russia has largely been accounted for in the GloNAF database of the world's naturalized floras (see van Kleunen et al. 2015; Pyšek et al. 2017 for details), as were some regions in the Far East. However, data from the Asian region of Russia is largely missing. The floristic information is mostly scattered in grey literature (Grigorevskaya et al. 2004; Borisova 2007; Morozova et al. 2008; Krylov and Reshetnikova 2009; Khorun et al. 2012) and primarily published in the Russian language. The comparability of the lists often suffers from the lack of standardized terminology and some data sources focus only on subsets of naturalized plants such as those that are considered to cause negative impacts on the environment or human livelihoods (such as Black Books: Vinogradova et al. 2010, 2011; Vinogradova and

Kuprianov 2016). Indeed, despite numerous local papers and reports on the presence of alien plant species in different subregions of Russia (Mayorov et al. 2012; Rzhevuskaya 2012; Tremasova et al. 2012; Antonova 2013; Panasenko 2013; Silaeva and Ageeva 2016), no summarizing inventory of invasive species in individual regions of this country has been compiled so far. In this paper we aim at closing this gap for a large part of Russia. Given the vast size of the country and the variation in environmental conditions and human impacts, these data provide an excellent opportunity to explore the effects of natural and human-related factors on the regional levels of plant invasions in an important but understudied part of the globe.

We provide, for the first time based on standardized inventories of invasive plant species covering over 80% of its territory, (1) an account of plant invasions in Russia, and (2) we explore the basic taxonomic, biogeographic and ecological characteristics of its invasive flora. We also elucidate (3) the differences between the invasive species composition in different biogeographic regions of Russia, and (4) analyse the importance of environmental and socioeconomic drivers on the variation in regional invasive plant species richness.

Methods

Lists of invasive plant species and their attributes

To compile the inventories of invasive alien plant species for regions in Russia (Table 1), local experts for alien plants (see Electronic Appendix 1 for a list of regional contributors) were asked to provide lists of invasive alien species for the following groups: (1) transformers *sensu* Richardson et al. (2000), defined as invasive species with impact on ecosystem functioning and (2) alien species becoming naturalized and rapidly spreading. These two categories correspond to the definition of invasive species, widely accepted in the current literature (following the criteria of Richardson et al. 2000; Pyšek et al. 2004; Blackburn et al. 2011). The regional contributors coordinated the compilation of the lists of invasive species for their regions on the basis of data provided by local botanists, working in defined small districts, by using the same guidelines (Notov et al. 2011). These lists were based on field knowledge, literature, herbarium and unpublished records. We considered also aliens of Russian origin, i.e. species that are native in a part of Russia but alien to another part (similar as aliens *in* and *to* Europe in Lambdon et al. 2008).

Data on life form and geographic origin of the species were extracted from the working database GloNAF (van Kleunen et al. 2015; Pyšek et al. 2017) and verified by inspecting local floras and other sources. To link the list obtained to the GloNAF database, the taxonomy of "The Plant List" (version 1.1; http://www.theplantlist.org) was used to standardize the original names (i.e. synonyms were replaced by accepted scientific names; see van Kleunen et al. 2015) using the R package Taxonstand (Cayuela et al. 2017). As to life form, species were classified into the following categories: annual herb, perennial herb (including biennials, to group species that survive winter in other form than seed), shrub, tree, climber, and aquatic plants. To classify the region of origin, each species was assigned to one or more of the major biogeographically defined areas (continents) of the Taxonomic Databases Working Group (Brummit 2001). Species whose native range is unknown as they are only known from cultivation and species that originated through recent human-mediated hybridization are listed as a separate category. Data on the origin of species were primarily extracted from GRIN (https://npgsweb.ars-grin.gov) and then checked by literature and web searches (e.g. www.botany.cz, www.plants.jstor.org, www.issg.org).

Study region

Forty-five regions were covered by our survey (Table 1) accounting for 83% of the territory of Russia. Twenty-eight regions belong to the European part of Russia (accounting for 14% of the Russian territory), 12 to Siberia (59%) and two to the Far East (10%) (Fig. 1).

