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Effect of the Rooting Activity of Wild Boar *Sus scrofa* on Plant Communities in the Middle Taiga of Western Siberia

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Abstract—Wild boar is an ecological engineer whose feeding activity can significantly influence the structure and composition of plant communities. The purpose of this study was to analyze the restoration of plant cover on wild boar rootings in areas recently colonized by wild boar in the north of Western Siberia compared to other parts of its range. The data were collected in four types of plant communities typical for the middle taiga subzone in Western Siberia. The rooting activity of wild boar led to a decrease in the projective cover and species richness of the herbaceous–dwarf-shrub and moss–lichen layers in the forest communities in the middle taiga of Western Siberia. The plant cover on the rootings was regenerated only by species that are typical of the original plant community. Unlike most other parts of the range of wild boar, in our study area we did not observe an increase in floristic species richness due to colonization or rootings by explerent plant species. This probably resulted from the initial low species richness of the northern plant communities.

Keywords: wild boar, *Sus scrofa*, Western Siberia, range expansion, plant communities, rooting activity
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INTRODUCTION

Some biological species can change, create, and maintain their habitats during their life activity (Jones et al., 1994). One of these edificator species is wild boar *Sus scrofa* L., 1758; its trophic activity is a strong factor determining the heterogeneity and dynamic processes of the vegetation cover of its habitats (Toropova, 1994; Kotanen, 1995; Onipchenko and Golikov, 1996; Evstigneev et al., 1999; Barrios-Garcia and Ballari, 2012). Wild boars not only modify the vegetation of the herbaceous layer but also can influence the formation of deciduous and coniferous forest stands (Lebedeva, 1956; Dinesman, 1961; Ickes et al., 2001; Siemann et al., 2009). Within the historical range, wild boar proves to be a necessary component of biogeocenoses; its ecological engineering activity contributes to an improvement of the quality of restoration processes in the ecosystem and an increase in its stability (Bulakhov, 1975; Bulakhov et al., 2015) and preconditions the normal development of populations of some plant species (Gornov, 2005; Evstigneev and Ekimova, 2008; Gornov, 2014).

However, the spread of edificator species (keystone species) beyond their range and their penetration into native ecosystems can lead to changes in the characteristics of natural communities and their destabilization (*A Global Strategy…*, 2001). This also applies to wild boar, which began to actively spread from the western and southern remote areas of Russia to the north and east (Danilkin, 2002) and develop new habitats from the mid-20th century. In the early 1980s, wild boars were first recorded in the northern part of Western Siberia, namely, in the Khanty-Mansi autonomous okrug–Yugra (KhMAO–Yugra) (Azarov, 1995) and have formed a stable population in the western and southern parts of the autonomous okrug to date (Markov et al., 2019). The issue of the response of local ecosystems to the appearance of the new species (wild boar), a polyphage that is much more highly specialized in searching for food below the ground than brown bear typical of this area (Vasin et al., 2015), is of great interest in terms of the conservation of natural communities in the taiga zone under the conditions of the penetration of the new "ecological engineer" species.

The purpose of this study is to assess the pattern of restoration of vegetation cover on wild boar rootings in ecosystems that are typical of middle taiga in Western Siberia. In particular, we (1) consider the species composition of plants and the state of the plant cover in sites disturbed by wild boar compared to the control,

(2) analyze changes on boar rootings of different ages with respect to these parameters, and (3) compare the trends in vegetation variation on wild boar rootings in different regions.

STUDY AREA

We carried out studies in the subzone of middle taiga in the northwestern part of Western Siberia, namely, in two sites in Berezovsky and Sovetsky districts (Khanty-Mansi autonomous okrug–Yugra).

The study area is characterized by severe snowy lengthy winters, short summers, and late spring and early autumn frosts. The average annual air temperature was –2.1°C in the nature reserve (1950–1969, Khangokurt Station). Since 1981, the average annual air temperature has increased by about 0.5°C from decade to decade. The average annual temperature has been –1.3°C over the past 30 years. The coldest month is January (–20.5°C) and the warmest one is July (17.4°C). The average period of snow cover is 194 days (over 6 months) and its height reaches 40–87 cm. The average duration of the frost-free season is 90 days (from June 6 to September 4) and that of the growing season is 140 days (Talanova, 2018).

Site 1 was in the Malaya Sosva River basin, in the northern part of the Malaya Sosva Nature Reserve (coordinates of the site center: 62°22′ N, 64°05′ E), where wild boars have been recorded since 1998. The northern part of the reserve is located within the Lower Ob depression and characterized by a flat relief (with the general slope to the north) disturbed by natural levee and ridge systems. The main plant communities include forests dominated by Scots pine (*Pinus sylvestris*) and Siberian pine (*Pinus sibirica*), lingonberry (*Vaccinium vitis-idaea*), and green mosses (*Pleurozium schreberi*, etc.), as well as swampy sphagnum pine forests.

