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The impact of *Sorbaria sorbifolia* invasions on soil seed banks in the southern taiga of Eurasia

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This study aimed to assess how the invasion of the shrub *Sorbaria sorbifolia* affects the soil seed bank in the urban forests of Ekaterinburg (Middle Urals, Russia). We compared species composition and abundance in the above-ground vegetation and seed banks across three forest vegetation types: those dominated by the invasive shrub *S. sorbifolia*, those dominated by the native shrub *Rubus idaeus*, and those without either species. In the presence of *S. sorbifolia*, the total cover of plants in the herb-dwarf shrub layer decreased by two orders of magnitude, the species richness decreased by 4-6 times, and the number of above-ground vegetation species decreased by 3-4 times. The species composition of the seed banks differed qualitatively from that of the above-ground vegetation and showed little relationship with the different vegetation types. While the species composition and richness of the seed bank remained unaltered by the *S. sorbifolia* invasion, its size was significantly decreased by 2.0-2.4 times. The ability to negatively affect the abundance of soil seed banks demonstrates that *S. sorbifolia* can be reasonably categorized as a transformer species. Therefore, this invasive plant requires special attention, as its further dispersal could have major consequences for native vegetation.

Keywords: Alien Plants, Invasive Plants, Biodiversity, Urbanized Forests, Clonal Plants, Above-ground Vegetation, Seed Bank, *Sorbaria sorbifolia*

Introduction

The influence of invasive plants on natural communities has been studied primarily at the level of above-ground vegetation composition and structure (Vilà et al. 2011). Few studies have examined the impact of invasive plants on seed banks, which are reservoirs of propagules for community recovery after disturbance (Wearne & Morgan 2006, Gioria et al. 2014, Anju et al. 2022). The impact of invasive plants on seed banks can be low (Gioria et al. 2014, Kundel et al. 2014), but it is more commonly observed to cause decreases in seed bank density, species richness, or species diversity (Ferreras et al. 2015, Cofer et al. 2018). Seed bank composition can be affected by seed contributions from invasive species (Thompson et al. 1997), changes in the overstory community composition, and the availability of basic resources (Gioria et al. 2011).

Invasive plants with active seed propagation often form seed banks that provide the genetic diversity necessary to overcome various barriers to their persistence (Gioria et al. 2012). However, the invasion of some plant species can occur exclusively through vegetative propagation. An example of such a species is the perennial *Reynoutria japonica* Houtt., which originated in East Asia and has become one of the three most invasive terrestrial plants in the UK, with no recorded seed deposition (Manchester & Bullock 2000).

Sorbaria sorbifolia (L.) A. Braun is an invasive shrub that propagates mainly vegetatively outside its native habitat, but it has high seed productivity and germination rates. Based on the species ontogenesis analysis, we classified *S. sorbifolia* as a geoxylic, vegetatively mobile shrub (Veselkin et al. 2020). Its natural range covers Western and Eastern Siberia, the Far East, Kamchatka, Japan, Korea, China, and Central Asia. It grows along shores, in forests, and at forest edges (Firsov & Tkachenko 2016). Outside its natural range, it is considered an invasive species (colonophyte) in central Russia (Vinogradova et al. 2010) and a transformer species in the European part of Russia (Panasenko 2013), where *S. sorbifolia* can be found on roadsides, in suburban forests, parks, and wastelands. This species was introduced in Europe as an ornamental plant in the mid-XVIII century (Vinogradova et al. 2010), but has now been recorded as invasive in Poland (Tomaszewski 2001), Latvia (Jurševska 2007), Lithuania (Dobravolskaite & Gudzinskas 2011), and Finland (Lanta et al. 2013). In Latvia, *S. sorbifolia* is seen as a threat to native species (Jurševska 2007), while in Belarus, it poses a high invasion risk, with extensive thickets reported in some regions. Additionally, it is recognized as capable of becoming adventive in North America (Govaerts 2025).

S. sorbifolia naturally ranges 1000-1500 km east of Ekaterinburg, where it was introduced in the late 1950s and has since spread as thickets to many forest parks. It is known for its pollution resistance (Li-Qiang et al. 2004), and it is commonly used in landscaping, leading to its expansion beyond its native range and resulting in invasions of natural vegetation. However, the impacts of *S. sorbifolia* invasion on local plant communities remain underexplored.

