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**GENETIC STRUCTURE OF *SOLIDAGO* × *NIEDEREDERI* (ASTERACEAE)  
POPULATION IN THE «ALEKSIN BOR» NATURAL MONUMENT  
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*Solidago* × *niederederi* (Asteraceae) is a natural hybrid of the native *S. virgaurea* and the alien invasive *S. canadensis*, originated in Europe. Its naturalisation potential is still questionable. One of the largest (more than 20 ramet clusters, treated as individuals) known population of this nothospecies, is located in the «Aleksin Bor» Natural Monument (Aleksin town, Tula Region, Russia) in the floodplain of the River Oka. We studied its genetic structure with the help of chloroplast and nuclear markers. Analysis of sequence of nuclear ribosomal internal transcribed spacer ITS 1–2 showed that all individuals with intermediate morphology are actually hybrids. Data on the intergenic chloroplast non-coding spacer rpl32–trnL showed that *S. canadensis* is the maternal species in 60% of the studied individuals. It was shown that even closely located individuals were not clones; therefore, they were results of sexual, rather than vegetative reproduction. Analysis of ISSR markers showed that the studied individuals of *S.* × *niederederi* in this population are not only F<sub>1</sub> hybrids, but also their descendants (F<sub>2</sub> hybrids and/or backcrosses, mostly with *S. canadensis*). We conclude that *S.* × *niederederi* has successfully been naturalised in the studied community and, possibly, is outcompeting its native parental species, *S. virgaurea*, through introgression.

**Key words:** alien species, biological invasions, hybridisation, nothospecies, ISSR, ITS 1–2, rpl32–trnL**Introduction**

*Solidago* × *niederederi* Khek (Asteraceae) is a European hybrid of the native *S. virgaurea* L. and the alien invasive *S. canadensis* L. of North American origin. Morphological traits of this hybrid are intermediate, which makes it easy to distinguish it in nature from both parental species in most cases (Nilsson, 1976; Gudžinskas & Žalneravičius, 2016; Vinogradova & Galkina, 2020). Despite the fact that this taxon was described as early as the beginning of the XX century (Khek, 1905), and the oldest finding, apparently, dates back to 1899 (Skokanová et al., 2020a), its findings in Europe became relatively frequent only at late XX – early XXI centuries (Skokanová et al., 2020b). Its hybrid nature has been confirmed genetically in 2016, with a hybridisation process occurring in both directions (Pliszko & Zalewska-Gałosz, 2016). Now, the questions of the naturalisation degree of *S.* × *niederederi*, its invasion potential, and its potential threat to native *S. virgaurea* remain unresolved (Skokanová et al., 2020b; Vinogradova & Galkina, 2020; Skokanová et al., 2022).

In most cases, the findings of *S.* × *niederederi* are single individuals (Skokanová et al., 2020b). It suggests that they appeared as a result of new hybridisation acts, rather than the reproduction of already existed individuals of this hybrid. This is consistent with the available data on the reduced pollen viability (Migdalek et al., 2014), and the absence of long rhizomes, which facilitate vegetative propagation of this nothospecies (Pliszko & Kostrakiewicz-Gierałt, 2019). At the same time, data on seed germination are contradictory; existing estimates of germinated seeds percent range from extremely low (Vinogradova & Galkina, 2020) to high values (Pliszko & Kostrakiewicz-Gierałt, 2017). These results allow suggesting that in most cases *S.* × *niederederi* individuals appear as *de novo* inter-species hybrids rather than as a result of self-reproduction of the hybrid species. It should be noted that this does not affect its status as a nothospecies in accordance with Article H3.1 of the International Code of Nomenclature for Algae, Fungi and Plants (Turland et al., 2018).

In this regard, each more or less large population is of particular interest for clarifying the

problem of reproduction mechanisms and possible expansion of *S. × niedereideri*. Its population has been discovered in 2020 in the floodplain of the River Oka in the «Aleksin Bor» Natural Monument (northwest of the Tula Region, European Russia) (Lysenkov & Galkina, 2022). It looks like a promising object for studying this issue. The initial analysis of the two discovered individuals had already shown that this population emerged as a result of at least two hybridisation acts (Lysenkov & Galkina, 2022). Later, more than 20 individuals with intermediate morphology were found in the study area, which makes this population of *S. × niedereideri* one of the most numerous within the known distribution area (Skokanová et al., 2020b).