Site 2 was in the basin of the upper current of the Konda River, on the territory of the Upper Konda Nature Reserve (coordinates of the site center: 60°45′ N, 63°23′ E). The relief is flat. There are elevated areas (steep slopes) along the river channels. The stand is formed mainly by Scots pine; lichens (*Cladonia* sp.) and green (*Pleurozium schreberi*, etc.) and sphagnum (*Sphagnum* sp.) mosses prevail in the ground layer. There are dark-coniferous forests formed by Siberian spruce (*Picea obovata*) and Siberian pine in the floodplains of rivers, in swampy lowlands, and on loams. Deciduous forests—birch forests (*Betula pubescens*) and aspen forests (*Populus tremula*)—are widespread along the banks of rivers and streams and in burned and cleared areas. The southern part of the territory is characterized by vast swampy areas. A large area in the nature reserve is occupied by various types of bogs.

MATERIALS AND METHODS

The works were carried out in July 2017 and 2018 during the period of maximum vegetation development. We studied areas where wild boars or signs of their activity were previously recorded.

Soil surface areas with signs of ground cover removal and other signs of the activity of this species in the nearby area were considered wild boar rootings. The rooting intensity of the animals was estimated by calculating the rooting areas. If the damaged surface was round or almost round, two perpendicular diameters were measured and the rooting area was calculated as the product of the two measurements. If the shape of rooting was oval, its maximum length and width were measured at three points: in the center and near the edges. In this case, the rooting area was calculated using the arithmetic mean of the three width measurements, multiplied by the length. The rooting type (litter type or soil types (continuous, diffuse, or point rooting) was determined according to Lebedeva (1956).

To compare the feeding activity of wild boars in different habitats, we estimated the area (S) of separate rootings and index of rooting intensity as the area of rootings per 1000 m^2 of the studied plots.

Rootings were divided into three groups with respect to their "age": fresh (of the current year), 1–2 years old, and 2–3 years old. Rootings were classified into these groups according to their external appearance, the presence/absence of last year's litter, soil looseness, the presence/absence of plant regeneration, and the age of coniferous seedlings. Rootings with clear animal footprints or rootings that were not covered with last year's leaf or needle litter were considered "fresh." The age of rootings that were not defined as "fresh" was determined by the age of coniferous seedlings found in the rooting. Since it is almost impossible to reveal winter rootings in summer, it is highly probable that all the recorded vegetation disturbances were made by wild boars in the snowless period.

Changes in the state of plant communities in rootings older than one year were evaluated by comparing the composition of the vegetation cover on the rooting with a 0.25 m^2 site located in the same biotope at a distance of no less than 1 m from the rooting. Plants from each revegetating rooting were recorded in the form of a species list; the total projective cover (in %) and projective cover (hereinafter, PC) of each plant species (or group of plant species) were determined; the control site adjacent to the rooting was described in the same way. We also made a general geobotanical description of habitats in which rootings were found (*Metody geobotanicheskikh issledovanii*..., 1996).

Vegetation on rootings was described for four types of forest habitats (Table 1) where the rooting activity of wild boar was revealed: mixed coniferous–deciduous forest (N = 18), lichen Scotch pine forest (N = 45),

Table 1. Characteristics of the studied types of wild boar habitats in the Konda–Sosva Ob region

Habitat type	Number of plant descriptions on rootings	Prevailing plant species in the layer			Projective cover of the layer (min–max), %	
		tree layer	herbaceous–dwarf-shrub layer	moss–lichen layer	herbaceous–dwarf-shrub layer	moss–lichen layer
Mixed coniferous–deciduous forest	18**	*Pinus sylvestris*, *Betula pubescens*, *Larix sibirica*	*Vaccinium vitis-idaea*, *Vaccinium myrtillus*, *Diphasiastrum complanatum*, *Maianthemum bifolium*, *Oxalis acetosella*, *Linnaea borealis*	*Pleurozium schreberi*	40–85	0–70
Lichen Scotch pine forest	45**	*Pinus sylvestris*	*Festuca ovina*	*Cladonia* sp.	5–25	45–100
Grass birch forest	7*	*Betula pubescen*	*Maianthemum bifolium*, *Trientalis europaea*, *Orthia secunda*, *Pyrola minor*	–	25–35	–
Green-moss Siberian pine forest	13*	*Pinus sibirica*	*Vaccinium vitis-idaea*, *Equisetum sylvaticum*, *Oxalis acetosella*, *Linnaea borealis*	*Pleurozium schreberi*	40–80	20–100

* One year of observations.
** Two years of observations.

grass birch forest ($N = 7$), and small-grass Siberian pine forest ($N = 13$). The sample size was determined by the number of wild boar rooting. The dynamics of vegetation restoration was observed on the basis of repeated (in 2017 and 2018) descriptions of plots established on rootings in mixed forests ($N = 7$), birch forests ($N = 7$), and lichen pine forests ($N = 15$).

The cenotic significance of plant species on rootings of different ages was estimated using the frequency of occurrence calculated as the ratio of the number of plots where the species was recorded to the total number of plots (Tikhodeeva, 2015). This index was chosen for reason of the very low values of the projective cover for all plant species in the revegetating.