Few studies have examined the impact of *S. sorbifolia* on the species composition of the herb and dwarf shrub layer within its thickets. Research indicates that species richness and coverage are significantly reduced beneath its crowns (Lanta et al. 2013, Veselkin et al. 2020) due to its ability to form dense thickets (Lipikhina et al. 2022) and high shading capacity (Veselkin et al. 2022). Lanta et al. (2015) reported that within *S. sorbifolia* thickets, the litter's chemical makeup differs from that of the

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native *Rubus idaeus*, leading to a slower decomposition rate of the leaf litter. This effect may be associated with high levels of toxic hydrogen cyanide in the leaves of *S. sorbifolia* (Kim & Zee 2000), which may have ecosystem-wide effects.

Invasive species can significantly affect the species composition of seed banks (Gioria et al. 2014, Lamb et al. 2021). A greater understanding of the long-term consequences of *S. sorbifolia* invasion is required to develop effective measures to contain it. A previous study indicated that *S. sorbifolia* did not affect the composition of soil seed banks (Veselkin et al. 2020). However, this initial research depended on a relatively small number of observations, which may have led to underestimating small but significant effects. The objective of this study was to characterize changes in the soil seed bank associated with the invasion of *S. sorbifolia*. Specifically, the following questions were formulated: (i) How are the species composition of the seed bank and the above-ground vegetation of the studied forest vegetation types related to each other? (ii) Is the seed bank species composition or seed number altered in *S. sorbifolia*-dominated vegetation types relative to non-invaded vegetation types?

Materials and methods

Study area

The study was conducted in Ekaterinburg (Russian Federation), a large city with a population of 1.5 million, in the southern taiga subzone of the boreal zone of the Middle Urals. The climate is moderately continental; the annual average temperature is +3 °C, with a January average of -12.6 °C and a July average of +19.0 °C, and the average annual precipitation is 537 mm. Pine herb forests, pine herb-dwarf shrub forests, and pine green moss forests on sod-podzolic and brown forest soils prevail in the vicinity of the city. Pollution levels in the city are high due to the large number of industrial enterprises and a dense transportation network.

Forest vegetation was studied in Uktussky and Yugo-Zapadny Forest Parks. The prevailing vegetation in these territories consists of pine stands that are remnants of formerly primary *Pinus sylvestris* forests dating to before the onset of urban development. The stands are relatively even-aged, with most trees 90-120 years old. Uktussky Forest Park is located on the southern outskirts of the city, 7-11 km from the center, and partially borders suburban forests. The forest park lies in the northern part of the Uktus Mountains, where basic and ultrabasic rocks are exposed at the ground surface in some areas. Yugo-Zapadny Forest Park is located 5-7 km from the city center and is surrounded by areas that have been heavily developed over the last 45-50 years. The relief is gently sloping; soils are typical, podzolized, brown, slightly to medium stony, and well-drained.

Pine forests in Uktussky Forest Park have a herb-dwarf shrub layer (total cover: 70%-85%) with a high abundance of typical forest and forest-margin species (*Calamagrostis arundinacea, Vaccinium myrtillus, Brachypodium pinnatum, Carex digitata, Pteridium latiusculum, Rubus saxatilis*) and a shrub layer (total cover: 1%-50%) with native species such as *Rosa acicularis, R. majalis, Rubus idaeus* and alien species like *Cotoneaster lucidus, Ribes alpinum*, etc. The herb layer of pine forests in the Yugo-Zapadny Forest Park has a total cover of 40%-90% and is dominated by *Calamagrostis arundinacea, Carex montana, Glechoma hederacea, Aegopodium podagraria,* and *Urtica dioica*. A common feature of the communities in both forest parks is a pronounced layer of tall shrubs and understory trees that includes many alien species. The moss layer is fragmentary (Veselkin et al. 2020).

Experimental design

We selected several sites in the Uktussky and Yugo-Zapadny forest parks, taking care of including the three types of vegetation therein: those dominated by *S. sorbifolia* thickets (henceforth: "*S.sor.*") had sizes ranging from 20×30 m^2 to 50×100 m^2 and, on average, an above-ground density of 22 shoots m^2. Forest vegetation dominated by *Rubus idaeus* L. ("*R.ida.*") was chosen as a phylogenetically related species (family Rosaceae) with the same life form (geoxylic vegetatively mobile shrub). Forest vegetation without either of the above species ("*forest*") was selected for comparison.