This study was aimed to identify the naturalisation strategy of *S. × niedereideri* in this population. Specifically, we aimed: 1) to confirm the species affiliation of *Solidago* with intermediate morphology using methods of molecular genetics; 2) to determine the maternal and paternal species for the discovered hybrids; 3) to reveal the propagation mechanism of *S. × niedereideri* in this population.

### Material and Methods

The studied *S. × niedereideri* population is located on a *Solidago*-forb meadow with high abundance of *S. canadensis* in a floodplain on the right bank of the River Oka in the «Aleksin Bor» Natural Monument (Aleksin, Tula Region, Russia; 54.53° N, 37.06° E). At the studied site, the climate is humid continental with a mean temperature of +18.6°C in July, and -6.5°C in January; the mean annual temperature is +6.0°C, and the annual precipitation is 614 mm according to data for 2012–2022 from the weather station, located 2.8 km south-east from the study site ([https://rp5.ru/Архив\\_погоды\\_в\\_Алексине](https://rp5.ru/Архив_погоды_в_Алексине)). The soil is slightly acidic loam. In the study area, the first finding of three ramet clusters of *S. × niedereideri* was made in 2020 during the study of insect visitation. One of them has also been found in 2019, though it was not studied properly. In August 2021, the meadow was specially surveyed to discover *Solidago* specimens, which are phenotypically intermediate between *S. virgaurea* and *S. canadensis*. We treated them based on the inflorescence structure: the branches of the inflorescence are long and diverge at an acute angle; the size of the capitula is larger than in *S. canadensis* and smaller than in *S. virgaurea*.

All detected specimens with intermediate morphology (n = 21) were photographed and mapped using a Garmin GPS navigator with an accuracy of 3 m. For each individual, the number of generative ramets has been counted. One leaf was sampled from each individual for genetic analysis of nuclear and chloroplast markers. Some specimens were collected into herbaria (one ramet per collected individual). For genetic analysis, leaves have been sampled from *S. canadensis* (n = 15) and *S. virgaurea* (n = 8), located closely (at a distance of less than 0.5 m) to the hybrids. In August 2022, this meadow was thoroughly surveyed again. We searched with GPS for individuals found in 2021 as well as individuals that had not been seen before.

For molecular genetic analysis, DNA was extracted from the collected leaves using the Extran kit (Synthol, Russia). Polymerase chain reaction (PCR) was carried out in a T-100 amplifier (Biorad, USA). For the nuclear ribosomal internal transcribed spacer (ITS 1–2), primers nnc18s10 (AGGAGAAGTCGTAACAA), forward, and c26A (GTTTCTTTTCCTCCGCT), reverse (Wen & Zimmer, 1996) were used at an annealing temperature of 58°C. For the chloroplast highly variable intergenic non-coding spacer rpl32–trnL, primers rpl32 F (forward) and trnL UAG (reverse) were used at an annealing temperature of 57°C. Purification of the PCR product for sequencing was carried out with a mixture of ammonium acetate and ethanol (when preparing 96% ethanol for 50 ml of such a mixture, 1.5 ml of 5 M ammonium acetate, 4.7 ml of water and 43.8 ml of 96% ethanol are taken). DNA was sequenced with an automatic sequencer ABI 3500xl (Applied Biosystems) of the company Synthol (Russia). The obtained nucleotide sequences were processed with BioEdit v. 7.0.5.3 (Hall, 1999). The obtained data were deposited in the GenBank database (NCBI, 2022) (Table 1).

Four ISSR primers were also used, namely UBC841 [(GA8)YG], M2 [(AC)8(C/T)G], M7 [(AC)8(C/T)G], M11 [(CACACA)2 (A/G)]. Pre-denaturation took place for 3 min at 94°C. Elongation lasted 30 s at 94°C, then 30 s at 37°C with M11, at 45°C with UBC 841, at 50°C with M2, and at 55°C with primer M7. Then elongation took place for 1 min at 72°C. The described process was repeated 35 times, and each subsequent time the elongation lasted 2 s longer at 72°C. The final stage was elongated for 3 min at 72°C.

