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ОХРАНА РАСТИТЕЛЬНОГО МИРА

PULSATILLA VULGARIS (RANUNCULACEAE) CONSERVATION IN RUSSIA: HABITAT MANAGEMENT TO ENHANCE THE ONLY POPULATION

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Pulsatilla vulgaris is one of the rarest vascular plant species in Russia. In the Red Data Book of the Russian Federation, it is classified as critically endangered (category 1). The only population of *P. vulgaris* in Russia is known from the Leningrad Region and it is rapidly declining. The analysis of the population ontogenetic structure demonstrates low level of the population self-sustainment due to lack of seed reproduction. One of the factors that prevent *P. vulgaris* generative reproduction is the biotope transformation caused by succession. Typical habitats of *P. vulgaris* are heaths, sparse and low pine forests, dry low-grass meadows and pastures. Successful seed reproduction of the species requires the factors that inhibit woody vegetation development and lead to the damage of dense ground cover and soil (i.e. moderate grazing, weak ground fires etc.). To avoid a complete loss of the species in Russia, artificially damaged sites suitable for successful seed regeneration of *P. vulgaris* were formed in 2020–2021 in "Nizhnevolkhovskiy" Protected Area (Leningrad Region, Volkhovskiy District). Trees uprooting, grass vegetation removal or damage, soil damage were performed to form exposed and well-warmed sites with sparse vegetation ground cover. These measures have significantly increased germination capacity of the seeds on the managed plots compared to the left untreated (control) areas. Over a two-year period, the population of *P. vulgaris* has increased by more than 10%. The success of the measures applied allows to recommend them for the restoration of rare and highly specialized species populations growing in similar habitats.

Keywords: rare species, age structure, ecological restoration, seed regeneration effectiveness, species population decline, Leningrad Region

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One of the most serious threats to biodiversity today is the loss or degradation of some habitats suitable for rare and highly specialized vascular plant species (Leimu et al., 2006; Fischer, Lindenmayer, 2007).

In the Leningrad Region, such losses happen as a result of economic development (deforestation, peatlands mining, wetlands drainage, etc.) and changes in traditional agricultural land use. Among the habitats that we lose due to changes in rural life there are the old continental dunes – prevalent close to the Volkhov River mouth and the only known habitat of the protected species *Pulsatilla vulgaris* Mill. (Ranunculaceae) in Russia.

To preserve the specific natural complexes along the Volkhov River (Leningrad Region, Volkhovskiy District, coordinates: 60°5'52.9"N, 32°19'20.5"E) the "Nizhnevolkhovskiy" Protected Area (Sorokina, 2019) was established in 2016. The protected area (hereinafter "PA") consists of three cluster sites: "Yushkovo" (10.5 ha), "Berezye 1"

(18.8 ha), and "Berezye 2" (3.9 ha). Among the goals of the PA creation are (i) protection of *Pulsatilla vulgaris* population, (ii) conservation of dune pine forests, heathlands and dry meadows with coastal and southern pine forest species, (iii) conservation of rare and endangered species of animals and plants associated with these habitats. However, the established conservation regime preventing any vegetation and soil disturbance, as observed in recent years, is not sufficient to maintain the *P. vulgaris* population, since the species has been declining in number due to the natural transformation of the open dunes into young pine stands.

The range of *Pulsatilla vulgaris* s.l. covers Western, Central, Eastern Europe and also Southern Scandinavia: the plant is known from UK, France, Belgium, Switzerland, Austria, Germany, Poland, Czech Republic, Slovenia, Croatia, Slovakia, Hungary, Romania, Moldova, Ukraine, as well as from Southern Sweden, Finland, and Denmark (Walker, 2011; GBIF, 2021); there is evidence of a single species finding in Norway (Flora Nordica, 2001).

Due to a high degree of *Pulsatilla vulgaris* polymorphism, which is particularly evident between plants of small and isolated populations, there is no clear resolution on intraspecific delimitation of this taxon based on morphological features (Flora Europaea, 1993). Currently, three subspecies of *P. vulgaris* (Flora Europaea, 1993; Walker, 2011) are usually distinguished, geographically replacing each other. When moving from west to east, *P. vulgaris* subsp. *vulgaris* distributed from the United Kingdom and France in the west to Sweden and Norway in the north and western borders of Poland in the east, is gradually replaced by *P. vulgaris* subsp. *grandis* (Wender.) Zämelis, represented in Central and Eastern Europe (Austria, Germany, Slovenia, Hungary, Romania, Slovakia, Czech Republic, Ukraine, Moldova, etc.) (Walker, 2011). *P. vulgaris* subsp. *gotlandica* Zämelis et Paegle is found only on Gotland in Sweden, while *P. vulgaris* subsp. *vulgaris* is known from mainland Sweden (Mossberg, Stenberg, 2005). Plants of a small population represented in the Leningrad Region, Russia, which have been geographically isolated for a long time, morphologically correspond to the diagnostic features of the type subspecies, *P. vulgaris* subsp. *vulgaris* (Tzvelev, 1976).

The species is listed in the Red Data Book of the Russian Federation (2008) as "critically endangered" (category 1). It is known from the only locality in the Leningrad Region which is far away from the main geographic range of the species.

According to our observations, the size of *Pulsatilla vulgaris* population in the Volkhov River lower course has significantly decreased during the last years. In the Red Data Book of the Russian Soviet Federative Socialist Republic (1988) and the Red Data Book of the Leningrad Region nature (2000), there is information about 80–250 *P. vulgaris* individuals in the dune pine forests on the left bank of the Volkhov River (at present, "Yushkovo" cluster site). At the same time, it was mentioned that there were no young individuals in the population despite the fact that the plants produced viable seeds (Red..., 1988). According to the data of the quantitative field surveys carried out in 1998–1999 (Sorokina, 2000) and in 2005 (Sorokina, 2008), there were at least 10–15 thousand individuals in the population of *P. vulgaris* on the right side of the river (now "Berezye 1" and "Berezye 2" cluster sites). Besides, in 2005 the species was reported to play a significant role within various plant communities such as heathlands and dry low-grass meadows, sometimes being a co-dominant (Volkova, 2014). On the left side of the Volkhov River, no more than 30 plants had remained by 2005.

In 2019, only about 1300 individuals of *Pulsatilla vulgaris* were recorded from "Berezye 1" and "Berezye 2" cluster sites of the "Nizhnevolkhovskiy" Protected Area. In addition, about 1000–1200 plants grew outside of the PA borders, namely on the territory of the abandoned military unit, adjacent to the "Berezye 2" cluster site from the south. In this area, there are highly transformed ruderal habitats situated between the ruins of military buildings. In "Yushkovo" cluster site, which is bordered to Novaya Ladoga town and subjected to high anthropogenic press, single plants were noted in 2014.

Thus, the population of *Pulsatilla vulgaris* is declining dramatically in the Leningrad Region – from 10–15 thousands of individuals in 2005 to 2.5–3 thousands in 2019. The total area occupied by the species population is currently no more than 9.8 hectares. The risk of extinction of such small and isolated population is very high due to specific environmental requirements and the absence of genetic exchange (Fischer, Stöcklin, 1997; DiLeo et al., 2017; Gargiulo et al., 2019).

It is important to note that the populations and localities of *Pulsatilla vulgaris* s.l. are declining throughout its geographic range. The species (or its subspecies) is redlisted in the United Kingdom, Sweden, Austria, Switzerland, Germany, Slovakia, Ukraine and some other countries. In the United Kingdom only, the number of localities has reduced from 130 in 1750 to 17 today (Wells, Barling, 1971; Walker, Pinches, 2011). In Austria, 9 of the 32 known localities have disappeared during a short period from 1991 to 2005 (Essl, 2005). In the southern

part of Finland where the species was recorded in the first half of the 20th century, it has become extinct (Ketokylmänkukka, 2021). In Poland, the last finding of the species in nature dates no later than 1930 (Wójtowicz, 2001); during the 20th century the species was also extinct in the Netherlands (Walker, 2011).

Such rapid losses are associated with both direct destruction of habitats (through urbanization, development, intensive agriculture) and decrease of moderate grazing pressure on the biotopes which are the species habitats (Walker, Pinches, 2011; DiLeo et al., 2017). Woody heaths, sparse pine forests, low-grass meadows and pastures on sandy or calcareous soils are typical *Pulsatilla vulgaris* habitats within most of its range in Western, Central, and Eastern Europe (Wells, Barling, 1971). High level of light intensity, low abundance of tall forbs and grasses, absence of thick turf, leaf litter and thick moss and lichen coverage are the mandatory habitat characteristics for long-existing species populations (Wells, Barling, 1971; Walker, Pinches, 2011).

Decrease of grazing as well as disappearance of the other factors that prevent forest regeneration on the heathlands lead to the shifts of open biotopes to high-grass communities, followed by wooded areas and then by closed forests (Vasilevich, 2008). Successions are the main cause of the *Pulsatilla vulgaris* extinction in many previously known European localities (Essl, 2005; Hensen et al., 2005). Experimental shading had a significant negative impact on the plants survival and flowering (Walker, Pinches, 2011). *P. vulgaris* disappearance from the communities which have been changed during the successions is determined by competition for light from taller herbaceous plants (Online Atlas..., 2022), and also by formation of thick moss and lichen cover preventing seed reproduction.