The above-ground vegetation was recorded in June-July 2019 for each vegetation type at the three selected sites (two sites in Uktussky Forest Park and one in Yugo-Zapadny Forest Park) and six sites in

Fig. 1 - Seed bank vegetation pots in a polycarbonate greenhouse (a). Each pot (b) represents one independent soil sample (pot size 20 × 15 × 10 cm, soil volume in the pot 2 dm^3).

2020 (three in Uktussky and three in Yugo-Zapadny). At each site, three replicate 10 m^2 plots were used. In 2019, three sites were studied, and three relevés (in *S.sor.*, *R.ida.*, and *forest*) were made at each site, *i.e.*, nine relevés in total. In 2020, three more sites were added to the three previously studied sites, and three vegetation types were also studied at each site. The sites studied in 2019 were investigated again in 2020. A total of 18 relevés were completed in 2020.

The aboveground species composition and total plant cover (%) were recorded. Species richness was estimated as the number of species per 100 m^2, and the Shannon index was calculated. Species were grouped based on: (i) life forms, divided into the broad groups of shrubs (shrubs, dwarf shrubs, and dwarf semishrubs), herbs (dicotyledonous and monocotyledonous herbaceous plants with broad leaves), graminoids (grasses, sedges, and rushes), and cryptogams (ferns, club mosses, and horsetails); and (ii) seed dispersal mode, divided into autochores, anemochores, and zoochores (Vittoz & Engler 2007). Plant names were given according to Govaerts (2025).

The seed banks of each plot were assessed in the 0-5 cm layer where most viable seeds accumulated (Ferreras et al. 2015). After the removal of surface forest litter, three replicate samples of 2 dm^3 each were collected from each plot to obtain a representative measure of species diversity (Shen et al. 2014, Lamb et al. 2021). The samples were taken from plots separated by several meters. Overall, we collected 27 soil samples in 2019 (3 sites × 3 plots × 3 samples) and 54 in 2020 (6 sites × 3 plots × 3 samples). The distance between the sites was 140-300 m in Uktussky Forest Park and 70-2,570 m in Yugo-Zapadny Forest Park. The distance between the Forest Parks was ~ 7 km.

The seed bank samples were analyzed using the seedling emergence technique (Thompson & Grime 1979). Briefly, each soil sample was sieved through a 5-8 mm mesh sieve to remove residual litter, and then placed in a 20 × 15 × 10 cm pot (~2 dm^3 soil per pot) under greenhouse conditions with moderate irrigation (Fig. 1). Seedling germination was assessed once a month for four months after placement. Each month, emergent seedlings were removed for plant identification, which, in some cases, was limited to the genus level. Those that could not be taxonomically distinguished during germination were replanted in separate pots for later identification based on post-germinal aspects of morphology.

Statistical analysis

In the statistical analysis of the aboveground vegetation and seed bank data, significance testing was conducted using the STATISTICA v. 8.0 package (StatSoft Inc., Tulsa, OK, USA). Two-way ANOVA with Tukey's tests was used for pairwise comparisons of continuous mean values. The response variables were the richness and diversity of forest vegetation types, and the explanatory variables were forest vegetation types (*S.sor.*, *R.ida.*, *forest*) and years (2019, 2020). Categorical and proportional data were arcsine-transformed prior to ANOVA. χ^2 tests were used to compare fractions, and the Pearson's correlation coefficient (r) was calculated to assess the relationship between variables. The observation unit was; (i) the value of a variable in a relevé (*i.e.*, in one study plot) when analyzing the above-ground vegetation; (ii) the average value of a variable in three vegetation pots with soil from one vegetation type when analyzing data on seedlings grown from the soil seed bank. Variables expressed in fractions were arcsine-transformed prior to ANOVA. Rarefaction curves were evaluated using the software EstimateS v. 9.1.0 (https://osf.io/su57f/overview).

The relationship between the aboveground vegetation and the seed bank was examined using non-metric multidimensional scaling (NMDS), which is considered the best method for graphical representation of floristic relationships (Clarke 1993). NMDS was built using a Jaccard's similarity coefficient (J) based on the presence/absence of species to facilitate comparison of data types from the above-ground vegetation surveys (percent cover) and the below-ground soil seed bank surveys (count data). NMDS and J were calculated using PAST v. 2.17 software (Hammer et al. 2001). J coefficients were first used to compare species composition between the soil seed bank and above-ground vegetation at each study site. Sørensen's similarity index was then calculated as $J = [2C/(A + B - C)] \times 100$, where C is the number of species shared by both samples, and A and B are the number of species in samples A and B, respectively. The indices were statistically compared using a Kruskal-Wallis H test.