The amplification products have been separated by electrophoresis in 1.7% agarose gel with the addition of ethidium bromide in  $0.5 \times$  TBE buffer for 1 h. Then the DNA fragments have been photographed in ultraviolet light in GelDoc-It Imaging System (LCD/LM-26E, USA) (Fig. S1). To determine their lengths, a 100bp + molecular weight marker was used. Images with DNA fragments have been analysed using CrossChecker software (Buntjer, 2000), with compilation of binary matrices of the presence/absence of frag-

ments of the same length. The obtained data are presented in the form of a matrix of binary features, in which the presence or absence of a certain fragment has been coded as 1 or 0, respectively. The resulting matrix has been analysed, with the non-metric multidimensional scaling method using the Jaccard distance in PAST v. 4.06 (Hammer et al., 2001). The hybridity of the studied specimens has been analysed, based on the results of ISSR analysis with NewHybrids software (Anderson & Thompson, 2002).

**Table 1.** *Solidago* spp. specimens used for molecular genetic analysis

Species	Specimen code	Barcode	Specimen ID in GenBank	
			ITS 1–2	rpl32–trnL
<i>Solidago juncea</i> Aiton (outgroup)	Sj	MHA0095780	MT584230	MT587694
<i>Solidago canadensis</i> L.	ScTu	MW 1066856	MZ224518	MZ230669
	Sc2	MHA0454305	ON637729	ON677260
	Sc3	–	ON637730	ON677261
	Sc5	MHA0454303	ON637731	ON677262
	Sc6	MHA0454302	ON637732	ON677263
	Sc8	–	ON637733	ON677264
	Sc9	–	ON637734	ON677265
	Sc12	–	–	ON677266
	Sc13	–	ON637735	ON677267
	Sc14	MHA0454308	ON637736	ON677268
	Sc15	–	ON637737	ON677269
	Sc16	–	ON637738	ON677270
	Sc17	MHA0454304	ON637739	ON677271
	Sc20	MHA0454306	ON637740	ON677272
Sc21	MHA0454307	ON637741	ON677273	
<i>Solidago × niededereri</i> Khek	Sn1Tu	MW 1066857	MZ224519	MZ230670
	Sn2Tu	MW 1066858	MZ224520	MZ230671
	Sn2	MHA0454295	ON637742	ON677274
	Sn3	–	–	ON677275
	Sn5	MHA0454291	ON637743	ON677276
	Sn6	MHA0454290	–	ON677277
	Sn7	MHA0454299	ON637744	ON677278
	Sn8	MHA0454297	–	ON677279
	Sn9	–	ON637745	ON677280
	Sn10	–	ON637746	ON677281
	Sn11	–	–	ON677282
	Sn12	–	–	ON677283
	Sn13a	–	–	ON677284
	Sn13b	–	–	ON677285
	Sn14	MHA0454294	ON637747	ON677286
	Sn15	–	ON637748	ON677287
	Sn16	–	ON637749	ON677288
	Sn17	MHA0454292	ON637750	ON677289
	Sn19	MHA0454296	ON637751	ON677290
	Sn21	–	ON637752	ON677291
	<i>Solidago virgaurea</i> L.	Sv1Tu	MW 1066859	MZ224521
Sv2Tu		MW 1066859	MZ224522	MZ230672
Sv1		–	ON637753	ON677292
Sv2		MHA0454273	ON637754	ON677293
Sv3		–	ON637755	ON677294
Sv4		–	–	ON677295
Sv5		–	ON637756	ON677296
Sv6		MHA0454274	ON637757	ON677297
Sv16	–	ON637758	ON677298	

To investigate the propagation mechanism of *S. × niedereideri*, we used ITS 1–2 and ISSR data to distinguish between vegetative propagation (in this case, some of closely located individuals would be genetically identical) and sexual reproduction. In the latter case, we can distinguish between two hypotheses: i) all individuals are a result of *de novo* hybridisation events, i.e. F<sub>1</sub> hybrids (in this case, *S. × niedereideri* specimens would be intermediate in nuclear markers, with no overlap between parental species); ii) some individuals are resulted from sexual reproduction of existing hybrid individuals, i.e. F<sub>2</sub> hybrids and/or backcrosses (in this case, some *S. × niedereideri* specimens would be closer to one of parental species).

