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Review article

Main directions of the study of plant invasions in Russia

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ABSTRACT

This article is focused on the analysis of major approaches to plant invasion research used by Russian researchers. They fall within three main groups: 1. Conventional approaches to floristic analysis based on the Russian scientific tradition of floristic research, 2. Approaches focused on the study of the fraction of invasive flora, making blacklists and regional Black books, 3. New comprehensive approaches based on a synthesis of methods used in botany, geo-information technology and population genetics. Multivariate statistical methods allow for the visualization of various data, including those on alien species group structures in various regions. They make it possible to identify boundaries of ecological niches occupied by plants in respect to climate-and-environmental or ecological variables. An assessment of current statistical interdependence between alien plant characteristics and scores of factors limiting their dissemination facilitates the making of predictive models of plant invasion. Examples of multivariate statistical methods used in invasion biology were analyzed, along with different approaches to the study of the variability of alien species. Alien and invasive fractions of the flora of the Trans-Siberian Railway were analyzed not by administrative units but by natural biomes. This approach allowed us to assess the correlation between the number of invasive species with different natural-climatic and floristic characteristics of biomes. The publication of "Black Books" of various administrative subjects of Russia according to a unified methodology allowed us to make an inventory of invasive species over the vast territory of the country. The experience gained by Russian researchers may be further used for developing universal approaches to plant invasion research.

KEY WORDS: alien plant species, invasion, invasion biology, Russia

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1. Introduction

The influence of alien organisms on other flora and fauna, as well as on people's lives, is developing into a global issue. It takes a global effort to solve challenges posed by their dispersal. Therefore, invasion research is becoming a priority in the scientific and political agenda (HULME ET AL., 2009, RUSSEL, 2012, GENOVESI ET AL., 2015, IPBES, 2019). It is crucial to work out unified solutions to common problems, as well as to exchange information on major approaches to plant invasion research used by scholars in various countries. This article focuses on providing a review of some approaches to the study of alien plant species in Russia.

2. Study area

Russia covers over 17 million square kilometers. It contains all the natural zones of the temperate

Holarctic region. Its business and economic infrastructure is highly heterogenous. The European part of Russia is largely represented by densely populated areas and highly developed industry. This is where purposeful research of alien plants and biological invasions was initiated (VINOGRADOVA ET AL., 2010, 2011). A lot of factual evidence has been accumulated and systematized. Due to this, the European part of Russia has become the key model area for developing approaches to assessing the invasion status, determining naturalization mechanisms and multi-year dynamics of the alien flora fraction (NOTOV A. & NOTOV V., 2009, VINOGRADOVA ET AL., 2021b). More recently, the research focus has been placed on plant invasion in Siberia and the Far East. Academic articles have been published which significantly generalize the research findings (EBEL ET AL., 2016, VINOGRADOVA ET AL., 2020a). The activities of Russian scholars have made it possible to accumulate multi-year experiences in using various approaches to plant invasion study. The importance of their further development is also explained by the need to consolidate the legal framework and intensify measures to reduce the invasion impact.

3. Materials and methods

This article summarizes the experience gained by the authors over many years of developing regional Black books, assessing the invasive status of species, compiling an inventory of the invasive fraction of the railway flora, analyzing the dynamics of the alien and invasive flora fractions and using multivariate statistical methods in invasion biology (NOTOV ET AL., 2009, 2011, VINOGRADOVA ET AL., 2010, 2011, TOKHTAR ET AL., 2020a,b; etc.).

We have analyzed major academic sources devoted to plant invasion in Russia, with special attention to articles which are of methodological importance. A more detailed study has been given to methods of assessing the invasion status and invasibility of plant communities, approaches to studying transformers and polemochores, as well as methods for studying alien species variability and cases where multivariate statistical methods were used.

4. Results and discussion

The main approaches to the study of alien plants may be conveniently classified into three groups formed at different stages of the development of the invasion biology in Russia.

1. Conventional approaches to floristic analysis based on the methods used by the Russian school of comparative floristics (YURTSEV, 1987, YURTSEV & KAMELIN, 1991). These methods allow for the determination of taxonomic and bio-morphological specifics of the alien flora fraction, analysis of its components depending on the time of invasion, degree of naturalization etc. (MAKAROV & IGNATOV, 1983, CHICHEV, 1985, TUGANAEV & PUZYREV, 1988, POPOV, 1995).