Results

Species richness of aboveground vegetation and seed banks

The lowest species diversity and total aboveground cover were found in *S.sor.* sites, with 4-6 times lower species richness (average number of species per 100 m^2), a 2-2.5 times lower Shannon index, and 100-200 times lower ground cover in the herb-dwarf shrub layer (Tab. 1). Considering the data from all three types of forest vegetation, estimates of species richness and shrub layer cover showed a negative and significant correlation ($r = -0.67$; $n = 27$; $p = 0.0001$), whereas species richness and coverage by the herb-dwarf shrub layer were positively related ($r = 0.90$; $n = 27$; $p < 0.0001$).

The species richness in seed banks did not differ significantly among the three vegetation types, although the Shannon indices were slightly higher in soils from *S. sor.* than in *R.ida*. However, the viable seed density (estimated over four months from germination tests) was 2-2.4 times lower in *S.sor.* than in the other vegetation types. Species richness and the density of viable seeds in seed banks were not correlated with each other ($r = 0.06$; $n = 27$; $P = 0.7843$).

Species compositions of aboveground vegetation and seed banks

The species composition of aboveground vegetation and seed banks differed qualitatively, as indicated by a low mean J coeffi-

Tab. 1 - Species richness and mean abundance estimates (± standard error) of forest vegetation types without *Sorbaria sorbifolia* and *Rubus idaeus* (*forest*), dominated by *Rubus idaeus* (*R.ida.*), and dominated by *Sorbaria sorbifolia* (*S.sor.*).

Component	Characteristics	Forest vegetation types			Significance (P) in two-way ANOVA		
		forest	*R.ida.*	*S.sor.*	Vegetation type (1)	Year (2)	(1)×(2)
Aboveground vegetation	Number of species of all layers per 100 m^2	54.0 ± 2.8	37.2 ± 3.9	8.2 ± 1.5	<0.0001	0.9801	0.4691
	Shannon index for the herb-dwarf shrub layer	2.3 ± 0.1	1.9 ± 0.1	0.9 ± 0.1	<0.0001	0.6695	0.3170
Total cover of aboveground parts, %	Shrubs and understory	54.1 ± 16.2	109.8 ± 9.9	123.1 ± 9.0	0.0044	0.6461	0.8045
	Herb-dwarf shrub layer	74.4 ± 5.2	43.2 ± 10.0	0.3 ± 0.1	<0.0001	0.4669	0.2538
Seed bank	Number of species in three pots	15.1 ± 1.2	12.1 ± 0.9	13.1 ± 1.7	0.3946	0.5060	0.7636
	Shannon index	1.9 ± 0.2	1.3 ± 0.1	2.0 ± 0.2	0.0183	0.3895	0.8445
	Number of seedlings in three pots, ind.	109.0 ± 17	129.0 ± 24	53.0 ± 9	0.0136	0.9637	0.1672