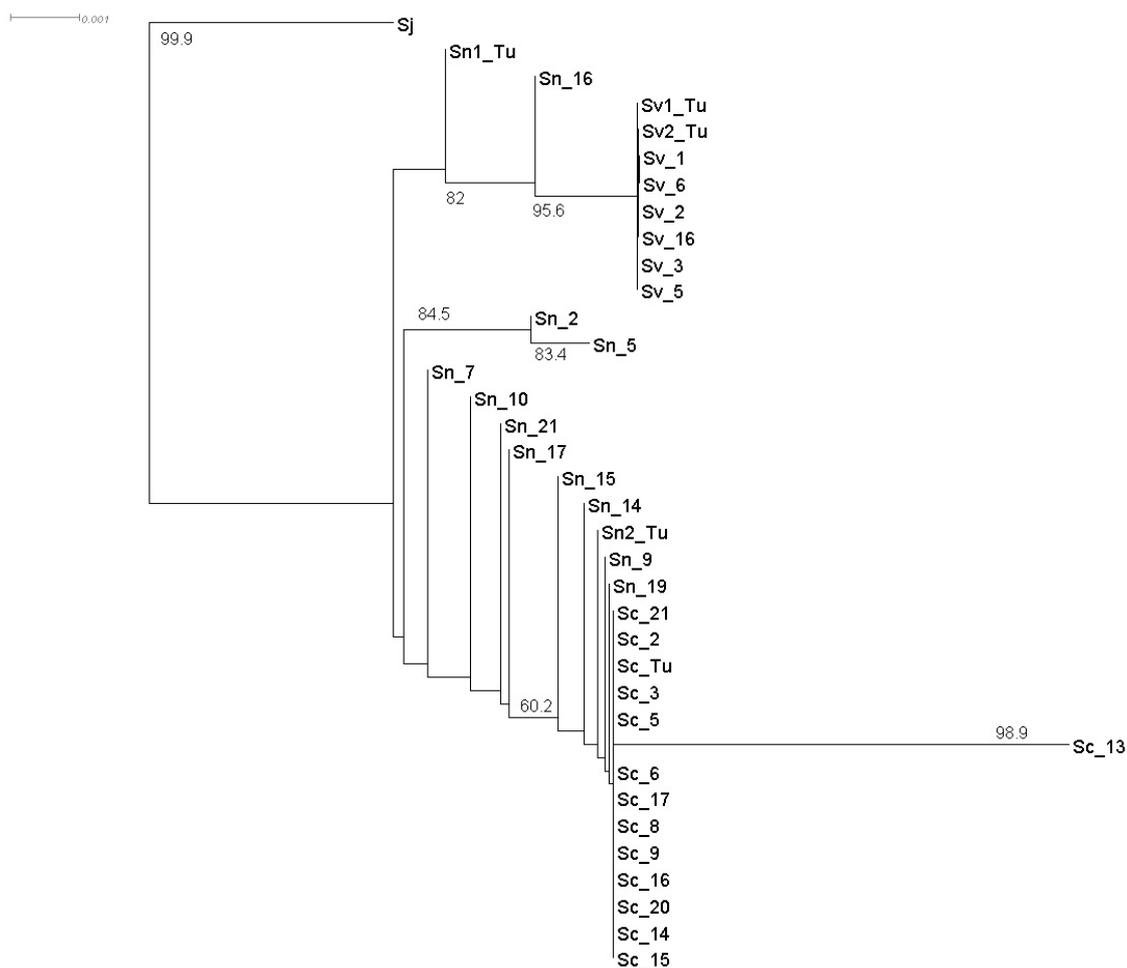
### Results

In 2021, 21 clusters of ramets with morphology intermediate between *S. canadensis* and *S. virgaurea* have been found. The number of ramets per cluster varied from 1 to 24, with a mean value of  $8.8 \pm 6.7$  (standard deviation); median and quar-

tiles are 7 (4–13). Henceforth we treated these ramet clusters as separate individuals.

Individuals with intermediate morphology were located either far from other *Solidago* individuals (by several metres) or close to *S. canadensis* clusters (at a distance of less than 1 m). Only in one case, both *S. virgaurea* and *S. canadensis* were located at close proximity.