The climatic conditions of Russia vary widely along the north-south gradient as well as from west to east. To characterize the climate in individual regions, we used 19 bioclimatic variables available through the WorldClim database (Hijmans et al. 2005). We performed a principal component analysis (PCA) with the first three axes explaining nearly 85% of the variation present in the original 19 variables (Dupin et al. 2011). The resulting PCA axes represent three uncorrelated linear

Table 1 The numbers of invasive species and geographic characteristics of the 45 Russian regions used in this study

Region	No. of invasive species	Biog. region	Area (km^2)
Adygey	23	eur	8136
Aga Buryat	4	sib	563,974
Altay	25	sib	184,258
Astrakhan'	18	eur	46,932
Bashkortostan	29	eur	145,883
Belgorod	62	eur	28,374
Bryansk	26	eur	34,382
Buryat	5	sib	443,570
Evenk	21	sib	851,364
Gorno-Altay	13	sib	105,467
Irkutsk	19	sib	923,495
Ivanovo	42	eur	23,712
Kaliningrad	31	eur	13,758
Kaluga	71	eur	29,114
Karelia	0	eur	175,821
Kemerovo	16	sib	106,119
Khabarovsk	41	feast	1,139,345
Khakass	14	sib	67,599
Komi	8	eur	418,782
Kostroma	24	eur	60,285
Krasnodar	49	eur	77,244
Leningrad	20	eur	144,952
Maga Buryatdan	41	feast	647,038
Mordovia	29	eur	26,212
Moscow	37	eur	47,999
Murmansk	4	eur	143,621
Nizhegorod	56	eur	74,930
North Ossetia	22	eur	7255
Novosibirsk	13	sib	190,094
Omsk	16	sib	146,123
Pskov	33	eur	56,962
Sakha	3	sib	3,819,822
Samara	30	eur	53,593
Saratov	44	eur	101,093
Sverdlovsk	61	eur	196,532
Tomsk	15	sib	337,399
Tula	30	eur	25,503
Tuva	1	sib	19,7918
Tver'	34	eur	85,533
Udmurt	45	eur	41,729
Ul'yanovsk	23	eur	36,887
Vladimir	33	eur	29,128
Volgograd	28	eur	260,453
Voronezh	29	eur	51,721
Yaroslavl'	40	eur	35,939

Biogeographic region: *eur* European part, *sib* Siberia, *feast* Far east

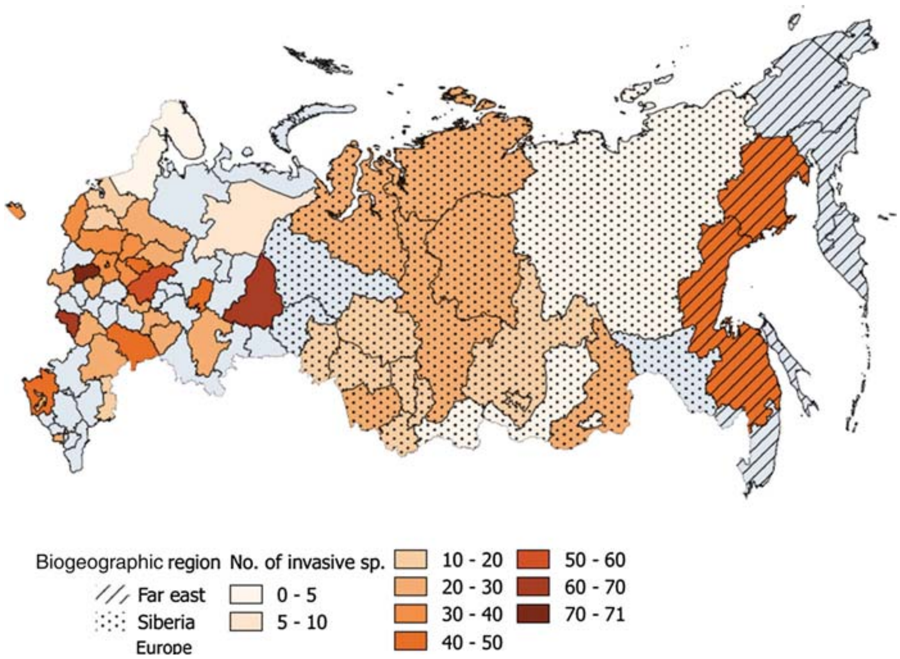

Fig. 1 Map of the study area with indication of the numbers of invasive plant species in the Russian regions, with location in the European, Siberian and Far East parts of the territory indicated. Grey areas indicate the absence of data on invasive species

combinations of the original data, with the first one (PCA score 1) related mainly to mean annual temperature, the second (PCA score 2) mainly to precipitation during wet or warm periods, and the third (PCA score 3) to precipitation during dry seasons.