To estimate the species similarity of rootings 1–2 years old and undisturbed sites, we calculated two coefficients:

(1) The number of herbaceous plant species (regardless of the number of individuals).

(2) Jacquard species similarity coefficient (JC). This index was calculated for the series of control plots, which were pairwise compared with each other (JC1). This made it possible to estimate the variability of the herbaceous cover within the same habitat type. The Jacquard coefficient was also calculated for "control–rooting" pairs of plots by evaluating changes in the species composition of plants on the rooting compared to the undisturbed site (JC2). The Jacquard coefficients were calculated using the PAST 3.0 software package. The average values of JC1 and JC2 were then compared to test the hypothesis that the difference in the species composition of plants should be greater between the rooting and control than between the control plots. The comparison was based on the Mann–Whitney test using the STATISTICA 6.0 software package.

Revegetation on wild boar rootings in Western Siberia and in other parts of the range of the species was compared by analyzing data from the published reviews (Danilkin, 2002; Barrios-Garcia and Ballari, 2012; *Ecology*, *Conservation*..., 2018). The analysis involved sources that contained data on changes in the plant projective cover, species number, and species composition of plants on rootings compared to the control sites.

RESULTS

The highest rooting intensity and largest area of rootings were observed in the green-moss pine forest (Table 2), where extensive rootings of different ages were recorded (mainly under Siberian pine trees). The disturbances were superficial (the soil was rooted only to 5 cm). Fresh rootings often overlapped older ones (rootings 1–2 years old). The average PC of the herbaceous–dwarf-shrub layer on rootings was 2.9 ± 0.5% (from 0.5 to 5.0%); seven of the ten plant species typical of the original community (*Equisetum sylvaticum*, *Luzula pilosa* (L.) Willd., *Maianthemum bifolium* (L.)

Table 2. Main characteristics of wild boar rootings in different types of plant communities in Western Siberia

Parameter	Grass birch forest	Green-moss Siberian pine forest	Lichen Scotch pine forest	Mixed coniferous–deciduous forest
Number of rootings	49	44	69	18
Rooting area, m^2: median (minimum–maximum)	4.8 (0.06–8.8)	32.3 (0.7–1103)	11.2 (0.1–18.1)	20.3 (0.24–24.6)
Rooting intensity (rooting area in m^2 per 1000 m^2)	1.9	25.3	3.0	1.7

F.W. Schmidt, etc.) were involved in revegetation. The moss layer was absent in the rooting areas.

Wild boar rootings were smaller (Table 2) and not more than 10–15 cm deep in the mixed forest. In 2017, we found fresh rootings (presumably made in the spring of that year) ($N = 11$) and rootings 1–2 years old ($N = 7$). No revegetation was observed on fresh rootings. The average PC of the herbaceous–dwarf-shrub layer was 2.6 ± 0.7% (from 0.5 to 5.0%) on rootings 1–2 years old; 84.0% of the plant species (16 of the 19 species) recorded in the control plots were involved in revegetation. The moss layer was absent in the rooting areas. The repeated description of these rootings in 2018 (when they reached the age of 2–3 years) showed an increase in the average PC of the herbaceous–dwarf-shrub layer to 7.8 ± 1.1% (11.0% of the control) and an increase in the number of species to the level of the control plots. Seedlings of nine tree and shrub species, dominated mostly by *Picea obovata*, were also found on the rootings of this age.

In 2017, fresh (summer) rootings were found in the grass birch forest; they were mostly small and shallow (up to 5 cm). The descriptions made one year later showed that 56% (13 of 23) of plant species found at control plots were presented in rooted sites. The PC was no more than 1.0%.

In 2017–2018, rootings of different ages (from fresh to 2–3 years old) were found in lichen Scotch forests. In undisturbed sites, herbaceous plants were represented by six species (*Arctostaphylos uva-ursi* (L.) Spreng., *Calamagrostis epigeios* (L.) Roth, *Carex ericetorum* Poll., *Festuca ovina* L., *Silene nutans* L., and *Vaccinium vitis-idaea* L.); among them, only *Carex ericetorum* and *Festuca ovina* were more or less abundant (their projective cover reached 10.0%). The other plant species were found occasionally. There was almost no vegetation (PC = 0), except single individuals of *Festuca ovina*, *Carex ericetorum*, and *Silene nutans*, on 1-year-old rootings in the lichen Scotch pine forest ($N = 19$). Therefore, the species composition of herbaceous plants on rootings differed little from that in the control; however, seedlings of Scotch pine (0.45 ind. per 1 m^2) and larch, which were not recorded in the tree layer of the original plant community, were found in this area. The growth density of Scotch pine seedlings increases to 1 ind. per 1 m^2 on rootings made more than two years ago (2–3 years old, $N = 26$). The herbaceous–dwarf-shrub layer was also almost completely absent and the average projective cover of the moss-lichen layer was about 7.2 ± 1.3% (2.0–20.0%) of the control. There were no fruticose lichens of the genus *Cladonia* in the disturbed sites; mosses of the genus *Polytrichum* were the only plants involved in revegetation at this stage (Fig. 1).