Analysis of ITS 1–2 showed that all *S. virgaurea* individuals belong to the same group, while all *S. canadensis* individuals belong to the other group (Fig. 1). Individuals of *S. × niedereideri*, with heterozygosity at many (but not all) sites, segregating between parental species (e.g. see Fig. S2), are divided into two groups. One group is close to *S. virgaurea*; the second one is sister to the clade containing *S. canadensis*. At the same time, most of the hybrid individuals are close to *S. canadensis*. It is interesting that the individual with intermediate morphology, which is closest to *S. canadensis* according to ITS 1–2, has chloroplast DNA of *S. virgaurea* haplotype. This excludes its identification as *S. canadensis*.



**Fig. 1.** Phylogenetic tree of *Solidago* specimens from «Aleksin Bor» Natural Monument (Tula Region, European Russia) based on comparison of sequences of nuclear ribosomal internal transcribed spacers ITS 1–2, constructed with Neighbour Joining algorithm. Numbers at nodes are bootstrap values (%). Indices denote specimens' codes (see Table 1).

Analysis of the chloroplast marker *rpl32-trL* showed that 12 (60%, 95% confidence interval 36–81%) plants had *S. canadensis* as a mother plant. Individuals with intermediate morphology with different chloroplast DNA origin did not differ in the number of ramets (median; min – max): 4; 2.5–13.5 for *S. virgaurea* vs. 7; 4.5–13.0 for *S. canadensis* ( $p = 0.52$ , according to the Mann-Whitney test). Five individuals with chloroplast DNA of *S. virgaurea* were situated near the dense groups of *S. canadensis*.

The distance between *S. × niedereideri* individuals in the population was (mean  $\pm$  SD)  $5.3 \pm 3.7$  m with min–max at 0.5–161.5 m. In this case, three groups of closely located individuals (separated by less than 1 m from each other) can be distinguished (3, 4, and 5 individuals in each group). In none of these groups, the plants were genetically identical, according to the ISSR analysis. Moreover, in some cases, closely located individuals turned out to be genetically distant from each other.

Ordination of the ISSR analysis results (Fig. 2) showed that all studied individuals of the parental species (except for one *S. virgaurea* specimen) fall into clearly defined clusters, while *S. × niedereideri* specimens overlap with both of them, tending to be close to *S. canadensis*. The lack of allele segregating between parental species did not allow performing adequate hybrid analysis using NewHybrids software.

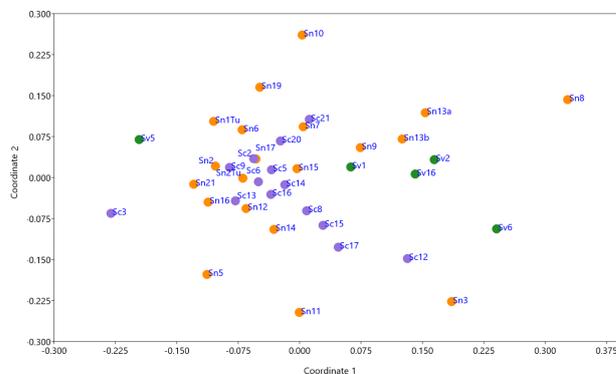
## Discussion

All the studied specimens with intermediate morphology can indeed be attributed to the nothospecies *S. × niedereideri*, based on their position on the ITS 1–2 tree (Fig. 1). These data, together with ordination of ISSR data (Fig. 2), suggest that many specimens with intermediate morphology are not  $F_1$  hybrids, but are backcrosses predominantly with *S. canadensis* or  $F_2$  hybrids, all of which should be assigned to nothospecies *S. × niedereideri* according to the botanical nomenclature (Article 4.1; Turland et al., 2018). Altogether, these results suggest introgression in this three-species system. Possibly, individual Sv5, phenotypically identifiable as *S. virgaurea*, distinct from other conspecifics according to ISSR (Fig. 2), but not according to ITS (Fig. 1), also has an admixture of genes from *S. canadensis* due to the introgression. So, here we have a «hybrid swarm», previously not reported for these three species. In contrast to our results, analysis of the relative DNA content, carried out in mixed populations in Eastern Europe, showed that all studied *S. × niedereideri* individuals are likely  $F_1$  hybrids, and only some individuals

phenotypically identifiable as *S. canadensis* could be backcrosses, but the authors themselves pointed to the weak validity of this conclusion (Skokanová et al., 2022). In addition, this situation differs from that, for example, with hybrids of *Arctium* spp. (Asteraceae), where all nothospecies individuals turned out to be  $F_1$  hybrids, which, apparently, do not reproduce sexually (see Fig. 2 in the present paper, and Fig. 2 in Replinger et al., 2007).