In addition to climate, we collated data on factors related to land use and human pressure for each region. The following characteristics of land use were obtained: proportion of agricultural land (Federal State Statistics Service 2015), and the average size of roadless areas (i.e. patches) within the region (http://roadless.online; Ibisch et al. 2017). Other proxies related to propagule pressure and land use were human population density and the proportion of the population living in urban areas (Federal State Statistics Service 2015).

As data on invasive species were collected on a regional scale while data on the above factors were sometimes available at a finer grain of subregions, the latter were summed (e.g. human population from several subregions within a region, or subregions' areas) or averaged (climate factors, size of roadless areas).

Statistical analysis

Two approaches were used to analyse the geographical and life-form patterns in the invasive flora of Russia. To test whether there are differences in the numbers of invasive species among regions in Europe, Siberia and the Far East, in terms of representation of species with different life forms and of different origin, their counts were analysed by row × column contingency tables, using generalized linear models (GLMs) with the log-link function and a Poisson distribution of errors (e.g. Crawley 2007). For the models that significantly explained the effects, adjusted standardized residuals of G-tests were then compared with critical values of the normal distribution to ascertain for which species groups the counts are lower or higher than expected by chance (Řehák and Řeháková 1986).

To test the effect of environmental and socioeconomic variables (climate PCA scores, human population density, percentage of urban population, proportion of agricultural land and roadless area) on the number of invasive species in individual regions, regression trees were applied (Breiman et al. 1984; De'ath and Fabricius 2000). To account for variation in size of the regions, the area of each region was taken as a weighing factor. Regression trees were constructed using binary recursive partitioning, with the default Gini index impurity measure used as the splitting index, in CART v. 7.0 (Breiman et al. 1984; Steinberg and Colla 1995). To find an optimal tree, a sequence of nested trees of decreasing size, each being the best of all trees of its size, was produced, and their resubstitution relative errors, corresponding to residual sums of squares, were estimated. Ten-fold cross-validation was used to obtain estimates of cross-validated relative errors for these trees.

Clustering (Ward method) (Crawley 2007) was used for visualizing the patterns in differences between the regions according to the species composition. The calculations were done in R 3.0.2 (R Development Core Team 2017).

Results

Invasive alien species in Russian regions

The invasive alien flora of the 45 Russian regions included in this study consists of 354 species (see Electronic Appendix S2 for the complete list of species and their distribution in the regions). The invasive species richness varied across the regions (Table 1, Fig. 1), ranging from zero in Karelia to 71 in Kaluga (both these regions are in the European part). In the European part of Russia, there are 277 invasive species in total, in Siberia 70 and in the Far East 79. The average number of invasive species per region in Russia is 27 ± 17 (mean ± SD; median = 26). The most widespread species are *Acer negundo* and *Echinocystis lobata* (recorded in 34 regions) followed by *Erigeron canadensis* and *Elodea canadensis* (30 regions). The vast majority of species has a very limited distribution; 228 of the 354 species were recorded in only one region (Fig. 2).

Cluster analysis (Ward method; Fig. 3) based on the invasive alien species lists in regions reflected the biogeographical position of regions, placing the majority of European ones in a separate cluster that is most distant from the two Far East regions. The Siberian regions formed a separate cluster that includes some European regions that border Siberia.

Taxonomic composition, origin and life forms

The 354 species belong to 65 families and 221 genera. The greatest numbers of invasive species are found in Compositae (62 species), Poaceae (40) and Rosaceae (35) (Table 2), while 25 families are represented by only one species. The genera richest in invasive species are *Prunus* (9), *Bromus* (6), *Salix* (6), *Atriplex* (5) and *Lepidium* (5), while 37 genera are represented by two species and 144 by one species.