Therefore, the revegetating areas in all four habitat types were characterized by the reduction of the PC (see Fig. 1). No more than 5.0% of the initial PC of the herbaceous–dwarf-shrub layer recovered over 1–2 years after the disturbance. The degree of restoration of the species composition was the highest in the mixed forest (84.0%) and lowest in the lichen Scotch pine forest (40.0%). The number of species was significantly lower on rootings in the disturbed sites than in the undisturbed sites; the difference was statistically high for the birch and Scotch pine forests ($p < 0.01$) and close to statistically significant values for the Siberian pine forest and mixed forest (Table 3).

There were no significant differences between the undisturbed sites and rootings with respect to the species composition (Table 4). This indicates that the representatives of indigenous communities on rootings are almost the only individuals involved in revegetation.

Let us consider changes in the occurrence of representatives of the herbaceous–dwarf-shrub layer in areas with rootings of different ages by the example of a mixed forest (Table 5). The rootings 1–2 years old contained mainly single plants that had survived rooting or developed from vegetative parts (rhizomes and bulbs) left by wild boars in the soil. The occurrence of almost all species at this stage is lower than that in the control plots. In rootings 2–3 years old, the occurrence of most plants increases owing to their vegetative and generative regeneration; in particular, the occurrence of *Carex globularis*, *Dactylorhiza hebridensis*, *Equisetum sylvaticum*, *Luzula pilosa*, *Melampyrum pratense*, and *Trientalis europaea* is significantly higher in these rootings than in the control (Table 5). All the aforementioned species are typical taiga-forest species and can obviously exhibit explorent features (R-strategists) during the disturbance of their habitats (Degteva and Novakovskii, 2011).

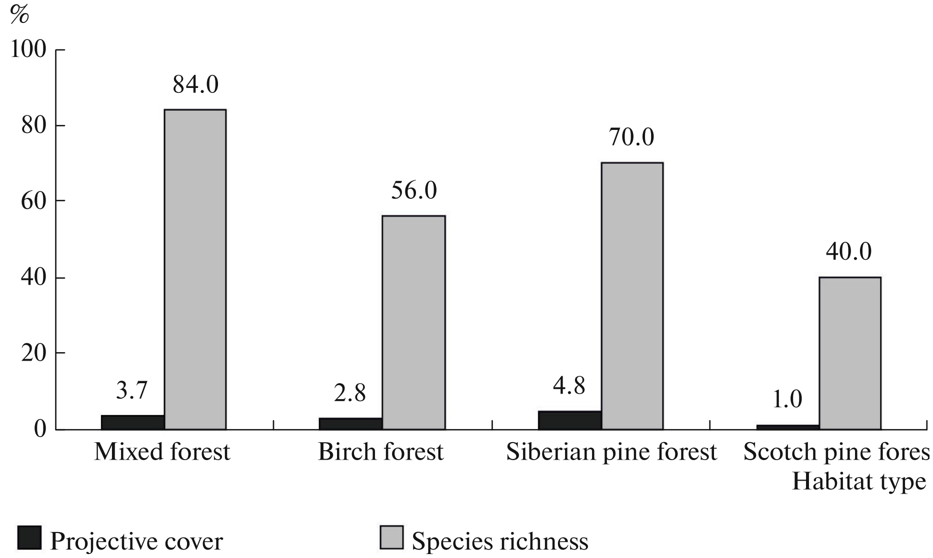

Fig. 1. Revegetation (projective cover and species richness) on rootings 1–2 years old in different habitats (% of the control) in Western Siberia.

The results of comparing the revegetation processes on wild boar rootings in different parts of its range are given in Table 6.

The table shows that the pattern of the wild boar effect on plants is generally similar in very diverse natural communities. The main consequence of the rooting activity of wild boar in all regions is a reduction of the projective cover of the herbaceous–dwarf-shrub and moss layers in the rooting areas. The rates of PC restoration can vary depending on the properties of the original community. Thus, up to 40.0% of the cover in floodplain broad-leaved forests regenerates in the second to third year and 90.0–100.0% regenerates in the fourth to fifth year after the disturbance (Evstigneev et al., 1999). Rootings in meadows are overgrown even faster: here, 40.0% of the projective cover regenerates in only one year (Bol'shakov et al., 2009). The rates of overgrowth of disturbed areas were significantly lower in the middle taiga communities of Western Siberia: 11.0% of the initial projective cover regenerated on rooting 2–3 years old in the mixed forest; 7.0% recovered in lichen Scotch pine forests, which, however, was determined only by the overgrowth of mosses of the genus *Polytrichum*, since fruticose lichens grow very slowly (Abdul'manova, 2014). The restoration of low-productive communities on poor and dry soils is particularly long. For example, wild boar rootings in the alpine lichen heaths of the Teberda Nature Reserve were clearly defined even 15 years after the disturbance (Onipchenko and Golikov, 1996).