2. Approaches focused on the study of the invasive flora fraction. Their methodological basis was developed alongside compiling blacklists and regional Black books (NOTOV ET AL., 2009, 2011, VINOGRADOVA ET AL., 2010, 2011). Some of the articles reviewed are devoted to the analysis of the alien flora fraction formation dynamics (MARKELOVA, 2004, NOTOV, 2009, MAYOROV ET AL., 2020, TOKHTAR & KURSKOY, 2020). Significant attention is also paid to monitoring (PANASENKO, 2013, MININZON ET AL., 2020).

3. New approaches synthesizing methods of botany, mathematical statistics, geo-information technologies and population genetics. Examples include the use of multivariate statistics, satellite data and hyperspectral indices of plants (TOKHTAR ET AL., 2011, TOKHTAR, 2018, EGOSHIN, 2020). A combination of conventional methods with those used in other branches of science allows for a deeper understanding of alien plant emergence and naturalization patterns (TOKHTAR & VINOGRADOVA, 2009, MOROZOVA, 2018, VESELKIN ET AL., 2020). The study of factors determining alien plant dissemination has been recently intensified. Forecasting the impact of global climate change on these processes and revealing bio-indicational characteristics of ecological and climatic areas of species are also of immediate importance (SELEDETS & PROBATOVA, 2007).

4.1. Approaches to assessing the invasion status of alien species

"The Black book of flora of Central Russia" (VINOGRADOVA ET AL., 2010) determines the main criteria enabling certain alien species to be categorized as invasive ones. These criteria include the wide-spread occurrence in the respective region, a high degree of naturalization and a trend toward intensive dispersal. This approach, though slightly modified, is also used by other scholars (KRYLOV & RESHETNIKOVA, 2009, NOTOV ET AL., 2011, VINOGRADOVA ET AL., 2011, RZHEVUSKAYA, 2012, MININZON & TROSTINA, 2013, KHORUN, 2013; etc.). A number of authors specify a group of prospective invasive plants which may potentially be included in the Black book (VINOGRADOVA ET AL., 2011, RESHETNIKOVA ET AL., 2019) and assess the degree of naturalization according to a 10-point scale (N0–N9) (KRYLOV &

Reshetnikova, 2009). In some cases, the Black books include alien species which are not quite stable in regional ecosystems, for instance, annual and biennial plants invading ecosystems on a regular basis and which are incapable of self-reproduction, as well as seedless perennials with intensive vegetative propagation (Mininzon & Trostina, 2013).

"The Black book of flora of the Tver region" (Vinogradova et al., 2011) suggests methods for assessing invasive species activity in administrative and business-and-economic districts of the region. Grid mapping of the region's territory has been provided, with 4×4 km cell size. The species activity was assessed according to a 3-point scale. Thus, *I* denotes singular finds in individual quadrants, or non-routine finds in less than 25% of quadrants, with the species abundance presumably low; *II* means regular finds in many quadrants (at least 50% of all quadrants), with various abundance levels and occurrence frequency; *III* denotes common species in the majority of quadrants (at least 75%), with a high abundance level. The aggregate activity of invasive flora fraction in each administrative district of the Tver region was calculated by summing the activity scores of all invasive species (Notov et al., 2011, Vinogradova et al., 2011).

In order to assess the phytocoenotic activity (the ability of an invasive species to invade various plant communities) and naturalization of alien species, 5–8 km long floristic routes were laid in Bryansk region. The following data were recorded along these routes: plant occurrence frequency, habitat and plant communities comprising species under study (Panasenko et al., 2011, Panasenko, 2014). A combined five-point scale was also suggested, with a view to reflecting stability and cover abundance indices (Bulokhov et al., 2012).

Thus, the degree of naturalization of an alien species is determined by its behaviour (activity) and habitat type (Starodubtseva et al., 2014). The blacklists should specify the habitat where one or another species has been found in the respective region. Species activity may only be described based on a quantitative assessment of its occurrence frequency and participation in plant communities (Notov et al., 2011).