Using the Biodiversity Information Standards (TDWG) delineation of continents, most invasive species originate from temperate Asia (274 species) and Europe (241). In terms of proportional contribution to the total invasive flora, 78% of the species have their native range in temperate Asia, 68% in Europe, 31% in North America, 31% in Africa and 29% in tropical Asia. Despite a trend for a higher proportion of plants originating from North America and tropical Asia in the Far East, the differences among the European, Siberian and Far East regions were not significant ($\chi^2 = 4.45$, $df = 10$, $p = 0.92$). Among the top 10 species recorded in the Russian regions, eight have native ranges in North America.

The invasive flora of Russia consists of 41% perennial herbs (203 species), 28% annuals (138), 15% shrubs (77), 11% trees (57), 5% climbers (24) and 1.4% (4) aquatic species. There were significant differences in the representation of life forms among the biogeographical regions ($\chi^2 = 29.78$, $df = 10$; $p < 0.001$; Fig. 4). Perennials were marginally ($p < 0.1$) significantly over-represented in the Far East, and shrubs in the European part of Russia. Highly significantly ($p < 0.01$) under-represented were shrubs and trees in the Far East (Fig. 4).

Factors associated with regionally high numbers of invasive species

The regression tree revealed that climatic factors (average annual temperature and precipitation during the dry season), human population density and the percentage of urban population are highly important factors for shaping the richness of invasive alien flora in a Russian region (Fig. 5). There were also other factors contributing to the patterns of regional invasive species richness, as indicated by surrogates that were closely associated with the primary splitting variables: the percentage of population living in a region that is urban, and the extent of roadless area.

The three regions with PCA axis 3 scores lower than −0.79 (regions with very little precipitation in the dry season) harbour the lowest numbers of invasive species, i.e. only three on average. The surrogates for this split were the percentage of urban population, population density and PCA axis 1. Regions with a

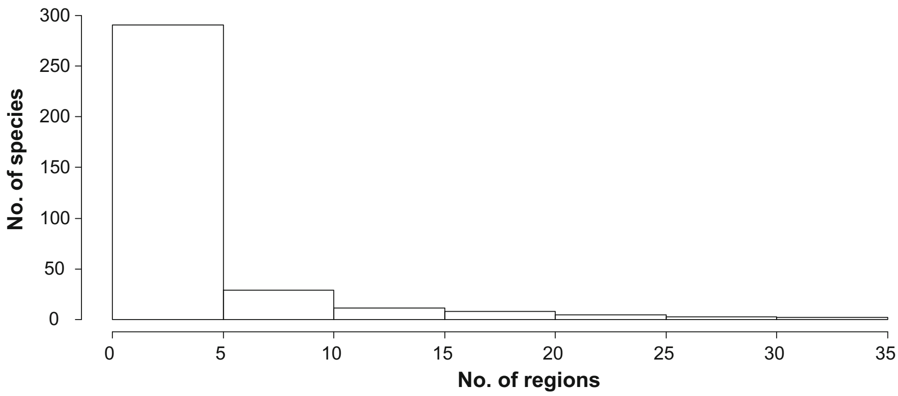

Fig. 2 Frequency distribution of invasive plant species in Russian regions (n = 45)