The overwhelming majority of publications report an increase in the number of species on rootings compared to the control plots. The opposite trend is described for beech forests in North Carolina (United

Table 3. Comparison of rootings and undisturbed sites by the number of herbaceous plant species

Habitat type	Number of descriptions of plants on rootings	Average number of species ± standard deviation		Mann–Whitney *U**	*p***
		rooting	control		
Grass birch forest	7	4.2 ± 2.4	9.2 ± 2.3	0.5	0.0010
Lichen Scotch pine forest	15	0.2 ± 0.4	4.5 ± 0.5	0.0	0.0001
Green-moss Siberian pine forest	4	2.8 ± 1.5	5.5 ± 1.3	1.0	0.0850
Mixed coniferous–deciduous forest	7	5.0 ± 1.9	7.3 ± 1.9	10.0	0.0740

* The value of the Mann–Whitney test showing the difference between the numbers of herbaceous plant species on rootings and in undisturbed sites.
** The level of statistical significance of differences between rootings and undisturbed sites in the average number of species.

Table 4. Comparison of coefficients of species similarity of herbaceous plants on wild boar rootings and in undisturbed areas

Habitat type	Jacquard coefficient (mean ± standard deviation)		Mann–Withney *U****	*p*****
	JC1*	JC2**		
Grass birch forest	0.31 ± 0.187	0.18 ± 0.122	43.5	0.11
Lichen Scotch pine forest	–	–	–	–
Green-moss Siberian pine forest	0.51 ± 0.148	0.53 ± 0.452	12.0	1.00
Mixed coniferous–deciduous forest	0.42 ± 0.185	0.32 ± 0.148	48.5	0.19

* Mean value of the coefficient of species similarity between undisturbed sites.
** Mean value of the coefficient of species similarity between rootings and undisturbed sites.
*** Value of the Mann–Whitney test for the difference between the average Jacquard coefficients for the "control–control" and "control–rooting" series.
**** Level of statistical significance of differences in the average Jacquard coefficients for the "control–control" and "control–rooting" series.

Table 5. Changes in the occurrence (o) of plant species in the herbaceous–dwarf-shrub layer on revegetating wild boar rootings in the mixed forest compared to the control plots (S_o, occurrence error)

Plant species	Control		Rooting 1–2 years old		Rooting 2–3 years old	
	o	S_o	o	S_o	o	S_o
Calamagrostis arundinacea (L.) Roth	1.00	0.00	0.43	0.12	0.57	0.12
Carex globularis L.	0.29	0.11	0.00	0.00	0.57	0.12
Chamerion angustifolium (L.) Scop.	0.14	0.08	0.00	0.00	0.14	0.08
Dactylorhiza hebridensis (Wilmott) Aver.	0.14	0.08	0.14	0.08	0.57	0.12
Diphasiastrum complanatum (L.) Holub	0.14	0.08	0.14	0.08	0.29	0.11
Equisetum sylvaticum L.	0.14	0.08	0.14	0.08	0.71	0.11
Gymnocarpium dryopteris (L.) Newm.	0.57	0.12	0.29	0.11	0.14	0.08
Galium boreale L.	0.29	0.11	0.29	0.11	0.29	0.11
Linnaea borealis L.	0.86	0.08	0.86	0.08	1.00	0.00
Luzula pilosa (L.) Willd.	0.57	0.12	0.43	0.12	1.00	0.00
Lycopodium annotinum L.	0.43	0.12	0.29	0.11	0.29	0.11
Maianthemum bifolium (L.) F.W. Schmidt	0.43	0.12	0.29	0.11	0.57	0.12
Melampyrum pratense L.	0.29	0.11	0.29	0.11	0.71	0.11
Orthilia secunda (L.) House	0.43	0.12	0.14	0.08	0.14	0.08
Oxalis acetosella L.	0.57	0.12	0.29	0.11	0.14	0.08
Rubus humilifolius C.A. Mey.	0.14	0.08	0.00	0.00	0.14	0.08
Trientalis europaea L.	0.29	0.11	0.00	0.00	0.71	0.11
Vaccinium myrtillus L.	0.14	0.08	0.14	0.08	0.29	0.11
Vaccinium vitis-idaea L.	1.00	0.00	0.86	0.08	1.00	0.00

States), alpine heaths, and plant communities in the north of Western Siberia, where the number of species remained lower on the rootings than in the control. Another feature of the studied region was that explerent species were absent on the revegetating rootings and almost completely absent in the control (except single larch seedlings on rootings in lichen pine forests). This trend was also observed in two other regions; however, the species composition of plants in disturbed sites mostly differed from that in the control in these regions.

DISCUSSION

While digging for animal and plant food, wild boar creates areas with no vegetation in closed cenoses, thereby triggering demutation processes (Evstigneev et al., 1999).

Soil areas exposed by wild boars recover in different ways in biogeocenoses that differ in their geographic location, soil richness, and topography. A reduction of the projective cover was common to all studied plant communities in the middle taiga of Western Siberia.