4.2. Approaches to the detection and study of transformers

D.M. Richardson describes transformers as "invasive plants which change the character, condition, form and nature of ecosystems over substantial areas". However, the book "Fifty years of invasion ecology: the legacy of Charles Elton" does not contain the second part of the definition concerning the area occupied by invasive species (Richardson et al., 2011).

Twenty types of transformers have been specified for Central Russia (Vinogradova et al., 2011). However, what are identified as transformers in some regions may not be considered as invasive species or have another invasion status in other ones (Panasenko, 2013). Differences in assessing the species status depend on both objective and subjective reasons, the former including differences in the time of invasion, dissemination rate and the region's natural environment, while the latter are represented by various criteria for categorizing species as alien ones (Vasyukov, 2012, Panasenko, 2013).

Panasenko (Panasenko, 2013) has developed a scale for the Bryansk region enabling plant species to be referred to the transformer category (Table 1). It may well be used for other regions within the forest zone.

Lists of invasive species have been made for three large regions of Russia: 1) the centre of the country's European part – 100 species, including 48 potentially invasive ones (Vinogradova et al., 2010); 2) Siberia (12 subjects of the Siberian federal district) – 58 invasive species (Ebel et al., 2016); 3) The Far Eastern Federal district –117 invasive species (Vinogradova et al., 2020a).

The first general analysis of Russia's invasive species was undertaken by Vinogradova et al. (2018) with standard criteria used for 45 regions (83% of the country). As a result, 354 alien species were found. The most wide-spread ones (in what concerns the number of regions) include *Acer negundo* L., *Echinocystis lobata* (Michx.) Torr. & A. Gray (recorded in 34 regions), *Erigeron canadensis* L. and *Elodea canadensis* Michx. (recorded in 30 regions) (Vinogradova et al., 2018).

The number of invasive species was determined for three towns of Udmurtia: Votkinsk (30 species), Mozhga (26 species) amd Kombarka (29 species) (Baranova & Bralgina, 2016). This is comparable with that in the city of Izhevsk (37 species) and the Republic of Udmurtia (48 species) (Baranova et al., 2014a, b).

4.3. Use of multivariate statistical methods in the study of alien species

A combination of numerous factors prevents efficient forecasting of the impact of alien species on natural ecosystems. Though some forecasts of alien species dissemination are already available, there is an evident lack of research work on this issue in Russia. As a rule, such studies focus mostly on individual taxa (genera, species) with similar eco-biological characteristics (VINOGRADOVA ET AL., 2010, TOKHTAR ET AL., 2011). Conventional methods enable scholars to determine the dynamics of species dissemination in time and space. However, multivariate statistical methods are suitable for studying processes of conjugated migration of plant groups into various types of macroecotopes (TOKHTAR & VINOGRADOVA, 2009, TOKHTAR, 2018, TOKHTAR ET AL., 2020b). These methods include factor and discriminant analysis, Canonical Correspondence Analysis, cluster analysis and correspondence analysis. Apart from visualizing a large body of data on correlational relationships of variables, their use allows for revealing latent factors which influence the formation of alien species groups in various conditions (TOKHTAR, 2018).

Table 1. Scale for including invasive species into the transformer category (acc. to: Panasenko, 2013, revised)

No.	Criteria and characteristics	Score
	I. Specifics of native plant communities	
1	Invades zonal climax communities: spruce forests, mixed spruce and deciduous forests, deciduous forests	5
2	Invades main zonal-and-azonal communities: pine, birch, aspen and alder forests; swamps	4
3	Invades other zonal-and-azonal communities: riverside willow stands; meadows; water and coastal communities	3
4	Invades semi-natural habitats (parks, sown meadows, fallow lands, tree belts, ponds and dam lakes)	1
5	Unintentional introduction and dissemination	3
	II. Introduction consequences	
6	Disrupts succession	5
7	Displaces and (or) prevents regeneration of native plants	3
8	Changes the indicators of native plant communities (for instance, lighting intensity)	2
9	Changes the ecosystem configuration	1
	III. Specifics of alien plants invading natural plant communities	
10	The species has become an edificator, a violent type; it forms monodominant communities in natural ecotopes	5
11	The species has become an edificator, a violent type; it forms monodominant communities in semi-natural ecotopes	3
12	The species has become an assectator, an explerent type; the species role and abundance depend on the plant community disruption degree	1
	IV. Invasive species dissemination	
13	In areas exposed to minimal anthropogenic load (nature reserves, wildlife sanctuaries etc.)	3
14	In the vicinity of inhabited localities and main lines (highways, railways, power lines)	1
	V. Position of plant communities with a dominant invasive species	
15	In areas exposed to minimal anthropogenic load (nature reserves, wildlife sanctuaries etc.)	3
16	In the vicinity of inhabited localities and main lines (highways, railways, power lines)	1