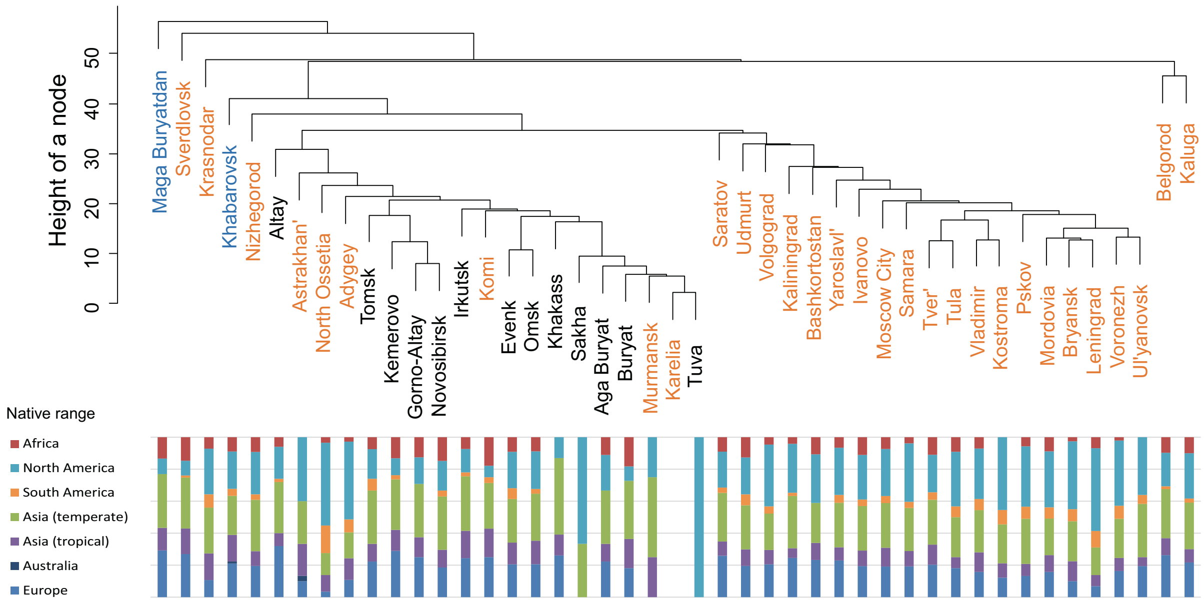

Fig. 3 Cluster tree (Ward method) showing the similarity of regions based on the invasive species composition. Regions marked by red are from the European part of Russia, black from Siberia and blue from Far East. Below the tree is shown a bar graph visualizing the proportions of origins

score above −0.79 on PCA axis 3 are richest in invasive species if, at the same time, the score on PCA axis 1, reflecting mean annual temperature, is lower than −1.26. Regions with low human population density harbour few invasive aliens, especially if there is a large extent of roadless area (Fig. 5).

Discussion

Our research yielded a dataset of 354 alien plant species that have become invasive in at least one of the 45 Russian regions for which we had data. Given that we covered more than 80% of the territory of Russia, this number is conservative and the total number of invasive plant species in Russia is likely to be higher. Nevertheless, the value of the dataset is that it is the first comprehensive treatment of the invasive flora of Russia using a standardized terminology (Richardson et al. 2000; Blackburn et al. 2011). This is important because up to now, many papers in the Russian literature on alien species (Lysenko 2010; Fomina and Tokhtar 2012) were using traditional Central-European terminology stemming from the approach of Thellung (1912) and his followers (e.g. Holub and Jirásek 1967; Schroeder 1969; see Kowarik and Pyšek

Table 2 The most represented species in the invasive flora of Russia, with information on the number of regions where they occur, continent of origin and life form

Species	Family	No. of regions	Continent of origin	Life-form
Acer negundo	Sapindaceae	34	N America	Tree
Echinocystis lobata	Cucurbitaceae	34	N America	Annual
Erigeron canadensis	Compositae	30	N America	Annual
Elodea canadensis	Hydrocharitaceae	30	N America	Perennial herb
Bidens frondosa	Compositae	24	N America	Annual
Epilobium ciliatum	Onagraceae	23	N & S America, Asia temperate	Perennial herb
Impatiens glandulifera	Balsaminaceae	23	Asia tropical	Annual
Heracleum sosnowskyi	Apiaceae	21	Asia temperate	Perennial herb
Juncus tenuis	Juncaceae	21	N & S America	Perennial herb
Solidago canadensis	Compositae	20	N America	Perennial herb
Impatiens parviflora	Balsaminaceae	19	Asia temperate	Annual
Amelanchier spicata	Rosaceae	18	N America	Shrub
Sambucus racemosa	Adoxaceae	18	N America	Shrub, tree
Erigeron annuus	Compositae	17	N America	Annual
Lupinus polyphyllus	Leguminosae	17	N America	Perennial herb
Oenothera biennis	Onagraceae	17	N America	Perennial herb
Helianthus tuberosus	Compositae	16	N America	Perennial herb
Elaeagnus rhamnoides	Elaeagnaceae	16	Asia temperate & tropical, Europe	Shrub, tree
Amaranthus retroflexus	Amaranthaceae	14	N America	Annual
Lepidium densiflorum	Brassicaceae	14	N America	Annual, perennial herb
Matricaria discoidea	Compositae	14	Asia temperate	Annual
Epilobium pseudorubescens	Onagraceae	13	Asia temperate, Europe	Perennial herb
Fraxinus pennsylvanica	Oleaceae	13	N America	Tree
Hordeum jubatum	Poaceae	13	Asia temperate	Perennial herb
Symphyotrichum salignum	Compositae	13	hybrid	Perennial herb
Xanthium albinum	Compositae	13	N America	Annual
Acorus calamus	Acoraceae	12	Asia temperate & tropical	Perennial herb
Parthenocissus inserta	Vitaceae	12	N America	Climber
Solidago gigantea	Compositae	12	N America	Perennial herb
Aronia mitschurinii	Rosaceae	11	Hybrid	Shrub
Oenothera rubricaulis	Onagraceae	11	N America	Perennial herb
Echinochloa crus-galli	Poaceae	10	Africa, Asia temperate & tropical, Europe	Annual
Saponaria officinalis	Caryophyllaceae	10	Asia temperate	Perennial herb
Ulmus pumila	Ulmaceae	10	Asia temperate	Shrub, tree