The biological features of *Pulsatilla vulgaris* seed germination is one of the additional causes for the species reduction in the northern parts of its range where heat resources are limited. According to experimental data (Butuzova, 2018), *P. vulgaris* seeds germinate at relatively high temperatures (about 23°C). In addition, *P. vulgaris* seeds undergo a process of prior development before germination that lasts for 17–18 days at temperatures of 20–22°C. Seed germination at optimal temperature takes 24–60 days (Pereboychuk, 2016; Butuzova, 2018). The experiment shows that even though the rate of germinated seeds is sufficiently high (92%), the survival rate is much lower (25%): seedlings loss is determined by the influence of both biotic and climatic factors (Butuzova, 2018). Soil moisture is crucial to the success of the plants rooting: seedlings survive only in wet summers (Walker, 2011). The combination of low survival rate and extremely slow growth of the seedlings results in *P. vulgaris* relatively poor seed reproduction efficiency.

Considering the high risk of degradation and possible eventual extinction of the only *Pulsatilla vulgaris* population in Russia, the main goal of our research is to develop a conservation strategy for this population. The objectives of our research are: (i) to identify causes of the population decline, (ii) to develop scientific and practical measures to maintain the population and increase it in number, (iii) to implement activities aimed at management of the biotopes which are the species habitats, (iv) to create sites suitable for the species successful seed reproduction.

In European countries, ecological restoration of endangered habitats is a widely accepted method to ensure maintenance of rare taxa populations including species of *Pulsatilla* (Langenauer, Keel, 2004; Piqueray et al., 2013). But in Russia the method is still not common. Our work on biotope management is one of the first in the country.

MATERIALS AND METHODS

Study area. The areas near the Volkhov River mouth, that are parts of "Nizhnevolkhovskiy" Protected Area and the only known *Pulsatilla vulgaris* locality in Russia, are situated within the boundaries of Priladozhskaya Lowland. Priladozhskaya Lowland landscapes were being formed during the Holocene under the influence of the changing shape of Ladoga Lake (Kvasov, 1974). They acquired their present form only about 2.0–2.5 thousand years ago as a result of sequence of Ladoga Lake regressions and transgressions. For a long time, sandy coastal ridges of the Volkhov River and small relic dunes with poor soil cover were the habitat of the whole complex of rare vascular plant species, such as *P. vulgaris*, *Armeria maritima* (Mill.) Willd., *Botrychium matricariifolium* (Retz.) A. Braun ex W.D.J. Koch, *Helictochloa pratensis* (L.) Romero Zarco, *Rosa mollis* Sm., *Silene tatarica* (L.) Pers., etc. (Sorokina, 2008) (hereinafter, the names of vascular plant taxa are given mainly according to POWO (2023), of bryophytes – according to the "Check-list of mosses of East Europe and North Asia" (Ignatov et al., 2006) and of lichens – according to the latest summary for Fennoscandia (Westberg et al., 2021)).

Till the end of the 20th – beginning of the 21st century, these lands were involved in traditional agriculture – both for grazing and for cattle movements from the nearby villages of Nemyatovo and Berezye to the meadows and forest pastures adjacent to the open woodlands and sparse pine

forests. In addition, in the second half of the 20th century, the sand dunes were constantly subjected to mechanical disturbance caused by trainings of the military personnel from the neighboring military base. In the plant communities, the richness of herbaceous plant species was relatively high for such habitats in Northwestern European Russia (12–15 species per 2 × 2 m plot). Among the herbaceous plants, a group of psammophyte species, typical of more southerly pinewood and sandy habitats stood out: *Armeria maritima*, *Festuca trachyphylla* (Hack.) Hack., *Potentilla inclinata* Vill., *Scleranthus perennis* L., *Thymus serpyllum* L. The unique characteristic of the heathland communities was *Pulsatilla vulgaris* that sometimes dominated (15–20% of cover). Among permanent species of these communities, *Artemisia campestris* L., *Carex ericetorum* Pollich, *Festuca ovina* L. were abundant, while the species like *Calamagrostis meinshausenii* (Tzvelev) Vilyasoo, *Linaria vulgaris* Mill., *Solidago virgaurea* L., *Antennaria dioica* (L.) Gaertn., *Sedum acre* L. were less abundant but still permanent. Moss and lichen layer was formed by common species: *Niphotrichum canescens* (Hedw.) Bednarek-Ochyra & Ochyra (*Racomitrium canescens* (Hedw.) Brid.), *Polytrichum piliferum* Hedw., *Ceratodon purpureus* (Hedw.) Brid., *Dicranum polysetum* Sw., *Abietinella abietina* (Hedw.) M. Fleisch., *Cetraria islandica* (L.) Ach., *Cladonia* spp. The cover of mosses and lichens was 60–70%.

At the beginning of the 21st century, human activity leading to vegetation and soil cover disturbance of the heaths inhabiting old continental dunes (Fig. 1) gradually decreased: local residents stopped keeping cattle and the military unit was disbanded. Along with a significant decrease of spring grass fires this led to the overgrowing of the heaths, development of young pine forests (Fig. 2) and the reduction of the biotopes suitable for the specialized vascular species survival. If before 1998–2005 it was still possible to find sites of exposed poorly fixed sands with non-closed vegetation on the study area, by 2020 such sites were fixed by vegetation and the dunes and sand terraces became covered to a large extent by pine forests.

Dune stabilization and successions are accompanied by nitrogen accumulation and decrease in the calcium content in the soil (Management..., 2008), that determines the changes in species composition of the communities of overgrowing open woodlands. In 2021, *Pulsatilla vulgaris* was recordered in very small numbers in open woodlands. *Avenella flexuosa* (L.) Drejer became the main dominant of the herb layer; in some communities it covers up to 75%. The number of herb species in the communities decreased down to 7–9 for a plot of 2 × 2 m. Gradual changes of environmental conditions during successions led to decrease in number or disappearance of some xeromesophytic species (such as *Armeria maritima*, *Herniaria glabra* L., *Festuca trachyphylla*, *Potentilla inclinata*, *Scleranthus perennis*, *Silene tatarica*, *Thymus serpyllum*, etc.). The cover of mosses and lichens reached up to 90% in some communities. Shading caused by the pine crowns closing led to the extinction of most *Juniperus communis* L. individuals, previously abundantly grown on the heathlands.

During the succession, the meadow communities on the coastal ridges of the Volkhov River in the southern part of the territory (the cluster site "Berezye 2"), which are also the habitat of *Pulsatilla vulgaris*, were transformed as well. There, on the sod sandy soils, sometimes with a buried massive humus horizon, the communities with rich species composition, counting both common meadow species and psammophytic ones (including coastal) were formed. Among the meadow communities, small areas on the coastal ridge are occupied by the communities with dominance of *Helictochloa pratensis*, rare and protected species in the Leningrad Region. The composition of these communities changed significantly over the past 15 years. The cover of the main dominant *Helictochloa pratensis* has decreased from 40% to 15–20%. Like on the dunes, the participation of *Avenella flexuosa* and other grasses (*Agrostis capillaris* L., *Calamagrostis meinshausenii*, *Festuca ovina*) has significantly increased. *Pulsatilla vulgaris* cover in such communities in the early 2000s ranged from 10 to 20%, and currently it is 5%. Such species as *Armeria maritima*, *Silene tatarica*, *Thymus serpyllum* have disappeared from the communities.

Almost complete loss of the open habitats in "Nizhnevolkhovskiy" Protected Area as a result of heathland shifts to meadows of perennial grasses and dense moss and lichen carpets accompanied by the following forest regeneration have determined the need to develop measures to manage and maintain the habitats suitable for *Pulsatilla vulgaris* survival and generative reproduction.

Population structure analysis. 12 control plots were fixed in 2020 to assess the effectiveness of *Pulsatilla vulgaris* seed reproduction and to carry out long-term observations of changes in the species abundance due to succession shifts. The plots 2 × 2 m were allocated in the areas that were not involved in the restoration activities, and were characterized by a maximum number of *P. vulgaris* generative plants at the time of the research: six plots (C1–C6) were chosen outside the "Nizhnevolkhovskiy" Protected Area in the territory of the abandoned military unit adjacent to the PA southern boundaries, and the other six plots (C7–C12) were chosen within the PA boundaries (Table

Fig. 1. Chains of dunes in the northwestern part of "Berezye 1" cluster site (September 2005). Photographer: V.N. Khramtsov.
Рис. 1. Дюнные гряды в северо-западной части кластерного участка "Березье 1" (сентябрь 2005 г.). Фотограф: В.Н. Храмцов

Fig. 2. Young pine forest on the dune chains replaced heathland in the course of succession, northwestern part of "Berezye 1" cluster site (May 2020). Photographer: I.A. Sorokina.
Рис. 2. Молодой сосновый лес на дюнных грядах, сменивший в ходе сукцессии боровую пустошь в северо-западной части кластерного участка "Березье 1" (май 2020 г.). Фотограф: И.А. Сорокина

1). These two groups of plots have significant differences in the intensity and age of anthropogenic disturbances of vegetation and soil cover. The pH of sandy soil on the control plots varies from slightly acidic to neutral (Table 1). Within the PA, significant impacts such as grazing and military exercises were stopped no later than in 2005–2007 (and since 2017 the area is strictly protected), while on the territory of the abandoned military unit extensive disturbances of soil and vegetation continued until recently. Only one of the control plots (C9) within the PA is now subjected to a significant disturbing impact as it is situated close to the trail and near a resting place of anglers and tourists.