Table 6. Features of revegetation processes on wild boar rootings according to the literature sources and our data

Habitat type	PC reduction compared to the control	Growth in the number of species on rootings compared to the control	Involvement of explerent species absent in the control in revegetation
Floodplain ash oak grove, Bryansk Region (Evstigneev et al., 1999)	+	+	+
Floodplain swamps, Central Florida (Arrington et al., 1999)	+	+	+
Coastal meadows, California (Kotanen, 1995)	+	+	+
Floodplain meadows, Sverdlovsk Region (Bol'shakov et al., 2009)	+	+	+
Alder and pine forests, Sweden (Welander, 1995)	No data	+	+
Beech forests, North Carolina (Bratton, 1975)	+	–	–
Sorrel spruce forest, Vologda Region (Pilipko, 2015)	+	+	+
Middle taiga forests, Western Siberia (our data)	+	–	–
Alpine lichen heath, North Caucasus (Onipchenko and Golikov, 1996)	+	–	–

The communities differed mainly in the rates of restoration of the projective cover and plant species richness. These processes were most intense in the mixed forest, where the original communities were characterized by the highest species richness and diversity. This process was the slowest in the communities of lichen Scotch pine forests with the lowest species richness. The low rates of revegetation and the attractiveness of lichen Scotch pine forests for wild boars, which remove the ground cover in search for chafer larvae (Danilkin, 2002), make these communities particularly vulnerable. The increased pressure of wild boars on lichen Scotch pine forests can negatively affect the food supply for forest reindeer, for which ground lichens are an important food resource in winter (Laptev, 1958). However, the effect of wild boars on this biotope is not always negative, since they exterminate en masse chafer larvae, which act as pine pests that infect the roots of young trees and prevent the restoration of pine forests in area of fires and clearings (Berezina, 1960). Wild boars also contribute to pine regeneration; their rooting activity creates conditions for seed rooting, as already shown in the literature (Khodzinskii, 2007). Researchers also note a positive effect of the rooting activity of wild boar on the regeneration of some tree species in other forest types, since the competition of tree and shrub species with the ground vegetation cover decreases in disturbed areas (Dinesman, 1961). This is particularly noticeable in communities with a dense moss cover, which prevents tree seeds from taking root. Thus, spruce seeds abundantly germinated on rootings in the moss spruce forests of the Tian Shan (Korelov, 1947, cit. by Dinesman, 1961). Spruce undergrowth was recorded on wild boar rootings in green-moss spruce forests of Bialowieza Forest (Lebedeva, 1956). In the green-moss spruce forest in Vologda Region, the number of seedlings of tree species increased by 39.7% on old rootings compared to the control (Bulakhov et al., 2015). Studies in the southeast of the United States (Texas) showed that disturbances made by wild boars increased the population of Chinese tallow tree *Sapium sebiferum* by a factor of two, which was an exotic species for that area (Siemann et al., 2009).

As a result, the rooting activity of wild boar creates open soil areas, thereby allowing different plant species to colonize them. The highest adaptive capacity for colonizing rooting areas is characteristic of plant species with a pronounced R-strategy ("reactive" explerent species, i.e., plants that have a low competitive capacity and, at the same time, can quickly capture free areas). Their appearance in disturbed sites leads to a significant increase in the species richness in these areas compared to that in undisturbed sites, as was observed in a number of meadow and forest plant communities of Eurasia and North America (see Table 6) (Kotanen, 1995; Welander, 1995; Evstigneev et al., 1999; Arrington et al., 1999; etc.). According to some researchers, fresh boar rootings are a necessary condition for the existence of "nomadic" reactive species in a cenosis, which are adapted to rapidly colonize zoogenic disturbances (Evstigneev et al., 1999). In such cases, the activity of wild boar contributes to an increase in the species richness and cenotic mosaic. This response to the effect of wild boar is characteristic of plant communities in which the species pool was formed under the conditions of regular moderate zoogenic or anthropogenic vegetation disturbances and contains a significant number of explerent species.

The picture was different in middle taiga forests in Western Siberia, where the level of transformation (anthropogenic or zoogenic transformation) was minimal. The open soil areas created by wild boars proved to be actually unused because of the absence of plant communities with the explerent life strategy in the species pool. The vegetation gradually (in the second vegetative season after the disturbance) began to recover owing to the growth of taiga species that were typical of the original community. As a result, the species richness even decreased rather than increasing on rootings 1–2 years old (40.0–84.0% of the control, depending on the community type). In the deciduous forest (Evstigneev et al., 1999), the number of species increased by 2.5–3 times on rootings of the same age owing to the invasion of R-strategists. Bratton (1975) also notes the decrease in the species richness on rootings without explerents for beech forests in North Carolina affected by the invasive wild boar.

A similar scenario was observed for the revegetation on lichen heathlands in the Teberda Nature Reserve (Onipchenko and Golikov, 1996). The floristic saturation in the disturbed sites reached the control level only the tenth year after the disturbance. As in upland lichen Scotch pine forests in Western Siberia, these are low-productive communities, which exist under extremely poor soil conditions; their flora is represented by perennial species with a low competitive ability (S-strategists). Some of them (*Festuca ovina* and *Polytrichum juniperinum*) have explerent features and are more actively involved in rooting overgrowth than the other species.