The importance of morphological characteristics of plants as bioindicator markers in relation to different environment factors was determined by studying correlation characteristic matrices and factors. The selection of different correlative matrices of morphological traits for analysis in the *Conyza canadensis* populations made it possible to obtain the most accurate separation of populations of semi-natural, natural, technogenic habitats in factor space (TOKHTAR & MAZUR, 2011).

It has been established by Canonical Correspondence Analysis methods that the phylogenetically separate lines of small- and large-flowered *Oenothera* L. species prefer more humid and warm climatic conditions. Probably, that is why there is a numerical reduction of their occurrence and abundance in the direction from Western to Eastern Europe. Based on these results, we can conclude that a significant factor influencing the species composition of evening primrose on different territories of Europe, are conditions of humidity and temperature (TOKHTAR & GROSHENKO, 2017).

Multivariate statistical methods are suitable for studying the processes of conjugated migration of species and plant groups into various types of macroecotopes (TOKHTAR & VINOGRADOVA, 2009, TOKHTAR, 2018, TOKHTAR ET AL., 2020b).

Factor analysis has revealed that alien species are capable of occupying various habitats using a group strategy, depending on the degree of natural and anthropogenic impacts. This method also allows us to determine groups of invasive species formed in steppe, chalk, forest and anthropogenic habitats (Fig. 1). Invasive species have been found to colonize the region's natural and anthropogenic ecotopes selectively, depending on the ecological and coenotic conditions of the environment. As a result, various ecotopes may have a similar species pool (TOKHTAR, 2018, TOKHTAR ET AL., 2020b) (Fig. 1).