The plastid markers showed that initial hybridisation events leading to the studied population of *S. × niedereideri* took place in both directions. The bidirectional hybridisation between *S. canadensis* and *S. virgaurea* was stated in the first research, confirmed the hybrid nature of *S. × niedereideri* (Pliszko & Zalewska-Gałosz, 2016), as in the first description of the studied population (Lysenkov & Galkina, 2022). Descendants of hybridisation events of both directions are in nearly equal proportions (though small sample size brought about low power). Hence, we did not see any evidence that one of the directions is more probable, or it leads to fitter individuals.

In the studied population, *S. × niedereideri* tends to grow closer to *S. canadensis* rather than to *S. virgaurea*. In the original description of the hybrid Khek (1905) pointed out that it grows «next to *S. canadensis* and not far from *S. virga aurea*». Since five individuals with chloroplast DNA of *S. virgaurea* were located near *S. canadensis*, their emergence cannot be explained by the seed abscission resulted from pollination of *S. canadensis*, which is unsurprising, given that *Solidago* fruits are wind-dispersing. However, in the studied plant community, the abundance of *S. virgaurea* is rather low. Therefore, its preferential proximity to *S. canadensis* can be just consequences of its higher abundance rather than any special affinity.



**Fig. 2.** Non-metric multidimensional scaling of studied *Solidago* spp. individuals based on ISSR results with Jaccard distances. Designations: green dots – *Solidago virgaurea*, purple dots – *S. canadensis*, orange dots – *S. × niedereideri*. Indices denote specimens' codes (see Table 1).

Even closely located ramet clusters are genetically different. Hence, we can reject the clonal propagation. This is consistent with the results of a study conducted in Poland, where no long rhizomes were found in *S. × niedereideri* (Pliszko & Kostrakiewicz-Gierałt, 2019). It was also hypothesised that *S. × niedereideri* can reproduce vegetatively through physical separation of ramets from a single clone due to *Sus scrofa* Linnaeus, 1758 rooting or plowing (Pliszko & Kostrakiewicz-Gierałt, 2019), but none of these possible processes took place in the studied meadow. So, the high amount of *S. × niedereideri* is explained by sexual reproduction.

Thus, the studied *S. × niedereideri* individuals can apparently be called a population that at least partially self-reproduces. Besides genetic data, this conclusion is supported by the fact that *S. × niedereideri* specimens are distributed in a small part of the field within the *S. canadensis* population, rather than evenly over the entire meadow. The age of this population is unknown, but it longs at least four year (2019–2022). Therefore, the conservative assessment of its invasion status according to Pyšek et al. (2004) is «casual alien plant». But we believe, that this population is naturalising now, since new individuals establish through sexual reproduction. However, *S. × niedereideri* does not seem to be invasive here, since we do not have evidence of offspring at considerable distances.

In the meadow, the soil texture and pH is within the range of those reported for *S. × niedereideri*, which is not surprising, given this range is rather wide, from sand to loam and from strongly acidic to slightly alkaline, respectively (Pliszko et al., 2023). In the study area, climatic conditions are also suitable for *S. × niedereideri*. So, the average annual temperature is 25°C, which is higher than 18°C, and the temperature of the coldest month is lower than 0°C (Jaźwa et al., 2018).

The parental *Solidago* species are obligate outcrossers (Werner et al., 1980; Kudo, 2022). Hence, self-pollination is also unlikely in *S. × niedereideri*. However, the hybrid is actively visited by anthophilous insects, common with parental species. For instance, Syrphidae and *Bombus* species can be the most important agents of the pollen transfer among all three species in the studied population (Lysenkov & Galkina, 2021).