CONCLUSIONS

The rooting activity of wild boars that colonized middle taiga forests in Western Siberia less than half a century ago led to the formation of areas with a low projective cover of the herbaceous–dwarf-shrub layer and moss–lichen layers. The species diversity was also low in the disturbed sites; rootings were overgrown here exclusively by species typical of the original community. Unlike other parts of the wild boar range, the rapid colonization of the disturbed areas by explerent species did not lead to an increase in the species richness on the fresh rootings. This is probably due to the low species richness of the northern communities under study, as well as due to the absence of diaspores of species with an appropriate life strategy.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain any studies involving animals performed by any of the authors.

REFERENCES

Abdul'manova, S.Yu., Dynamics of growth and productivity of fruticose lichens during recovery successions, *Ekologiya: Populyatsiya, vid, sreda. Mat. konf. molodykh uchenykh. Ekaterinburg, 14–18 aprelya 2014 g.* (Ecology: Population, Species, and Environment. Proc. Conf. Young Scientists, Yekaterinburg, April 14–18, 2014), Yekaterinburg, 2014, pp. 6–12.

Arrington, D.A., Toth, L.A., and Koebel, J.W., Effects of rooting by feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage, *Wetlands,* 1999, vol. 19, no. 3, pp. 535–544.

Azarov, V.I., *Redkie zhivotnye Tyumenskoi oblasti i ikh okhrana. Amfibii, reptilii, ptitsy i mlekopitayushchie* (Rare Animals of Tyumen Region and Their Protection. Amphibians, Reptiles, Birds, and Mammals), Tyumen: Vektor Buk, 1995.

Barrios-Garcia, M.N. and Ballari, S.A., Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review, *Biol. Invasions,* 2012, vol. 14, pp. 2283–2300.

Berezina, V.M., Geographic zoning of the stationary distribution of the eastern *Melolontha* on the territory of the USSR, *Tr. VIZR,* 1960, no. 15, pp. 87–128.

Bol'shakov, V.N., Korytin, N.S., Markov, N.I., and Pogodin, N.L., *Kopytnye (Mammalia, Artiodactyla) na Srednem Urale* (Ungulates (Mammalia, Artiodactyla) in the Middle Urals), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2009.

Bratton, S.P., The effect of the European wild boar, *Sus scrofa*, on Grey Beech Forest in the Great Smoky Mountains, *Ecology,* 1975, vol. 56, pp. 1356–1366.

Bulakhov, V.L., Effect of burrowing activity of wild boar on physicochemical and biocenotic properties of soils in forest biocenoses, in *Kopytnye fauny SSSR* (Ungulate Fauna of the USSR), Moscow: Nauka, 1975, pp. 159–161.

Bulakhov, V.L., Pakhomov, A.E., and Pilipko, E.N., Effect of burrowing activity of wild boar (*Sus scrofa* Linnaeus, 1758) on components of various biogeocenoses, *Izv. Irkutsk. Gos. Univ., Ser.: Biol., Ekol.,* 2015, vol. 13, pp. 16–26. https://cyberleninka.ru/article/n/vliyanie-royuschey-deyatelnosti-kabana-sus-scrofa-linnaeus-1758-na-komponenty-razlichnyh-biogeotsenozov. Accessed May 16, 2019.

Danilkin, A.A., *Mlekopitayushchie Rossii i sopredel'nykh regionov. Svinye (Suidae)* (Mammals of Russia and Adjacent Regions. Suidae), Moscow: GEOS, 2002.

Degteva, S.V. and Novakovskii, A.B., *Ekologo-tsenoticheskie gruppy sosudistykh rastenii v fitotsenozakh landshaftov basseina verkhnei i srednei Pechory* (Ecological-Cenotic Groups of Vascular Plants in Phytocenoses of Landscapes in the Upper and Middle Pechora Basin), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2011.

Dinesman, L.G., *Vliyanie dikikh mlekopitayushchikh na formirovanie drevostoev* (Effect of Wild Mammals on the Formation of Forest Stands), Moscow: Akad. Nauk SSSR Lab. Lesoved., 1961.

Ecology, Conservation and Management of Wild Pigs and Peccaries, Meletti, M. and Meijaard, E., Eds., New York: Cambridge Univ. Press, 2018.

Evstigneev, O.I. and Ekimova, G.A., The role of wild boars in the maintenance of coenopopulations of the lesser butterfly-orchid, in *Ekspeditsionnye issledovaniya: Sostoyanie i perspektivy. Pervye mezhd. nauch. chteniya pamyati N.M. Przheval'skogo (mat. konf.)* (Expeditionary Studies: The State and Prospects. First Int. Scientific Reading in the Memory of N.M. Przhevalsky (Proc. Conf.)), Smolensk, 2008, pp. 188–190.

Evstigneev, O.I., Korotkov, V.N., Braslavskaya, T.Yu., and Chupachenko, V.G., Wild boar and cyclic micro-successions in the herbaceous cover of broad-leaved forests (on the example of Nerussko-Desnyanskiy Polesye), *Byull. MOIP,* 1999, vol. 104, no. 6, pp. 3–8.