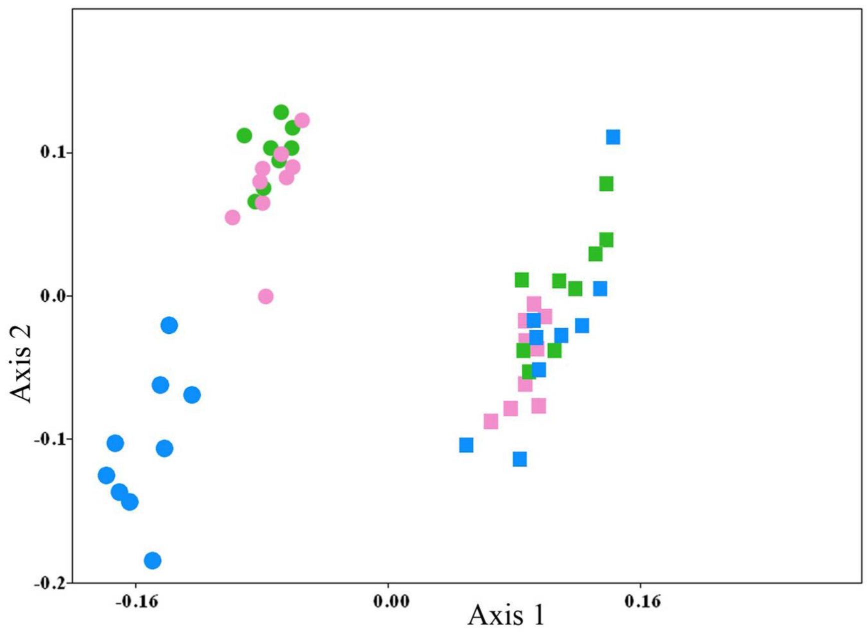

Fig. 2 - Two-dimensional non-metric multidimensional scaling (NMDS) ordination of soil seed banks and aboveground vegetation (stress value = 0.18). Ordination is based on presence/absence data. (Circles): above-ground vegetation; (squares): seed bank; (blue): forest vegetation type dominated by *Sorbaria sorbifolia*; (pink): dominated by *Rubus idaeus*; (green): without *Sorbaria sorbifolia* and *Rubus idaeus.*

cient (8.1% ± 4.7%) across vegetation types (Fig. 2). Two clusters of relevés stood out in the above-ground vegetation. A separate but not very compact cluster is the *S. sor.* relevés (the mean *J* similarity coefficient within this group was 31.0% ± 14.5%). The *R.ida.* and *forest* vegetation types were also not very homogeneous; the similarity coefficients within these types were 30.0% ± 9.4% and 37.5% ± 10.5%, respectively. The *S.sor.* differed significantly in species composition from the other types: the average *J* values were 8.8% ± 5.4% between *S.sor.* and *forest,* and 11.6% ± 7.1% between *S.sor.* and *R.ida.*, while the average *J* value 32.8% ± 10.1% between *R.ida.* and *forest* was higher (H=10.3; n=108; df=2; p=0. 0059).

No noticeable features were found in the species composition of seed bank seedlings from different vegetation types. Within types, the average *J* values were low (26.0% ± 11.6% for *S.sor.*, 28.9% ± 9.0% for *R.ida.*, 25.0% ± 7.2% for *forest*) and between types were low too (26.1% ± 10.2% for *S.sor. - R.ida.*, 23.6% ± 8.1% for *S.sor. - forest*, 25.8% ± 10.4% for *R.ida. - forest*). Seedling composition did not differ among *S.sor.*, *R.ida.*, and *forest* vegetation types (*H*=3.6; n=108; *df*= 2; p=0.1681). This is evidenced by the lack of divergence of seed bank-related points in the ordination diagram (Fig. 2).

The similarity of seed bank species composition to above-ground vegetation within vegetation types was generally low, as indicated by a low mean *J* coefficient (8.1% ± 4.7%). However, in *R.ida.* and *forest* vegetation types, the average *J* values were 12.0% ± 4.0% and 10.2% ± 3.1%, respectively. The similarity in species composition was significantly lower in *S.sor.* (*J*=5.5% ± 3.9%; *H* =85.5; n=243; *df*=2; *p*<0.0001).

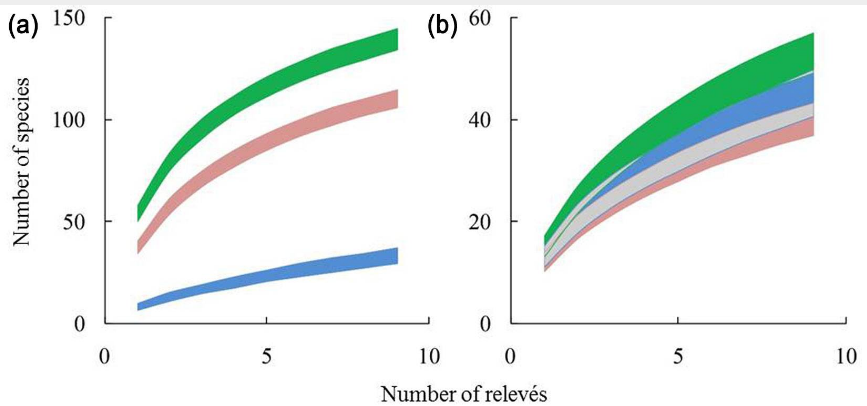

Fig. 3 - Rarefaction curves of the number of detected aboveground vegetation species (a) and species from the soil seed bank (b) by increasing in the number of surveyed plots in forest vegetation types without *Sorbaria sorbifolia* and *Rubus idaeus* (*forest* - green fill), dominated by *Rubus idaeus* (*R.ida.*, pink fill), and dominated by *Sorbaria sorbifolia* (*S.sor.*, blue fill). The width of the bands correspond to 2×SD.