On the control plots, we described vegetation, assessed the number, density and ontogenetic structure of *Pulsatilla vulgaris* population. The age stages of plant individuals were classified according to the system proposed by V.I. Simachyov (1978) for *Pulsatilla vernalis* (L.) Mill.

We analysed the ontogenetic structure of *P. vulgaris* population using index of ageness (Uranov, 1975):

$$\Delta = \frac{\Sigma k_i \times m_i}{N},$$

k_i – the number of individuals in *i*-th ontogenetic group, m_i – ageness of one individual in *i*-th ontogenetic group, N – the number of all individuals.

To estimate the mean value of energy efficiency of a population (Zhivotovskiy, 2001) we calculated the efficiency index (ω) using the following formula:

$$\omega = \frac{\Sigma n_i e_i}{\Sigma n_i},$$

n_i – the number of individuals in *i*-th ontogenetic group, e_i – the efficiency of energy consumption by the plants at the *i*-th stage relative to that at the g_2 stage (Zhivotovskiy, 2001), $\sum n_i$ – the number of all individuals.

We used the index of regeneration (I_{reg}) and the index of replacement (I_{rep}) (Zhukova, 1987) to predict the population number dynamics.

The index of regeneration (I_{reg}) shows the number of pregenerative plants per one generative individual:

$$I_{reg} = \frac{j + im + v}{g_1 + g_2 + g_3},$$

j, im, v, g_1, g_2, g_3 – the number of plants in corresponding ontogenetic groups.

The index of replacement (I_{rep}) shows the number of offspring plants per one adult individual:

$$I_{rep} = \frac{j + im + v}{(g_1 + g_2 + g_3) + (s + ss + sc)},$$

Table 1. Main coenotic and environmental characteristics of the control plots
Таблица 1. Основные ценотические и экологические характеристики контрольных площадок

Plot Площадка	Vegetation Растительность	pH of soil solution pH почвенного раствора
C1	Grass-herb meadow. Grass cover 75%, moss cover <1%, lichen cover <1%. Number of species – 33. Most abundant: *Pulsatilla vulgaris*, *Solidago virgaurea*, *Avenula pubescen*s Злаково-разнотравный луг. Травяной покров 75%, моховой покров <1%, лишайниковый покров <1%. Количество видов – 33. Наиболее обильные: *Pulsatilla vulgaris*, *Solidago virgaurea*, *Avenula pubescen*s	6.42
C2	Moss-herb heathland. Grass cover 30%, moss cover 21%, lichen cover 6%. Number of species – 38. Most abundant: *Pulsatilla vulgaris*, *Carex ericetorum*, *Viscaria vulgaris*, *Abietinella abietina*, *Brachythecium albicans* Мохово-разнотравная пустошь. Травяной покров 30%, моховой покров 21%, лишайниковый покров 6%. Количество видов – 38. Наиболее обильные: *Pulsatilla vulgaris*, *Carex ericetorum*, *Viscaria vulgaris*, *Abietinella abietina*, *Brachythecium albicans*	7.07
C3	Fescue-herb meadow. Grass cover 70%, moss cover 7%, lichen cover 1.5%. Number of species – 36. Most abundant: *Festuca ovina*, *Pulsatilla vulgaris*, *Hieracium umbellatum*, *Pilosella officinarum* Овсяницево-разнотравный луг. Травяной покров 70%, моховой покров 7%, лишайниковый покров 1.5%. Количество видов – 36. Наиболее обильные: *Festuca ovina*, *Pulsatilla vulgaris*, *Hieracium umbellatum*, *Pilosella officinarum*	6.01
C4	Moss-fescue-herb heathland with sparse pine undergrowth; height – 2.5 m. Grass cover 50%, moss cover 35%, lichen cover 1.5%. Number of species – 35. Most abundant: *Viscaria vulgaris*, *Pulsatilla vulgaris*, *Festuca ovina*, *Pleurozium schreberi*, *Brachythecium albicans* Мохово-овсяницево-разнотравная пустошь с редким подростом сосны; высота 2.5 м. Травяной покров 50%, моховой покров 35%, лишайниковый покров 1.5%. Количество видов – 35. Наиболее обильные: *Viscaria vulgaris*, *Pulsatilla vulgaris*, *Festuca ovina*, *Pleurozium schreberi*, *Brachythecium albicans*	5.92
C5	Herb-moss heathland with aspen undergrowth (*Populus tremula*); height – 0.1–0.6 m. Grass cover 45%, moss cover 60%, lichen cover 1%. Number of species – 34. Most abundant: *Abietinella abietina*, *Pulsatilla vulgaris*, *Antennaria dioica*, *Festuca ovina* Разнотравно-моховая пустошь с подростом осины (*Populus tremula*); высота – 0.1–0.6 м. Травяной покров 45%, моховой покров 60%, лишайниковый покров 1%. Количество видов – 34. Наиболее обильные: *Abietinella abietina*, *Pulsatilla vulgaris*, *Antennaria dioica*, *Festuca ovina*	6.92
C6	Herb-moss heathland with aspen undergrowth (*Populus tremula*); height – 0.1–0.8 m. Grass cover 30%, moss cover 35%, lichen cover 3%. Number of species – 30. Most abundant: *Abietinella abietina*, *Pulsatilla vulgaris*, *Thymus serpyllum* Разнотравно-моховая пустошь с подростом осины; высота – 0.1–0.8 м. Травяной покров 30%, моховой покров 35%, лишайниковый покров 3%. Количество видов – 30. Наиболее обильные: *Abietinella abietina*, *Pulsatilla vulgaris*, *Thymus serpyllum*	6.16
C7	Herb-grass meadow. Grass cover 75%, moss cover 20%. Number of species – 25. Most abundant: *Avenella flexuosa*, *Helictochloa pratensis*, *Pulsatilla vulgaris*, *Achillea millefolium*, *Brachithecium albicans* Разнотравно-злаковый луг. Травяной покров 75%, моховой покров 20%. Количество видов – 25. Наиболее обильные: *Avenella flexuosa*, *Helictochloa pratensis*, *Pulsatilla vulgaris*, *Achillea millefolium*, *Brachithecium albicans*	5.89
C8	Grass-herb meadow. Grass cover 60%, moss cover 25%. Number of species – 24. Most abundant: *Veronica chamaedrys*, *Knautia arvensis*, *Fragaria vesca*, *Avenella flexuosa*, *Pleurozium schreberi*, *Brachithecium salebrosum* Злаково-разнотравный луг. Травяной покров 60%, моховой покров 25%. Количество видов – 24. Наиболее обильные: *Veronica chamaedrys*, *Knautia arvensis*, *Fragaria vesca*, *Avenella flexuosa*, *Pleurozium schreberi*, *Brachithecium salebrosum*	5.70

Table 1. Continue
Таблица 1. Продолжение

Plot Площадка	Vegetation Растительность	pH of soil solution pH почвенного раствора
C9	Moss-dwarf shrub-herb heathland. Grass cover 22%, dwarf shrub cover 13.5%, moss cover 10%, lichen cover 8%. Number of species – 34. Most abundant: *Avenella flexuosa*, *Antennaria dioica*, *Calluna vulgaris*, *Pleurozium schreberi*, *Cetraria islandica* Мохово-кустарничково-разнотравная пустошь. Травяной покров 22%, кустарничковый покров 13.5%, моховой покров 10%, лишайниковый покров 8%. Количество видов – 34. Наиболее обильные: *Avenella flexuosa*, *Antennaria dioica*, *Calluna vulgaris*, *Pleurozium schreberi*, *Cetraria islandica*	5.30
C10	Heath-herb-moss heathland. Grass cover 24%, dwarf shrub cover 20%, moss cover 30%, lichen cover <1%. Number of species – 19. Most abundant: *Calluna vulgaris*, *Melampyrum pratense*, *Avenella flexuosa*, *Pleurozium schreberi* Вересково-разнотравно-моховая пустошь. Травяной покров 24%, кустарничковый покров 20%, моховой покров 30%, лишайниковый покров <1%. Количество видов – 19. Наиболее обильные: *Calluna vulgaris*, *Melampyrum pratense*, *Avenella flexuosa*, *Pleurozium schreberi*	5.01
C11	Fescue-lichen-moss heathland with sparse pine undergrowth (*Pinus sylvestris*); height – 0.2 m. Grass cover 10%, moss cover 20%, lichen cover 10%. Number of species – 25. Most abundant: *Niphotrichum canescens*, *Cetraria islandica*, *Festuca ovina* Овсяницево-лишайниково-моховая пустошь с редким подростом сосны. Высота – 0.2 м. Травяной покров 10%, моховой покров 20%, лишайниковый покров 10%. Количество видов – 25. Наиболее обильные: *Niphotrichum canescens*, *Cetraria islandica*, *Festuca ovina*	5.02
C12	Hairgrass-moss-lichen heathland with sparse pine undergrowth (*Pinus sylvestris*); height – 0.5 m. Grass cover 15 %, moss cover 40%, lichen cover 45%. Number of species – 23. Most abundant: *Cladonia arbuscula*, *Pleurozium schreberi*, *Avenella flexuosa* Луговиково-мохово-лишайниковая пустошь с редким подростом сосны. Высота – 0.5 м. Травяной покров 15%, моховой покров 40%, лишайниковый покров 45%. Количество видов – 23. Наиболее обильные: *Cladonia arbuscula*, *Pleurozium schreberi*, *Avenella flexuosa*	5.49

j, *im*, *v*, g_1, g_2, g_3, *s*, *ss*, *sc* – the number of plants in corresponding ontogenetic groups.