Some *S. × niedereideri* individuals identified in 2021 were not found in August 2022; the only individual, known since 2019 (Lysenkov & Galkina, 2022), almost did not form shoots. At the same

time, in August 2022, ten previously undetected individuals, morphologically confidently identified as *S. × niedereideri* were found. It can evidence for a high turnover in this population, with some individuals dying (or at least not flowering, since we did not search for vegetative shoots), and some new ones appearing every year.

During 2019–2022, one of the parental species, *S. virgaurea*, practically disappeared in the studied meadow. Unfortunately, we did not measure accurately the percent cover of the vegetation. But, in 2019–2022, we observed insect visitations to all flowering plants in this plant community (Lysenkov, 2022). Therefore, we can try to use the number of insects visited this species as a rough estimate. In 2019, *S. virgaurea* accounted for 15% of all registered insect visits to flowers in the studied plant community, whereas in 2020 and 2021 for less than 5%. In 2022, only sparse *S. virgaurea* individuals remained in the meadow, which possibly reduces the opportunities for *de novo* formation of *S. × niedereideri* in new hybridisation events. There are known cases when an invasive species or its hybrid with a native species displaced the latter (e.g. Abbott et al., 2003; Bleeker et al., 2007; Zalapa et al., 2009). Due to the rarity of the hybrid, this threat from *S. × niedereideri* to the *S. virgaurea* in European Russia still seems to be insignificant (Vinogradova & Galkina, 2020), whereas in more Western European countries, where *S. × niedereideri* disperses more actively, this threat is considered significant (Skokanová et al., 2022). Almost full disappearance of *S. virgaurea* in this plant community, coupled with an increasing population size of *S. × niedereideri* and a high introgression rate, can be just a spurious correlation. So, special studies of causes are needed, but we suppose that these observations form evidence, though weak, in favour of a higher threat to native parental species from the hybrid.

## Conclusions

New individuals of *S. × niedereideri* in the studied population are formed not only as a result of new hybridisation events between parental species but are also a result of sexual reproduction of already existing individuals, including through backcrossing with parental species. The resulting introgression apparently may lead to the displacement of the native species by the hybrid. Thus, *S. × niedereideri* behaves like a stabilised hybrid, treated as a species.

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## Supporting Information

The information on genetic analysis results (Electronic Supplement. Examples of genetic analysis results of the studied specimens of *Solidago* spp.) may be found in the [Supporting Information](#).

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## ГЕНЕТИЧЕСКАЯ СТРУКТУРА ПОПУЛЯЦИИ *SOLIDAGO* × *NIEDEREDERI* (ASTERACEAE) В ПАМЯТНИКЕ ПРИРОДЫ «АЛЕКСИН БОР» (ЕВРОПЕЙСКАЯ РОССИЯ)

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*Solidago ×niederederi* – возникший в Европе гибрид между аборигенным *S. virgaurea* и инвазионным *S. canadensis*. Его способность к натурализации остается дискуссионной. Одна из самых больших известных популяций этого нотовида (более 20 кластеров рамет, рассматриваемых как особи) расположена в памятнике природы «Алексин Бор» (г. Алексин, Тульская область, Россия) в пойме р. Оки. Генетическая структура этой популяции была изучена с помощью хлоропластных и ядерных маркеров. Анализ последовательности ядерного рибосомального внутреннего транскрибируемого спейсера ITS 1–2 показал, что все особи с промежуточной морфологией действительно являются гибридами. Данные по межгенному хлоропластному некодирующему спейсеру rpl32–trnL показали, что *S. canadensis* является материнским видом для 60% изученных особей. Показано, что даже близко расположенные особи не являются клонами, т.е. они возникли в результате полового, а не вегетативного размножения. Анализ маркеров ISSR показал, что изученные особи *S. ×niederederi* в этой популяции – это не только гибриды F<sub>1</sub>, но и их потомки (гибриды F<sub>2</sub> и/или бэккроссы, преимущественно с *S. canadensis*). Мы пришли к выводу, что *S. ×niederederi* успешно натурализуется в изучаемом сообществе и, возможно, вытесняется его аборигенный родительский вид *S. virgaurea* за счет интрогрессии.

**Ключевые слова:** ISSR, ITS 1–2, rpl32–trnL, биологические инвазии, гибридизация, нотовид, чужеродный вид