Taxonomic diversity and group composition of aboveground vegetation and seed banks

Over both the study years, 155 species of higher plants belonging to 111 genera and 49 families were identified in the aboveground vegetation (Tab. 2). The seedling emergence assay indicated that seed banks contained half that number, with the identification of 72 species belonging to 53 genera and 24 families (see Tab. S1 in the Supplementary material for a complete list of species found in the above-ground vegetation and the seed banks).

Herbs formed the largest proportion of species (59%-78%) in both the aboveground vegetation and the seed banks. However, annual and biennial herbs were detected only in the seed banks. The proportion of woody plant species (including trees, shrubs, and dwarf shrubs) in the seed banks was also two times lower than in the aboveground vegetation. In terms of seed dispersal mode, the aboveground vegetation species were represented by autochores (including ballistae), anemochores, and zoochores in approximately equal proportions (29%-39% each). The seed bank was dominated by autochores (44%), with fewer anemochores (31%) and zoochores (25%). The proportion of autochores was significantly higher than the proportion of zoochores (χ^2=6.01; *df*=1; *p*=0.0143).

We identified 49 species common to both the seed bank and the above-ground vegetation, primarily consisting of forest and edge species, including perennial herbs, graminoids, and woody plants. The most consistently observed species were *Carex digitata, Fragaria vesca, Glechoma hederacea, Luzula pilosa, Poa palustris, P. pratensis, P. trivialis, Rubus idaeus, Urtica dioica, Veronica chamaedrys,* and *Viola nemoralis*.

There were 106 species recorded only in the above-ground vegetation. The dominant above-ground vegetation species, including *Aegopodium podagraria, Brachypodium pinnatum,* and *Rubus saxatilis,* were not identified in seed banks. Conversely, 23 species were detected only in seed banks and consisted mostly of perennial, annual, or biennial herbs that are considered edge or ruderal species. These species did not contribute to many seedlings and appeared due to accidental drift. The most consistently detected species in this group were *Androsace filiformis, Cardamine amara, Melilotus* sp. (*M. officinalis* + *M. alba*), *Sonchus arvensis,* and *Stellaria media*. Of the species detected in the seed banks, 69% were represented by few seedlings (1-

Tab. 2 - Taxonomic diversity and group composition of above-ground vegetation and seed banks of forest vegetation types without *Sorbaria sorbifolia* and *Rubus idaeus* (forest), dominated by *Rubus idaeus* (*R.ida.*) or *Sorbaria sorbifolia* (*S.sor.*). Cumulative data for 2019-2020. The proportion of different life forms and dispersal modes are reported in parenthesis.

Group	Characteristics	Above-ground vegetation				Seed bank			
		total	*forest*	*R.ida.*	*S.sor.*	total	*forest*	*R.ida.*	*S.sor.*
Taxonomy	Number of species	155	139	110	33	72	53	40	45
	Number of genera	111	105	80	31	53	38	32	38
	Number of families	49	47	43	20	24	22	20	21
Life forms	Trees	13 (8.4%)	11 (7.9%)	11 (10.0%)	8 (24.2%)	3 (4.2%)	2 (3.8%)	3 (7.5%)	1 (2.2%)
	Shrubs, dwarf shrubs	25 (16.1%)	19 (13.7%)	21 (19.1%)	6 (18.2%)	4 (5.5%)	2 (3.8%)	2 (5.0%)	4 (8.9%)
	Herbs	91 (58.7%)	84 (60.4%)	62 (56.4%)	11 (33.4%)	56 (77.8%)	43 (81.1%)	27 (67.5%)	34 (75.6%)
	Graminoids	16 (10.3%)	15 (10.8%)	10 (9.1%)	4 (12.1%)	9 (12.5%)	6 (11.3%)	8 (20.0%)	6 (13.3%)
	Cryptogams	10 (6.5%)	10 (7.2%)	6 (5.4%)	4 (12.1%)	0	0	0	0
Seed dispersal modes	Autochores	45 (29.0%)	42 (30.2%)	30 (27.3%)	6 (18.2%)	32 (44.4%)	23 (43.4%)	15 (37.5%)	20 (44.5%)
	Anemochores	60 (38.7%)	53 (38.1%)	35 (31.8%)	14 (42.4%)	22 (30.6%)	16 (30.2%)	14 (35.0%)	14(31.1%)
	Zoochores	50 (32.3%)	44 (31.7%)	45 (40.9%)	13 (39.4%)	18 (25.0%)	14 (26.4%)	11 (27.5%)	11(24.4%)

10). Of the seedlings, 73% belonged to five taxa: *Betula* sp. (6%, *B. pendula + B. pubescens), Rubus idaeus* (29%), *Veronica chamaedrys* (7%), *Viola nemoralis* (5%), and *Urtica dioica* (26%).