We used Kolmogorov–Smirnov test to verify samples on normality. Further, we used nonparametric analysis, as the distribution of values of variables, like the number of plants in various ontogenetic groups, was not normal.

We used Spearman's correlation analysis to reveal strength and direction of relationship between the number of plant individuals at a certain stage of development and (i) the level of anthropogenic pressure on habitats, and (ii) biotope conditions. We used Chaddock's scale to estimate the strength of relationship between parameters investigated (< 0.3 – weak; 0.3–0.5 – moderate; 0.5–0.7 – salient; 0.7–0.9 – high; > 0.9 – very high).

The average seed germination rate on the control plots was calculated on the basis of information on (i) the mean number of young generative, mature generative and old generative plants, (ii) their average seed productivity and (iii) the number of individuals of pregenerative groups, grown from seeds in the year of estimation (seedlings and juvenile plants) or in the previous year (immature plants).

Biotope restoration. In 2020–2021, we carried out fieldworks on the restoration of habitats suitable for *Pulsatilla vulgaris* seed reproduction, on the territory of "Nizhnevolkhovskiy" Protected Area. 19 plots were placed in "Berezye 1" cluster site and one plot was placed in "Berezye 2" cluster site. In 1998–2005, there was maximum abundance of *P. vulgaris* along with a complex of xeromesophytic plant species typical of the sandy dune habitats near Ladoga Lake in the clusters where the plots were placed. Now, these sites are covered with pioneer pine forests or *Avenella flexuosa* and moss (or lichen and moss) communities due to the lack of disruptive factors. The absence of bare sandy soil prevents *P. vulgaris* seed germination and seedling development. At the start of the habitat restoration works the individuals of *P. vulgaris* were absent from 17 managed plots out of 20 ones.

A number of practices have been proposed for restoration and management of European dunes and heaths

(Sedláková, Chytrý, 1999; Management..., 2008; Walker, Pinches, 2011), i.e. burning, sod-cutting, mowing, soil disturbance, removing shrubs and trees, moderate cattle grazing. Being applied these disturbances allow to maintain habitats such as dunes in dynamic state appropriate for specialised xeromesophyte and psammophyte plant species. Burning small patches of vegetation along with moderate cattle grazing (Sedláková, Chytrý, 1999; Management..., 2008) are the most effective ways to restore the mosaic biotopes of continental dunes and to create sites suitable for *Pulsatilla vulgaris* seed reproduction. Restoration by burning plant cover at our study area was not implemented as it had not been approved by regional authorities.

The creation of artificially disturbed sites followed by seed sowing is one of the effective ways to regenerate *Pulsatilla vulgaris* populations (Langenauer, Keel, 2004; Piqueray et al., 2013). We placed 14 plots (2 × 2 m) within the treeless areas of "Berezye 1" and "Berezye 2" cluster sites (moss, lichen-moss, *Avenella flexuosa*-moss, *Festuca*-moss communities). Virginile and generative individuals of *Pulsatilla vulgaris* were found on three of them. Six more plots sized from 6 × 6 m to 10 × 10 m were placed at the sites covered with pine forests.

We carried out the following activities in order to disturb vegetation and soil on the managed plots (Table 2)[1]:

I – removal of plant cover and sod followed by soil reversal (to a depth of about 20 cm) (6 plots);

II – removal of plant cover and sod with some harrowing (3–5 cm deep) (3 plots);

III – partial removal of plant cover and sod (on the sites sized 10 × 10 cm or 50 × 50 cm) (3 plots);

IV – partial removal of plant cover in order to create open soil sites around generative individuals of *Pulsatilla vulgaris* (2 plots);

V – tree uprooting with herb layer and sod removal (6 plots).

On the managed plots, the pH of soil solution was slightly acidic (Table 2). At 10 managed plots, we added dolomite powder (2 kg per 2 × 2 m plot) to decrease the soil acidity level and to estimate its impact on the *Pulsatilla vulgaris* seedling development (Table 2).

[1] All restoration activities (including seed collection) were implemented in accordance with regional and federal legislation and approved by the Ministry of Natural Resources and Environment of the Russian Federation, by the Federal Service for Supervision of Natural Resources, and by the Committee of Natural Resources of the Leningrad Region.

Seed sowing. We collected *Pulsatilla vulgaris* seeds outside the "Nizhnevolkhovskiy" Protected Area, on the territory of the abandoned military unit located south of "Berezye 2" cluster site.

The fruits of *P. vulgaris* are multiachenes of (45)60–80 single-seed achenes. In the study area, a young generative plant with 1–2 flowers produces on an average 70 to 140 seeds, a mature generative plant with 3–11 flowers produces 210 to 770 seeds, and an old generative plant with 5–7 flowers produces 350 to 490 seeds. We collected manually 20–30 achenes per generative shoot.

To make a control estimation of *Pulsatilla vulgaris* seed germination under indoor conditions, we planted seeds in unheated greenhouse on the 29th of June 2020. From July to August, the mean night temperatures were 17–23°C, and the mean day temperatures were 25–35°C. As a substrate, we used a mixture of turf soil and sand (in a ratio 1 : 3). The depth of seeding was 0–0.2 cm. Watering was carried out once every 10–14 days (10 liters per 1 m^2).

In 2020, the managed plots inside the "Nizhnevolkhovskiy" Protected Area were seeded on three dates. Freshly collected seeds were sown on the 23nd of June, 2020 on 7 managed plots, 2 × 2 m (M1, M2, M4, M7–10). 600 seeds were sown on each plot. Sowing took place in dry and moderately hot weather and followed by one-time watering at the rate of 20 liters per area 2 × 2.

Two other plots 6 × 6 m (M5) and 10 × 10 m (M6) were seeded on the 30th of July, the seeds were stored for more than a month at room temperature (+20...+22°C). One plot, 5 × 11 m (M3), was seeded on the 2nd of August, 2020. About 800 seeds were spread on each of the plots. The seeds on all the plots were sown at a depth of 0–0.2 cm. We did not water the plots seeded on the 30th of July, 2020 and the 2nd of August, 2020 (the soil was naturally wet).

In 2021, freshly collected seeds were sown on eight managed plots at a time, on the 21st of June, 2021. All plots were watered after sowing. The same amount of seeds was used: 600 seeds per a plot 2 × 2 m (M14–M18). At larger plots with previously uprooted vegetation (M11–M13), the amount of seed sown was significantly increased – up to 3600 per a plot. We did not seed two managed plots (M19, M20) where the generative individuals of *Pulsatilla vulgaris* occured, but we bared the ground near the flowering plants to allow the seeds fallen from the plant to germinate.

Table 2. Main coenotic and environmental characteristics of the managed plots
Таблица 2. Основные ценотические и экологические характеристики рабочих площадок

Plot Площадка	Plot size Размер площадки (m × m)	Vegetation Растительность	pH of soil solution pH почвенного раствора	Type of restoration works Тип реставрационных работ	Dolomite powder added (kg) Внесение доломитовой муки (кг)
1	2	3	4	5	6
		2020			
M1	2 × 2	Moss heathland. Moss cover 95%, lichen cover 2%, grass cover 1%. Number of species – 14. Most abundant: *Niphotrichum canescens* Моховая пустошь. Моховой покров 95%, лишайниковый покров 2%, травяной покров 1%. Количество видов – 14. Наиболее обильные: *Niphotrichum canescens*	5.83	II (removal of plant cover and sod with some harrowing) (удаление растительности и дерна и легкое боронование)	2
M2	2 × 2	Lichen-moss heathland. Moss cover 65%, lichen cover 25%, grass cover 3%. Number of species – 18. Most abundant: *Niphotrichum canescens*, *Cetraria islandica* Лишайниково-моховая пустошь. Моховой покров 65%, лишайниковый покров 25%, травяной покров 3%. Количество видов – 18. Наиболее обильные: *Niphotrichum canescens*, *Cetraria islandica*	5.45	I (removal of plant cover and sod followed by soil reversal) (удаление растительности и дерна с последующим оборотом грунта)	0
M3	5 × 11	Pine forest (*Pinus sylvestris*) with *Avenella flexuosa* and mosses (*Pleurozium schreberi*, *Dicranum polysetum*). Crown density – 0.4. Height – 10 m. Moss cover 45%, grass cover 25%. Number of species – 25 Сосняк луговиково-моховой. Сомкнутость крон – 0.4. Высота – 10 м. Моховой покров 45%, травяной покров 25%. Количество видов – 25	5.04	V (tree uprooting with removal of herb layer and sod) (корчевка деревьев с последующим удалением травяно-кустарничкового яруса и дерна)	0
M4	2 × 2	Lichen-moss heathland. Moss cover 50%, lichen cover 30%, grass cover 8%. Number of species – 36. Most abundant: *Barbilophozia attenuata*, *Pleurozium schreberi*, *Cetraria islandica*, *Cladonia arbuscula* Лишайниково-моховая пустошь. Моховой покров 50%, лишайниковый покров 30%, травяной покров 8%. Количество видов – 36. Наиболее обильные: *Barbilophozia attenuata*, *Pleurozium schreberi*, *Cetraria islandica*, *Cladonia arbuscula*	5.66	III (partial removal of plant cover and sod) (частичное снятие растительности и дерна)	0