Global Strategy on Invasive Alien Species, McNeely, J.A., Mooney, H.A., Neville, L.E., et al., Eds., Gland, Switzerland–Cambridge, UK: IUCN, 2001.

Gornov, A.V., The role of wild boars in maintaining populations of some species of meadow plants in the Nerusso-Desnyanskiy woodland, *Byull. Bryansk. Otd. RBO,* 2014, vol. 2, no. 4, pp. 42–47.

Gornov, A.V., Wild boar and features of self-maintenance of cenopopulations of *Dactylorhiza baltica* in the Nerusso-Desnyanskiy woodland, in *Izuchenie i okhrana biologicheskogo raznoobraziya Bryanskoi oblasti: Mat. po vedeniyu Krasnoi knigi Bryanskoi oblasti* (Investigation and Protection of Biological Diversity of Bryansk Region: Materials on Maintaining the Red Book of Bryansk Region), Trubchevsk, 2005, no. 1, pp. 86–91.

Ickes, K., DeWalt, S.J., and Appanah, S., Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest, *J. Trop. Ecol.,* 2001, vol. 17, no. 2, pp. 191–206.

Jones, C.G., Lawton, J.H., and Shachak, M., Organisms as ecosystem engineers, *Oikos,* 1994, pp. 373–386.

Khodzinskii, V.P., On the influence of the burrowing activity of mammals on the growth of seedlings of Scots pine, in *Sovremennye problemy prirodopol'zovaniya, okhotovedeniya i zverovodstva. Mat. Mezhd. nauch-prakt. konf., posvyashchennoi 85-letiyu VNIIOZ* (Current Problems of Nature Management, Hunting, and Fur Farming. Proc. Int. Sci.-Pract. Conference Dedicated to the 85th Anniversary of VNIIOZ), Kirov, 2007, pp. 460–461.

Kotanen, P.M., Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie, *Ecography,* 1995, pp. 190–199.

Laptev, I.P., *Mlekopitayushchie taezhnoi zony Zapadnoi Sibiri* (Mammals of the Taiga Zone of Western Siberia), Tomsk: Tomsk. Gos. Univ., 1958.

Lebedeva, L.S., Ecological features of the wild boar of Belovezhskaya Pushcha, *Uch. Zap. Mosk. Pedagog. Inst. im. V.P. Potemkina,* 1956, vol. 61, nos. 4–5, pp. 105–271.

Markov, N.I., Pankova, N.L., and Filippov, I.V., Wild boar (*Sus scrofa* L.) in the north of Western Siberia: history of expansion and modern distribution, *Mamm. Res.,* 2019, vol. 64, no. 1, pp. 99–107. https://doi.org/10.1007/13364-018-0378-9

Metody geobotanicheskikh issledovanii: Metodicheskoe posobie (Methods of Geobotanical Research: Methodological Manual), Bogolyubov, A.S., Ed., Moscow: Ekosistema, 1996.

Onipchenko, V.G. and Golikov, K.A., Demutational shifts after boar burrows on alpine lichen heaths in the Teberda nature reserve, *Byull. MOIP, Otd. Biol.,* 1996, vol. 101, no. 4, pp. 49–54.

Pilipko, E.N., Effect of the burrowing activity of the wild boar (*S. scrofa*) on the physicochemical parameters of the soil in the Ustyuzhsky district of Vologda Region, *Fundamental'naya nauka i tekhnologii, Perspektivnye razrabotki. Mat. V Mezhd. nauch.-prakt. konf.* (Fundamental Science and Technology, Promising Developments. Proc. V Int. Sci.-Pract. Conf.), 2015, vol. 2, pp. 7–9.

Siemann, E., Carrillo, J., Gabler, C.A., Zipp, R., and Rogers, W.E., Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US, *For. Ecol. Manage.,* 2009, pp. 546–553.

Talanova, G.I., Climate of the Malaya Sosva Reserve: long-term data, *Din. Okruzh. Sredy Izmen. Klim.,* 2018, vol. 9, no. 1, pp. 22–45.

Tikhodeeva, M.Yu., *Prakticheskaya geobotanika: Analiz sostava rastitel'nykh soobshchestv: Uchebnoe posobie* (Practical Geobotany: Analysis of the Composition of Plant Communities: Handbook), St. Petersburg: S.-Peterb. Univ., 2015.

Toropova, N.A., The role of heterotrophs in the organization of the mosaic-layer structure of forests, in *Vostochnoevropeiskie shirokolistvennye lesa* (East European Broad-Leaved Forests), Moscow, 1994, pp. 228–241.

Vasin, A.M., Lykhvar', V.P., Buidalina, F.R., Zaguzov, A.V., and Syzhko, V.V., *Pozvonochnye zhivotnye zapovednika "Malaya Sos'va" (Severnoe Zaural'e): Annotirovannyi spisok i kratkii ocherk* (Vertebrates of the Malaya Sosva Reserve (Northern Trans-Urals): Annotated List and Brief Outline), Izhevsk: IP Permyakov S.A., 2015.

Welander, J., Are wild boars a future threat to the Swedish flora?, *J. Mt. Ecol.,* 1995, vol. 3, pp. 165–167.

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