At the species level (Fig. 3), the taxonomic diversity in above-ground vegetation in *S.sor.* was four times lower (33 ± 4 species in nine relevés) than in the *forest* (139 ± 5 species in nine relevés). In contrast, the taxonomic diversity in seed banks differed little between the *S.sor., R.ida.,* and *forest* vegetation types (40 ± 3 to 53 ± 4 species in nine plots). Changes in the diversity characteristics of seedlings from the soil seed bank due to the high abundance of *S. sorbifolia* were not observed either in the first year of the study or at the end of the two-year period.

Discussion

Our results on the effect of *S. sorbifolia* invasion on species composition indicated that this invasive species had no significant impact on seed bank composition, which confirms our earlier study (Veselkin et al. 2020). However, aboveground taxonomic diversity in *S. sorbifolia* thickets was lower than in other forest habitats. In addition, the similarity between the aboveground vegetation and seed bank composition in the *S. sorbifolia*-dominated vegetation type was also lower than in other vegetation types in the local forest.

In both native vegetation types and *S. sorbifolia* thickets, the species composition of the seed bank and aboveground vegetation was observed to vary significantly. The presence of a small proportion of aboveground species in the seed bank is characteristic of forests (Petrov 1989, Anju et al. 2022) and other plant communities (Wearne & Morgan 2006). Seed banks in stable vegetation types are short-lived, and most forest species do not form a permanent seed bank (Thompson et al. 1998). According to our estimates, the seed bank species composition across the three studied vegetation types was more similar to each other than to that of the above-ground vegetation. This pattern has also been reported in other seed bank studies (Gooden & French 2014, Ferreras et al. 2015). Most species represented in the seed banks are herbaceous, while of the 13 tree and 25 shrub/dwarf shrub species observed in the aboveground vegetation, only 3 and 4, respectively, were detected in the seed banks. This agrees with the generally observed predominance of herbs and the low representation of woody species in forest seed banks (Anju et al. 2022). The composition of the above-ground vegetation and the seed banks differed in seed dispersal mode, with the seed banks showing a significantly higher number of autochores. The invasion of plant communities by *Stenotaphrum secundatum* (Walter) Kuntze was shown to reduce the number of seedbank zoochores in endangered coastal swamp forest seed banks of eastern Australia (Gooden & French 2014). However, our study indicated that the group ratio, based on seed dispersal mode in seed banks, was unaffected by *S. sorbifolia* invasion.

We observed inconsistencies between the species composition of aboveground vegetation and seed banks. Some dominant species in the herb and dwarf shrub layers were absent from their corresponding seed banks. This could be due to reduced seed production from asexual reproduction (e.g., *Aegopodium podagraria*) or because some species require specific germination conditions not tested in our assays (*Brachypodium pinnatum* needs long cold stratification), or both (*Rubus saxatilis*) (Nikolaeva et al. 1985). The most abundant and common species in the seed bank of pine forests are pioneer species such as *Betula* sp., *Luzula pilosa, Rubus idaeus,* and *Urtica dioica,* which usually germinate *en masse* when the tree canopy is disturbed. These species are often found in the seed banks of boreal forests that have experienced some anthropogenic impact (Granström 1982). The large number of seeds of these species in the soil can be explained by their survival from previous stages of community development and by the presence of fruiting individuals in the modern urbanized vegetation of Ekaterinburg.

Based on two years of observations (2,626 seedlings), we obtained statistically reliable evidence of a decrease in the seed bank abundance in *S. sorbifolia*-invaded forest vegetation. This contrasts with our earlier study, which was based on fewer observations and failed to detect any significant differences (Veselkin et al. 2020). However, the effects of *S. sorbifolia* invasion on seed bank density were not accompanied by any significant alterations to the seed bank species richness and diversity. This distinguishes *S. sorbifolia* from many invasive plants that negatively affect all seed bank characteristics (Gioria et al. 2014, Ferreras et al. 2015, Cofer et al. 2018, Alharthi et al. 2021). The effects of *S. sorbifolia* on the seed bank are consistent with those of the invasive shrub, *Cytisus scoparius* (L.) Link, which has also been reported to decrease seed bank density without significantly affecting species richness in subalpine vegetation (Wearne & Morgan 2006).