Table 2. Continue
Таблица 2. Продолжение

1	2	3	4	5	6
M5	6 × 6	Sparse pine forest (*Pinus sylvestris*) with *Avenella flexuosa* and mosses (*Pleurozium schreberi*) Crown density – 0.1. Height – 8 m. Moss cover 40%, grass cover 20%. Number of species – 37 Разреженный сосняк луговико-во-моховой. Сомкнутость крон – 0.1. Высота – 8 м. Моховой покров 40%, травяной покров 20%. Количество видов – 37	5.43	V (tree uprooting with removal of herb layer and sod) (корчевка деревьев с последующим удалением травяно-кустарничкового яруса и дерна)	0
M6	10 × 10	Sparse pine forest (*Pinus sylvestris*) with *Avenella flexuosa* and mosses (*Pleurozium schreberi*) Crown density – 0.1. Height – 8 m. Grass cover 50%, moss cover 20%. Number of species – 49 Разреженный сосняк мохово-луговиковый. Сомкнутость крон – 0.1. Высота – 8 м. Травяной покров 50%, моховой покров 20%, Количество видов – 49	5.62	V (tree uprooting with removal of herb layer and sod) (корчевка деревьев с последующим удалением травяно-кустарничкового яруса и дерна)	0
M7	2 × 2	Grass-moss heathland. Moss cover 50%, grass cover 45%. Number of species – 20. Most abundant: *Pleurozium schreberi*, *Dicranum polysetum*, *Avenella flexuosa*, *Festuca ovina* Злаково-моховая пустошь. Моховой покров 50%, травяной покров 45%. Количество видов – 20. Наиболее обильные: *Pleurozium schreberi*, *Dicranum polysetum*, *Avenella flexuosa*, *Festuca ovina*	5.58	I (removal of plant cover and sod followed by soil reversal) (удаление растительности и дерна с последующим оборотом грунта)	2
M8	2 × 2	Moss-hairgrass heathland. Grass cover 40%, moss cover 25%. Number of species – 19. Most abundant: *Avenella flexuosa*, *Pleurozium schreberi* Мохово-луговиковая пустошь. Травяной покров 40%, моховой покров 25%. Количество видов – 19. Наиболее обильные: *Avenella flexuosa*, *Pleurozium schreberi*	5.58	I (removal of plant cover and sod followed by soil reversal) (удаление растительности и дерна с последующим оборотом грунта)	0
M9	2 × 2	Hairgrass-moss heathland. Moss cover 90%, grass cover 20%. Number of species – 17. Most abundant: *Pleurozium schreberi*, *Dicranum polysetum*, *Thuidium recognitum*, *Avenella flexuosa* Луговиково-моховая пустошь. Моховой покров 90%, травяной покров 20%. Количество видов – 17. Наиболее обильные: *Pleurozium schreberi*, *Dicranum polysetum*, *Thuidium recognitum*, *Avenella flexuosa*	5.36	II (removal of plant cover and forest floor with some harrowing) (удаление растительности и дерна и легкое боронование)	2

Table 2. Continue
Таблица 2. Продолжение

1	2	3	4	5	6
M10	2 × 2	Hairgrass-moss heathland. Moss cover 45%, grass cover 40%. Number of species – 19. Most abundant: *Pleurozium schreberi*, *Avenella flexuosa* Луговиково-моховая пустошь. Моховой покров 45%, травяной покров 40%. Количество видов – 19. Наиболее обильные: *Pleurozium schreberi*, *Avenella flexuosa*	6.39	III (partial removal of plant cover and sod) (частичное снятие растительности и дерна)	0
2021					
M11	9 × 9	Fescue-moss heathland. Moss cover 25%, grass cover 20%, lichen cover 6%. Number of species – 32. Most abundant: *Niphotrichum canescens*, *Pleurozium schreberi*, *Avenella flexuosa* Овсяницево-моховая пустошь. Моховой покров 25%, травяной покров 20%, лишайниковый покров 6%. Количество видов – 32. Наиболее обильные: *Niphotrichum canescens*, *Pleurozium schreberi*, *Avenella flexuosa*	6.05	V (tree uprooting with removal of herb layer and sod) (корчевка деревьев с последующим удалением травяно-кустарничкового яруса и дерна)	0
M12	15 × 7	Pine forest (*Pinus sylvestris*) with *Avenella flexuosa* and mosses (*Pleurozium schreberi*, *Dicranum polysetum*). Crown density – 0.3. Height – 7–10 m. Grass cover 25%, moss cover 20%. Number of species – 25 Сосняк мохово-луговиковый. Сомкнутость крон – 0.3. Высота – 7–10 м. Травяной покров 25%, моховой покров 20%. Количество видов – 25	5.07	V (tree uprooting with removal of herb layer and sod) (корчевка деревьев с последующим удалением травяно-кустарничкового яруса и дерна)	0
M13	10 × 7	Pine forest (*Pinus sylvestris*) with *Avenella flexuosa*. Crown density – 0.2. Height – 6 m. Grass cover 45%, moss cover 8%. Number of species – 37 Сосняк луговиковый. Сомкнутость крон – 0.2. Высота – 6 м. Травяной покров 45%, моховой покров 8%, Количество видов – 37	5.42	V (tree uprooting with removal of herb layer and sod) (корчевка деревьев с последующим удалением травяно-кустарничкового яруса и дерна)	0
M14	2 × 2	Moss-grass heathland. Grass cover 60%, moss cover 20%. Number of species – 32. Most abundant: *Festuca ovina*, *Avenella flexuosa*, *Niphotrichum canescens* Мохово-злаковая пустошь. Травяной покров 60%, моховой покров 20%. Количество видов – 32. Наиболее обильные: *Festuca ovina*, *Avenella flexuosa*, *Niphotrichum canescens*	5.85	I (removal of plant cover and sod followed by soil reversal) (удаление растительности и дерна с последующим оборотом грунта)	2

Table 2. Continue
Таблица 2. Продолжение

1	2	3	4	5	6
M15	2 × 2	Hairgrass-moss heathland. Moss cover 70%, grass cover 10%. Number of species – 14. Most abundant: *Pleurozium schreberi*, *Avenella flexuosa* Луговиково-моховая пустошь. Моховой покров 70%, травяной покров 10%. Количество видов – 14. Наиболее обильные: *Pleurozium schreberi*, *Avenella flexuosa*	4.93	II (removal of plant cover and forest floor with some harrowing) (удаление растительности и дерна и легкое боронование)	2
M16	2 × 2	Lichen-hairgrass-moss heathland. Moss cover 45%, grass cover 30%, lichen cover 20%. Number of species – 30. Most abundant: *Pleurozium schreberi*, *Avenella flexuosa*, *Cladonia arbuscula*, *Cetraria islandica* Лишайниково-луговиково-моховая пустошь. Моховой покров 45%, травяной покров 30%, лишайниковый покров 20%. Количество видов – 30. Наиболее обильные: *Pleurozium schreberi*, *Avenella flexuosa*, *Cladonia arbuscula*, *Cetraria islandica*	5.28	III (partial removal of plant cover and sod) (частичное снятие растительности и дерна)	2
M17	2 × 2	Moss-hairgrass heathland. Grass cover 75%, moss cover 25%. Number of species – 19. Most abundant: *Avenella flexuosa*, *Pleurozium schreberi*, *Dicranum polysetum* Мохово-луговиковая пустошь. Моховой покров 75%, травяной покров 25%. Количество видов – 19. Наиболее обильные: *Avenella flexuosa*, *Pleurozium schreberi*, *Dicranum polysetum*	5.27	I (removal of plant cover and sod followed by soil reversal) (удаление растительности и дерна с последующим оборотом грунта)	2
M18	2 × 2	Moss-lichen-hairgrass heathland. Grass cover 40%, lichen cover 25%, moss cover 15%. Number of species – 29. Most abundant: *Avenella flexuosa*, *Cladonia arbuscula*, *Pleurozium schreberi* Мохово-лишайниково-луговиковая пустошь. Травяной покров 40%, лишайниковый покров 25%. моховой покров 15%,. Количество видов – 29. Наиболее обильные: *Avenella flexuosa*, *Cladonia arbuscula*, *Pleurozium schreberi*	5.17	I (removal of plant cover and sod followed by soil reversal) (удаление растительности и дерна с последующим оборотом грунта)	2