2012 for review; Pyšek et al. 2002 for comparison of terminologies). Another important feature of the present inventory is that it reflects the up-to-date current knowledge of invasive plants in individual regions because the team of authors include local experts who provided data and have the best knowledge of their territories. This makes the present dataset somewhat different from inventories that rely solely on literature sources and may therefore be in some cases outdated.

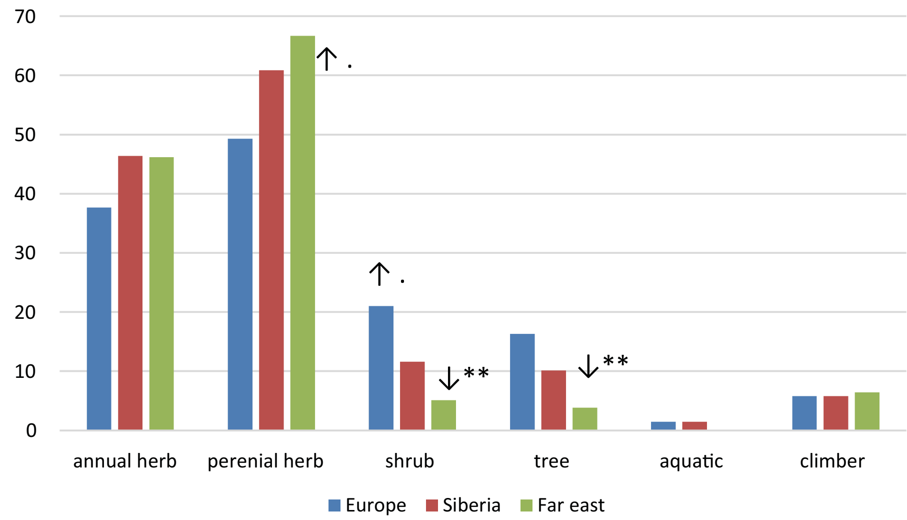

Fig. 4 Frequency distribution of life forms in the three biogeographical areas. Regions that significantly differ among the two groups (G-test, p ** < 0.01, . < 0.1) are marked by an arrow, with its direction indicating over- or under-representation within the group