According to our observations, *S. sorbifolia* contributes little to the seed banks in the local forests of Ekaterinburg (4 *S. sorbifolia* seedlings were identified in 2019 and 26 in 2020). This contrasts with other invasive shrubs such as *Cytisus scoparius* (Wearne & Morgan 2006), *Rhododendron maximum* L. (Cofer et al. 2018), and *Nicotiana glauca* Graham (Alharthi et al. 2021) and likely reflects the predominantly asexual propagation of *S. sorbifolia* outside its native range (Lipikhina et al. 2022). It is known that clonal invasive plant species usually have a stronger impact on the species richness of native communities compared to sexually reproducing invasive plants (Vilà et al. 2015), which is consistent with our observations.

Generally, it is acknowledged that without replenishing seed stocks from vegetation, the number of viable seeds in seed banks will decline exponentially due to aging, as well as the impacts of phytophages and pathogens. (Roberts & Feast 1973). The displacement of native species from communities due to conditions created by invasive species is considered the main cause of seed bank depletion (Gioria & Osborne 2009). Two reasons can be hypothesized for seed bank depletion in the *S. sorbifolia* thickets: (i) seed production is reduced due to the low abundance and diversity of plants in *S. sorbifolia* thickets (Veselkin et al. 2020), and (ii) seed deposition from surrounding forest plant communities is reduced due to the high stem density and dense canopy of *S. sorbifolia* (Lipikhina et al. 2022). The latter pattern has been demonstrated in *Cytisus scoparius* thickets (Wearne & Morgan 2006). Light competition is recognized as a major driver in the impact of invasive species on plant communities. Many invasive species form dense canopies, which can significantly reduce the amount of light available to native species (Cusack & McCleery 2014, Berg et al. 2017). In comparison to aggressive invaders like *Fallopia japonica, Gunnera tinctoria* and *Heracleum mantegazzianum* (Gioria et al. 2014), which have large, fully developed leaves, *S. sorbifolia* has leaves that are more openwork in structure. Nonetheless, it creates a dense, multilayered canopy that intercepts about 93% of the incident light (Veselkin et al. 2022). Thus, *S. sorbifolia* not only suppresses the growth of smaller native plants, reducing their contribution to the seed bank, but also likely physically hinders seed deposition from surrounding plant communities.

Conclusions

The invasion of *S. sorbifolia* into the forest vegetation of the Middle Urals has been accompanied by a noticeable transformation of the above-ground vegetation (species richness, total cover, composition). In contrast, *S. sorbifolia* has no significant impact on seed bank species composition, but it significantly reduces the total number of seeds present. The likely ways *S. sorbifolia* affects seed banks are through its influence on growth conditions, which in turn impacts seed production for native species, and by physically obstructing seed deposition from surrounding plant communities. Our studies indicate that seed banks in *S. sorbifolia*-invaded forest vegetation could significantly reduce the capacity of native communities to regenerate, even after complete removal of the invasive species. *S. sorbifolia* is one of the few invasive species in the Middle Urals capable of vegetative growth, and it has demonstrated long-term persistence in closed, relatively undisturbed forest communities. Understanding the mechanisms underlying the success of *S. sorbifolia* invasion is necessary for an objective assessment of its potential long-term consequences for natural plant habitats and its current popular use in urban landscaping. The ability to reduce seed abundance in the soil demonstrates that *S. sorbifolia* is reasonably categorized as a transformer species requiring special attention, as its further dispersal can have major consequences for native vegetation.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Author Contributions

Conceptualization: Veselkin DV, Zolotareva NV; Methodology: Zolotareva NV, Podgaevskaya EN; Formal analysis and investigation: Veselkin DV, Zolotareva NV, Podgaevskaya EN, Lipikhina YuA; Writing - original draft preparation: Zolotareva NV, Lipikhina YuA; Writing - review and editing: Veselkin DV, Zolotareva NV, Podgaevskaya EN, Lipikhina YuA; Funding acquisition: Veselkin DV; Resources: Kiseleva OA; Supervision: Kiseleva OA.

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Supplementary Material

Tab. S1 - The complete list of species found in the aboveground vegetation and seed banks of three types of forest vegetation, with the dominance of *Sorbus sorbifolia* (*S.sor.*), with the dominance of *Rubus idaeus* (*R.ida*), and without either species (forest).

Link: Lipikhina_4791@suppl001.pdf