Table 2. Continue
Таблица 2. Продолжение

1	2	3	4	5	6
M19	2 × 2	Moss-hairgrass heathland. Grass cover 45%, moss cover 40%. Number of species – 22. Most abundant: *Avenella flexuosa*, *Pleurozium schreberi* Мохово-луговиковая пустошь. Травяной покров 45%, моховой покров 40%. Количество видов – 22. Наиболее обильные: *Avenella flexuosa*, *Pleurozium schreberi*	4.97	IV (partial removal of plant cover in order to create open soil sites around generative individuals of *Pulsatilla vulgaris*) (частичное удаление растительности в целях создания участков с открытой почвой вокруг генеративных экземпляров *Pulsatilla vulgaris*)	2
M20	2 × 2	Grass-herb meadow. Grass cover 60%; Number of species – 32. Most abundant: *Achillea millefolium*, *Vicia cracca*, *Pulsatilla vulgaris*, *Avenella flexuosa*, *Helictochloa pratensis* Злаково-разнотравный луг. Травяной покров 60%. Количество видов – 32. Наиболее обильные: *Achillea millefolium*, *Vicia cracca*, *Pulsatilla vulgaris*, *Avenella flexuosa*, *Helictochloa pratensis*	5.62	IV (partial removal of plant cover in order to create open soil sites around generative individuals of *Pulsatilla vulgaris*) (частичное удаление растительности в целях создания участков с открытой почвой вокруг генеративных экземпляров *Pulsatilla vulgaris*)	2

RESULTS AND DISCUSSION

On the 12 control plots, we found 776 individuals of *Pulsatilla vulgaris*, 527 of which grew on the plots (C1–C6) located outside the "Nizhnevolkhovskiy" Protected Area, and 249 ones grew on the plots (C7–C12) located inside the PA. On the control plots, the density of individuals of *P. vulgaris* per 1 m^2 varies from 4.5 (C10) to 38.5 (C5) (Table 3) (mean = 16.2). However, the mean density of the individuals on the plots outside the PA is two times higher than that on the plots inside the PA (21.9 vs 10.4 individuals per 1 m^2).

We counted the number of plants of various ontogenetic groups on the control plots (Table 3). According to literature data, *Pulsatilla vulgaris* life span reaches 20 years (Walker, 2011), in the 4–5 years of life the plants reach generative stage (in the 1.5–3 years if cultivated (Yagovkina, Baranova, 2009; Walker, 2011)).

Some ontogenetic stages are missing from the *Pulsatilla vulgaris* coenopopulation. The majority of the control plots are characterised by the predominance of virginile or young generative plants with a great number of mature generative plants. On the five plots (C4 outside the PA; C7, C8, C10, and C12 inside the PA), seedlings, juvenile and immature plants were not found. On the plots C1 and C11, there were no seedlings and juvenile plants. Subsenile and senile individuals were absent from all the plots located outside the PA, while they were recorded on three out of six plots located inside the PA.

We determined the ontogenetic state of *Pulsatilla vulgaris* coenopopulations on the control plots based on the presence and predominance of the certain ontogenetic groups. The decline of the population was estimated based on the absence of pregenerative plants (Rabotnov, 1950; Smirnova et al., 2002) (Table 4).

We found that coenopopulations of *Pulsatilla vulgaris* on the most plots have left-handed ontogenetic spectrum what might indicate that they are relatively young. Formally, they should be assigned to the normal type of age state; however; as seven plots have no young plants (i.e. seedlings, juvenile and immature individuals) the regress process could be stated. The proportion of the pregenerative plants (mainly due to virginile individuals) on two control plots outside the PA (C2, C3) exceeds the share of generative plants. This circumstance makes them similar to invasive (pioneer) populations (Rabotnov, 1950). The coenopopulation of one of the control plots inside the PA (C9) has a fragmentary range with a predominance of immature and virginile plants. C9 is the only control plot inside the PA where plants of all pregenerative stages have been recorded. Probably, the

Table 3. Age structure of *Pulsatilla vulgaris* cenopopulations on control plots
Таблица 3. Возрастная структура ценопопуляций *Pulsatilla vulgaris* на контрольных площадках

Ontogenetic groups Онтогенетические группы	Number of individuals on control plots Количество особей на контрольных площадках											
	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12
p	0	1	2	0	1	6	0	0	3	0	0	0
j	0	3	9	0	3	5	0	0	1	0	0	0
im	1	14	18	0	3	14	0	0	11	0	4	0
v	12	33	38	6	55	23	16	6	10	3	6	17
g_1	20	32	18	18	56	20	42	23	2	12	9	6
g_2	15	13	18	3	36	26	18	13	0	3	5	6
g_3	2	0	0	1	0	2	3	3	0	0	6	11
ss	0	0	0	0	0	0	0	0	1	0	2	5
s	0	0	0	0	0	0	0	0	0	0	1	1
sc	0	0	0	0	0	0	0	0	0	0	0	0
Total number of individuals Общее число особей	50	96	103	28	154	96	79	45	28	18	33	46
Mean number of individuals per m^2 Среднее число особей на $м^2$	12.5	24	25.75	7	38.5	24	19.75	11.25	7	4.5	8.25	11.5

Note. Ontogenetic groups: *p* – seedling; *j* – juvenile; *im* – immature; *v* – virginile; g_1 – young generative; g_2 – mature generative; g_3 – old generative; *ss* – subsenile; *s* – senile; *sc* – dying.

Примечание. Онтогенетические группы: *p* – проросток; *j* – ювенильная; *im* – имматурная; *v* – виргинильная; g_1 – генеративная молодая; g_2 – генеративная средневозрастная; g_3 – генеративная старая; *ss* – субсенильная; *s* – сенильная; *sc* – отмирающая.

Table 4. Types of *Pulsatilla vulgaris* coenopopulations on the control plots
Таблица 4. Типы ценопопуляций *Pulsatilla vulgaris* на контрольных площадках

Control plots Контрольные площадки	Type of coenopopulation Тип ценопопуляции
C1, C4, C7, C8, C10–C12	normal incomplete with regression signs, left-handed spectrum нормальная неполночленная с признаками регрессии, спектр левосторонний
C2, C3, C5	normal incomplete, left-handed spectrum нормальная неполночленная, спектр левосторонний
C6	normal incomplete, bimodal spectrum (max *v* и g_2) нормальная неполночленная, спектр бимодальный (max *v* и g_2)
C9	fragmented, left-handed spectrum фрагментарная, спектр левосторонний

characteristics of this coenopopulation are determined by its location along the trail subjected to a significant recreational load.

The basic ontogenetic spectrum (Zaugolnova, 1976) of *Pulsatilla vulgaris* on all of the 12 control plots might be characterised as (i) normal, (ii) complete, and (iii) monomodal, with maximum number of young generative plants (Fig. 3).

The comparison of averaged ontogenetic spectra of *Pulsatilla vulgaris* between the control plots *inside* and *outside* the PA clearly shows their differences in number of various ontogenetic groups of plants (Fig. 4). On the plots *outside* the PA, the number of pregenerative, young, and mature generative plants is higher than that on the plots *inside* the PA, where the number of old generative and postgenerative plants is high.

The graph of averaged ontogenetic spectra of *Pulsatilla vulgaris* coenopopulations (in relative values) (Fig. 5) demonstrates that on the plots outside the PA (i) virginile and young generative plants predominate, (ii) there are no postgenerative plants, (iii) juvenile and immature plants seedlings play a more significant role. On the control plots inside the PA, young generative plants dominate

Fig. 3. Basic ontogenetic spectrum of *Pulsatilla vulgaris*.
Ontogenetic groups: *p* – seedling; *j* – juvenile; *im* – immature; *v* – virginile; g_1 – young generative; g_2 – mature generative; g_3 – old generative; *ss* – subsenile; *s* – senile.

Рис. 3. Базовый онтогенетический спектр *Pulsatilla vulgaris*.
Онтогенетические группы: *p* – проросток; *j* – ювенильная; *im* – имматурная; *v* – виргинильная; g_1 – генеративная молодая; g_2 – генеративная средневозрастная; g_3 – генеративная старая; *ss* – субсенильная; *s* – сенильная.

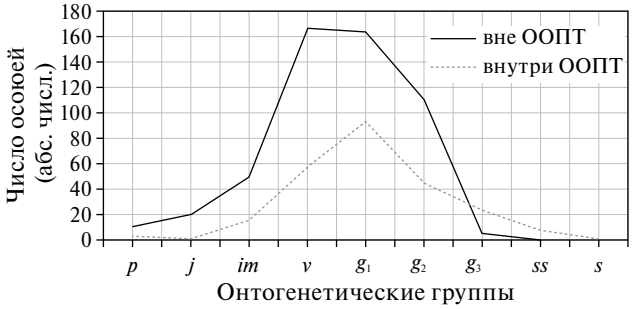

Fig. 4. Average ontogenetic spectra of *Pulsatilla vulgaris* on the control plots inside and outside the PA.
Ontogenetic groups: *p* – seedling; *j* – juvenile; *im* – immature; *v* – virginile; g_1 – young generative; g_2 – mature generative; g_3 – old generative; *ss* – subsenile; *s* – senile.