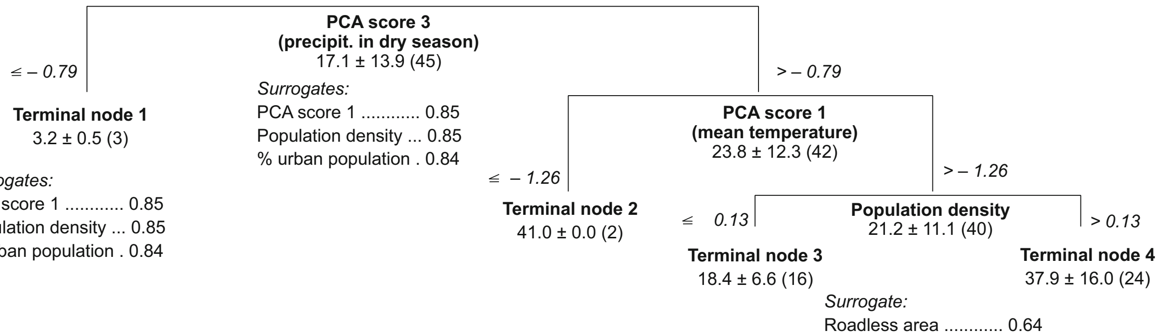

Fig. 5 Regression tree with the number of invasive plant species in a region as the explained variable. Each splitting node (splitting variable name and splitting criterion) and each terminal node show the number (mean ± SD; number of cases) of invasive species weighted by the area of the region. Surrogates are shown in cases where the association value is above 0.6

Our study, which combines data from several biogeographical regions, provides a reasonably robust picture of the most successful invasive alien plant species in Russia. Overall, we identified eight species that are present in at least half of the regions (*Acer negundo*, *Echinocystis lobata*, *Erigeron canadensis, Elodea canadensis*, *Oenothera biennis*, *Bidens frondosa*, *Epilobium adenocaulon* and *Impatiens glandulifera*). Interestingly, the four most widespread species belong to the families Sapindaceae, Cucurbitaceae, Compositae and Hydrocharitaceae, but the families with the largest numbers of invasive species are different, with the only exception of Compositae. Besides the Compositae family, which is richest in invasive species (62) and was shown in other studies to contain high numbers of alien plant species (Pyšek 1997, 1998; Daehler 1998; Pyšek et al. 2017), Poaceae (40 species) and Rosaceae (35 species) contribute most species to the invasive alien flora. This pattern is in accordance with many previous studies that explored the taxonomic structure of alien floras in the temperate zone (e.g. Lambdon et al. 2008; Pyšek et al. 2017), and might reflect that these families are among the largest ones globally.

Overall, the prevailing life forms in the Russian invasive flora are annual and perennial herbs, which account for 39% and 57% of the species, respectively. Shrubs (22%) and trees (16%) are less represented. However, there are differences in the representation of life forms among the broad biogeographical zones, with the invasive flora of the Far East having a significantly higher percentage of perennial herbs compared to shrubs and trees. We argue that this pattern is likely to be related to the particularly harsh climatic conditions in the Far East that are unfavourable for establishment and growth of woody species. This hypothesis seems to be supported by the fact that the two Far East regions are floristically somewhat distinct from other parts of Russia. Compared to the other parts of Russia, the Far East is characterized by tall herbaceous vegetation.

The highest numbers of invasive species were found in the Moscow region as might be expected due to intense human influence there. The overall pattern of invasive species richness is driven by the interaction of climate and socioeconomic factors reflecting human pressures such as the extent of roadless areas and the proportion of urban population. Human population density is a key factor positively correlated with invasive species richness, confirming the results of previous studies performed for Europe (Pyšek et al. 2010), and all other socioeconomic factors appear in our analyses only as statistical surrogates (Fig. 5). With regard to climate, results of our analyses show, that temperature is important but not the most important constraint to invasive plants in Russia; the first split in the regression tree indicates the significant role of the intra-annual distribution of precipitation in Siberia. Likewise, the two Far East regions, where the mean annual temperatures are particularly low, harbour rather rich invasive floras. One possible factor that is specific to these regions and could be partly responsible for an increased invasive species richness is the presence of ports, as coastal areas have been shown to act, in general, as invasion hotspots (Xu et al. 2012; Dawson et al. 2017). The expectations that harsh climatic conditions and low human population density act against the presence of invasive species, as found in the majority of the regions of Siberia, were confirmed by lower richness of invasive plant species than in European regions.

We conclude that despite the wide range of environmental and historical conditions, the invasive flora of Russia within each of the European, Siberian and Far East parts is rather homogeneous. This can be a result of synchrony between the historical development and limited trade within neighbouring regions and with other continents, but this situation may change rapidly in the future with changing climate and increasing trade (see e.g. Seebens et al. 2015). Such future trends might be best assessed by including data on complete alien floras, including all naturalized and casual species that are unfortunately not available at the moment.

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