Рис. 4. Усредненные онтогенетические спектры *Pulsatilla vulgaris* на контрольных площадках в границах и вне границ ООПТ.
Онтогенетические группы: *p* – проросток; *j* – ювенильная; *im* – имматурная; *v* – виргинильная; g_1 – генеративная молодая; g_2 – генеративная средневозрастная; g_3 – генеративная старая; *ss* – субсенильная; *s* – сенильная.

and postgenerative individuals appear. The increase in the role of young generative plants is accompanied by a decrease in number of individuals in all pregenerative groups, rather than their increase, as it usually occurs in the populations of normal complete ontogenetic spectrum (Smirnova et al., 2002). Thus, the regression phenomena typical of the part of the population growing inside the PA are determined by the environment impact, not by the age structure of the population.

Fig. 5. Average ontogenetic spectra of *Pulsatilla vulgaris* (in relative values) on the control plots inside and outside the PA.
Ontogenetic groups: *p* – seedling; *j* – juvenile; *im* – immature; *v* – virginile; g_1 – young generative; g_2 – mature generative; g_3 – old generative; *ss* – subsenile; *s* – senile.

Рис. 5. Усредненные онтогенетические спектры *Pulsatilla vulgaris* (в относительных величинах) на контрольных площадках в границах и вне ООПТ.
Онтогенетические группы: *p* – проросток; *j* – ювенильная; *im* – имматурная; *v* – виргинильная; g_1 – генеративная молодая; g_2 – генеративная средневозрастная; g_3 – генеративная старая; *ss* – субсенильная; *s* – сенильная.

For the majority of the control plots (9 out of 12), the ratio of ontogenetic groups of *Pulsatilla vulgaris* is similar to that of young coenopopulations (Table 5). Plots C3 and C9 are characterised by lower age level (maturing coenopopulation); plot C12 is mature. Generally, average age level is higher for the plots *inside* the PA (0.312) than for the plots *outside* the PA (0.248).

The efficiency index (ω) value varies from 0.297 (C9) to 0.799 (C8) (Table 5). At the same time, mean energy efficiency of coenopopulations at plots outside and inside the PA have similar values (0.636 и 0.647 correspondently).

According to (Δ – ω) classification of age state (Table 5) based on joint use of ageness index and efficiency index (Osmanova, Zhivotovsky, 2020), coenopopulations on six control plots are maturing, while young coenopopulations are characteristic to three plots outside the PA and for one plot inside the PA; inside the PA there is also one transitional coenopopulation and one is mature.

In order to predict the dynamics of *Pulsatilla vulgaris* population number, we assessed the efficiency of the population self-replacement by calculating indexes of regeneration (I_{reg}) and replacement (I_{rep}). In total, on all control plots the index of regeneration (I_{reg}) is 0.7, while on the control plots *outside* the PA it is 0.85, and *inside* the PA – 0.46. In total on all control plots the index of replacement (I_{rep}) is 0.69, while on the control plots *outside* the PA it is 0.85, and *inside* the PA – 0.43.

Table 5. Main characteristics of *Pulsatilla vulgaris* coenopopulations on the control plots
Таблица 5. Основные характеристики ценопопуляций *Pulsatilla vulgaris* на контрольных площадках

Plot Площадка	Ageness index (Δ) Индекс возрастности (Δ)	Age level Возрастной уровень	Efficiency index (ω) Индекс эффективности (ω)	Coenopopulation type according to "Δ – ω" classification Тип ценопопуляции по классификации "Δ – ω"
C1	0.316	young молодая	0.750	maturing зреющая
C2	0.206	young молодая	0.571	young молодая
C3	0.188	maturing взрослеющая	0.505	young молодая
C4	0.278	young молодая	0.731	maturing зреющая
C5	0.258	young молодая	0.675	maturing зреющая
C6	0.243	young молодая	0.583	young молодая
C7	0.308	young молодая	0.761	maturing зреющая
C8	0.346	young молодая	0.799	maturing зреющая
C9	0.113	maturing взрослеющая	0.297	young молодая
C10	0.282	young молодая	0.761	maturing зреющая
C11	0.391	young молодая	0.638	transitional переходная
C12	0.435	mature зрелая	0.626	mature зрелая

The averaged efficiency of self-replacement of *Pulsatilla vulgaris* population calculated for the control plots is significantly lower than 1, indicating a low ability of the population to replace itself (Osmanova, Zhivotovsky, 2020). Moreover, the efficiency of self-replacement of *P. vulgaris* population *inside* the PA is two times lower compared to the population *outside* the PA.

The absence or low number of pregenerative individuals of *Pulsatilla vulgaris* indicates low seed reproduction of the species even in the places with the highest number of generative plants. Seven of twelve studied coenopopulations (ageness index is 0.278 or higher) show traits of regress. At the same time, the emergence of seedlings, juvenile and immature plants is connected directly to the soil and plant cover disturbances and their age. By using Spearman's rank correlation coefficient we found positive relationship between disturbances and the number of pregenerative plants ($r_s = 0.698$ for seedlings; $r_s = 0.781$ for juvenile plants; $r_s = 0.816$ for immature plants; $r_s = 0.671$ for virginile plants). On the vast majority of the control plots *inside* the PA, where all disturbances are prohibited according to its regime, high number of young and middle-age generative plants occur, seed reproduction is absent. The phenomenon cannot be explained by the fruiting rhythm. The main reason for weak seed reproduction is formation of closed plant cover (including plant debris layer) and acidification of soil caused by decomposition of the large amount of needles and mosses debris. We found that the total number of *P. vulgaris* individuals on the control plots is significantly correlates to the increase of soil solution pH ($r_s = 0.797$), the same correlation was found for the number of juvenile plants ($r_s = 0.593$) and for virginile plants ($r_s = 0.748$), while for seedlings and immature plants the relationship was not significant ($r_s = 0.446$). For all pregenerative ontogenetic stages of *P. vulgaris*, we found negative correlation between the number of individuals and cover of plant debris, though it was not significant ($r_s = -0.044$ for seedlings; $r_s = -0.184$ for juvenile plants; $r_s = -0.194$ for immature plants; $r_s = -0.469$ for virginile plants).

Thus, the current unstable state and the dynamics of *Pulsatilla vulgaris* population proved the necessity of urgent actions to maintain effective seed reproduction of the species within "Nizhnevolkhovskiy" Protected Area.

We carried out the restoration actions within the "Nizhnevolkhovskiy" Protected Area largely based on the experience of the European colleagues (Sedláková, Chytrý, 1999; Walker, Pinches, 2011) and Natura 2000 habitat management program (Management..., 2008). In the course of the restoration works, we created lit and well-warmed sites with missing or disturbed plant cover that are suitable for seed reproduction of *P. vulgaris*.

In 2020, the first *Pulsatilla vulgaris* seedlings were recorded on the 22nd of August on three plots sown in June. During the recalculation done on the 7th of October, 2020 seedlings were found on nine out of ten managed plots (Table 6). There were no seedlings only on one plot (M3), seeded the last (2nd of August, 2020), but the seedlings of the protected species *Armeria maritima* were recorded. By the end of the growing season (2020), the total number of young plants was 141, their amount on the managed plots ranged from 5–6 (on the large uprooted plots seeded the last) up to 39–45 (on the plots seeded in June). By October 2020, juvenile plants had from one to three true leaves; most plants had two true leaves. In May 2021, new seedlings appeared on the managed plots: the largest number was recorded on the plots M3, M5, M6 seeded in late July-August 2020.

On the managed plots, seed germination rate varied from 1.5% to 9.7% (mean = 4.6%). In total, on the plots managed in 2020, 311 seedlings of *Pulsatilla vulgaris* appeared by spring of 2021. During the summer season of 2021, 12.5% of the seedlings died, and only 272 individuals, mostly immature and virginile, survived by the autumn of 2021 (Table 6). The first blossoming individuals were recorded on the 24th of May 2022, 13 on the plot M5 and 10 on the plot M6.

The control seed germination of *Pulsatilla vulgaris* in indoor conditions (unheated greenhouse) in 2020 was 60%. These values correspond to the average germination of freshly collected seeds obtained in the laboratory conditions: 47% for the seeds from Sweden (Walker, 2011), about 69.8% for material from Ukraine (Pereboichuk, 2016) and 75% for material from the UK (Walker, 2011). The first seedlings appeared 48 days after they were sown in the greenhouse. By the end of the first growing season, the plants reached the immature

Table 6. Results of *Pulsatilla vulgaris* seeds germination on managed plots in 2020
Таблица 6. Показатели всхожести семян *Pulsatilla vulgaris* на рабочих площадках в 2020 г.

Plot Площадка	Date of seeding Дата посева семян	Number of seeds sown Количество посеянных семян	Time of seedlings emergence Сроки появления всходов	Number of seedlings Количество всходов	Germination rate Всхожесть семян	Number of seedlings died by October 2021 Количество проростков, погибших к октябрю 2021 г.
M1	23.06.2020	600	end of August 2020 конец августа 2020 г.	15	2.5	4
M2	23.06.2020	600	end of August 2020 – May 2021 конец августа 2020 г. – май 2021 г.	58	9.7	0
M3	02.08.2020	800	May 2021 май 2021 г.	56	7	0
M4	23.06.2020	600	October 2020 – May 2021 октябрь 2020 г. – май 2021 г.	17	2.8	0
M5	30.07.2020	800	October 2020 – May 2021 октябрь 2020 г. – май 2021 г.	39	4.9	0
M6	30.07.2020	800	October 2020 – May 2021 октябрь 2020 г. – май 2021 г.	52	6.5	0
M7	23.06.2020	600	October 2020 октябрь 2020 г.	45	7.5	22
M8	23.06.2020	600	October 2020 октябрь 2020 г.	7	1.2	7
M9	23.06.2020	600	end of August 2020 конец августа 2020 г.	13	2.2	6
M10	23.06.2020	600	October 2020 – May 2021 октябрь 2020 г. – май 2021 г.	9	1.5	0

phase and formed 4–5 true leaves; by the end of the second season (2021) they entered the virginile phase and blossomed in May 2022.

In 2021, we recorded the first seedlings of *Pulsatilla vulgaris* on the managed plots by the 30th of August (plots M11, M14–M16). By the 2nd of October the seedlings appeared on two other plots (M12 and M17). In total, we recorded 70 seedlings of *P. vulgaris* on all managed plots. Seed germination rate varied from 0 to 9.2% (mean = 1.3%) (Table 7). By the end of October, nine seedlings (12.9% of all recorded in 2021) died. We believe that high temperatures and drought of summer 2021 negatively affected the germination rate of *P. vulgaris* on the exposed and well-lit plots compared to 2020.

On two managed plots (M19, M20) with generative individuals of *Pulsatilla vulgaris*, where no seeds were sown, in 2021 ten seedlings appeared, one died by the end of the vegetation season (Table 7). At the same time, on the control plot C7 located next to the managed plot M20, no seedlings were in 2021.

In total, by the end of the growing season, 70 young plants – seedlings and juvenile individuals (with one, less often two true leaves) grew on ten plots managed in 2021. In May 2023, the first plants blossomed.

In order to estimate the success of restoration activities made, we compared mean germination rate of *Pulsatilla vulgaris* between the control plots (*inside* the PA, *outside* the PA and the mean value for population) and managed plots in 2020 and 2021.

Mean number of seeds per a control plot is higher for plots outside the PA (12427) than for plots inside the PA (6920). According to the literature sources (Wells, Barling, 1971) and the authors' observations, the fruits (achenes) of *Pulsatilla vulgaris* having tenacious pinnate stylodia, mainly spread for no more than 20 cm from the parent plant. Most of the disseminated seeds (no less than 80%) do not spread out of the control plots. Mean seed germination rate (Table 8) was higher on the control plots *outside* the PA than on the control plots *inside* the PA, both in 2020 (0.08% vs. 0.05%) and in 2021 (0.05% vs. 0.01%). For the whole population of *P. vulgaris*, mean germination rate was 0.07% in 2020 and 0.03% in 2021. At the same time, it should be noted that mean germination rate for the species in optimal climatic conditions within the main part of its geographic range is much higher, about 16% (Walker, 2011).

Thus, the efficiency of seed reproduction on the managed plots, sown after the restoration activities, was significantly higher compared with the control plots left

Table 7. Results of *Pulsatilla vulgaris* seeds germination on managed plots in 2021
Таблица 7. Показатели всхожести семян *Pulsatilla vulgaris* на рабочих площадках в 2021 г.

Plot Площадка	Date of seeding Дата посева семян	Number of seeds sown Количество посеянных семян	Time of seedlings emergence Сроки появления всходов	Number of seedlings Количество всходов	Germination rate Всхожесть семян	Number of seedlings died by October 2021 Количество проростков, погибших к октябрю 2021 г.
M11	21.06.2021	3600	–	1	0.03	1
M12	21.06.2021	3600	October 2021 октябрь 2021 г.	7	0.2	0
M13	21.06.2021	3600	–	0	0	0
M14	21.06.2021	600	–	3	0.5	3
M15	21.06.2021	600	end of August 2021 конец августа 2021 г.	55	9.2	4
M16	21.06.2021	600	–	1	0.2	1
M17	21.06.2021	600	October 2021 октябрь 2021 г.	3	0.5	0
M18	21.06.2021	600	–	0	0	0
M19	no seeding без засева семян		–	1	–	1
M20	no seeding без засева семян		end of August – October 2021 конец августа – октябрь 2021 г.	9	–	0

Table 8. Average number and germination of *Pulsatilla vulgaris* seeds on the control plots in 2020 and 2021
Таблица 8. Среднее число и всхожесть семян *Pulsatilla vulgaris* на контрольных площадках в 2020 и 2021 гг.

Control plots Контрольные площадки	Mean number of seeds produced on the control plot Среднее число семян, образующихся на контрольной площадке	Mean number of seeds left within the control plot Среднее число семян, остающихся на контрольной площадке	Mean seed germination rate in 2020 (%) Средняя всхожесть семян в 2020 г. (%)	Mean seed germination rate in 2021 (%) Средняя всхожесть семян в 2021 г. (%)
Outside the PA Вне границ ООПТ	12427	9942	0.08	0.05
Inside the PA В границах ООПТ	6920	5536	0.05	0.01
Mean value for the whole population Среднее для всей популяции	9594	7675	0.07	0.03

without intervention for both years: 4.6% vs. 0.07% in 2020, and 1.3% vs. 0.03% in 2021, respectively.

We have not found a significant relationship between the types of restoration work and number of seedlings of *Pulsatilla vulgaris* on the plots, as the data obtained in 2020–2021 are limited. Based on our observations we suppose that (i) removal of plant cover and sod along with the reversal of the soil on the plots of 2 × 2 m and (ii) uprooting with subsequent removal of the herb layer and sod on the larger plots were the most successful. Moreover, the plots with generative plants of *P. vulgaris* where plant cover was disturbed to create open soil fragments were more 'effective' compared to the control plots.

CONCLUSION

Artificially disturbed sites on the unmanaged and overgrown heathlands allow to increase significantly the effectiveness of *Pulsatilla vulgaris* population seed reproduction in critical to the species survival climatic conditions of the Leningrad Region. In total, in the course of the restoration activities fulfilled in 2020–2021 we obtained 361 young plants (i.e. seedlings, juvenile and immature individuals), that increased the number of this declining population by 10%. By the spring of 2022, the first plant individuals became generative; in 2023, there were 119 blooming plants.

Based on the current results we recommend the implemented methods and techniques to maintain the population of *Pulsatilla vulgaris* and other *Pulsatilla* species. These techniques could be also applied for restoration and maintenance of some highly specialized rare species (e.g., *Armeria maritima*, *Dianthus arenarius*, *Silene tatarica* etc.) of sandy habitats such as heathlands, open pine woods, continental dunes in Northwestern Russia.

The results of the work demonstrate that it is necessary to provide the legal possibility for science-based habitat management, like controlled disturbances of plant cover and soil, in the regulation acts for PAs aimed at preservation of sandy habitats (i.e. heathlands, old continental dunes and alike) in order to restore biotope mosaic.

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СОХРАНЕНИЕ *PULSATILLA VULGARIS* (RANUNCULACEAE) В РОССИИ: УПРАВЛЕНИЕ МЕСТООБИТАНИЯМИ ДЛЯ ПОДДЕРЖАНИЯ ЕДИНСТВЕННОЙ ПОПУЛЯЦИИ

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Pulsatilla vulgaris является одним из наиболее редких видов сосудистых растений на территории России: категория статуса в Красной книге Российской Федерации – 1 (вид, находящийся под угрозой исчезновения). Численность единственной в России популяции *P. vulgaris*, известной из Ленинградской области, сокращается быстрыми темпами. Анализ онтогенетической структуры популяции показал слабую эффективность ее самоподдержания, связанную с ограниченными возможностями семенного возобновления. Одной из основных причин, затрудняющих семенное возобновление вида, является преобразование биотопов в ходе естественной сукцессии. Типичными местообитаниями *P. vulgaris* являются боровые пустоши, разреженные сосновые леса, сухие низкотравные луга и пастбища. Для успешного семенного возобновления вида необходимо воздействие факторов, приводящих к разрушению сомкнутого напочвенного покрова и препятствующих развитию древесной растительности (например, умеренный выпас

скота, слабые низовые пожары и др.). Во избежание полной утраты вида на территории России в 2020–2021 гг. в границах ООПТ “Нижневолховский” (Ленинградская область, Волховский район) созданы искусственно нарушенные участки, пригодные для семенного возобновления *P. vulgaris*. На площадках проводилась корчевка деревьев, удаление или нарушение травянистой растительности, оборот верхнего слоя почвы в целях формирования освещенных и хорошо прогреваемых участков с несомкнутым растительным покровом. Мероприятия позволили повысить полевую всхожесть семян по сравнению с контрольными участками, оставленными без вмешательства. За двухлетний период численность популяции *P. vulgaris* была увеличена более чем на 10%. Эффективность применяемых мер позволяет рекомендовать их для восстановления численности редких узкоспециализированных видов, произрастающих в сходных местообитаниях.

Ключевые слова: редкий вид, возрастная структура, экологическая реставрация, эффективность семенного возобновления, сокращение популяции вида.

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