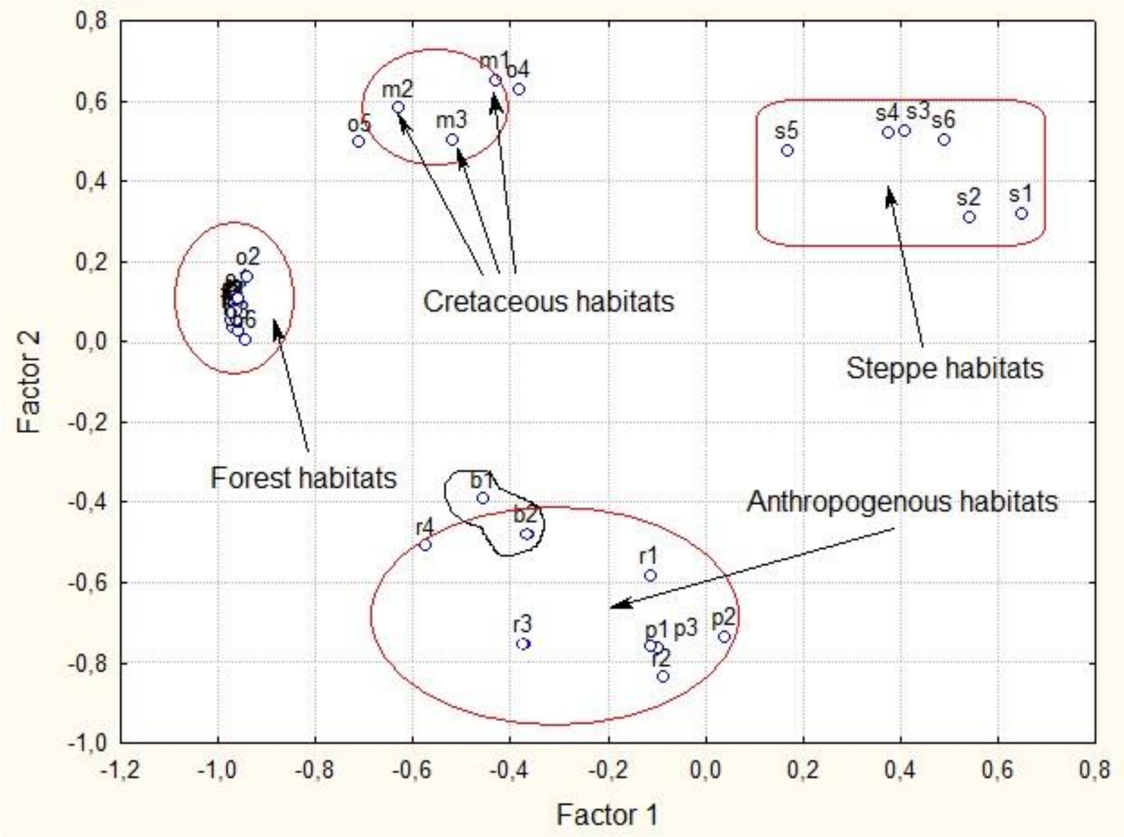

Fig. 1. Jaccard coefficient-based distribution diagram for groups of alien species colonizing various natural and anthropogenically transformed ecotopes in the two-factor space, symbols: b1–b2 – banks of water bodies and riverbanks; m1–m3 – chalk outcrops; f1–f8 – forest habitat areas; o1– o6 – gully systems; p1–p3 – parks; r1–r4 – railways; s1–s6 – steppe areas

Another issue of immediate importance is analyzing the variability of the correlational structure of the morphological characters of alien plants in various ecotopes (TOKHTAR & MAZUR, 2011). Depending on the research objectives, classification, historic and predictive models can be created.

The universality of the methods described gives them good prospects for further use. Various combinations of plant characteristics and environmental features may be studied. These methods make it possible to visualize a large body of heterogeneous data using state-of-the-art software packages (TOKHTAR & VINOGRADOVA, 2009), and thus, to reveal the factors which influence the formation of alien species groups along with various environmental gradients and their specifics.

4.4. Intraspecific variability of invasive plant species

In Russia, integrated methods based on classical and contemporary approaches are used for studying intraspecific variability and microevolution of plants. The pattern of the research stages is provided in "The Black book of flora of Central Russia" (VINOGRADOVA ET AL., 2010) and described below, with some significant alterations and addenda.

1. Studying the history of introduction and mapping primary and secondary ranges of species based on the academic articles and herbaria available. This enables us to determine the lag-phase and the period of evolutional differentiation in initial population which follows. For instance, the lag-phase lasted for 50 years for *Epilobium adenocaulon* Hausskn. and *Bidens frondosa*, 70 years for *Impatiens glandulifera* Royle, 120 years for *I.parviflora* DC., and 250 years for *Amaranthus albus* L.

2. Revealing the variability range of morphological characteristics in natural conditions by studying indigenous and invasive populations. The diagnostic characteristics require special attention.

3. Studying the biological peculiarities of seeds with various geographical origins by germinating them. In the laboratory, various temperature modes and stratification periods are used. On experimental plots, germination specifics are analyzed in the conditions of late fall, spring and summer sowings.

4. Growing plants from seeds of various geographical origins in homogenous edaphoclimatic conditions (creating introduced populations). Seeds are collected along the north-south transect of their secondary distribution range, from the

northernmost to southernmost boundaries of the species range in Russia. To determine the endogenous variability, seeds are collected separately from each individual plant. Intraspecific variability is assessed in the introduced populations grown from seeds collected in 4–6 micro-populations consisting of 10–15 plants each. Growing all samples in homogenous conditions makes it possible to assess genotypes instead of variations in phenotype. Moreover, this method allows for a more precise determination of the sample taxonomic rank. For instance, in cultivation on an experimental plot, *Bidens frondosa* var. *minor* Hook. (at least 5 cm tall) did not differ from the typiform in shoot height and achieved 80 cm. *Ribes aureum* Pursh and *R. odoratum* H.L. Wendl., which differ in the extensity of their pubescence are really the dominant and recessive form of *R.aureum*, respectively.

5. Studying the rate and duration of growth, phenorhythm and respective structural changes, as well as pollination types in introduced populations. For some species, it is necessary to analyze characteristics allowing us to refer to them as winter or spring biomorphs, as well as to study the photoperiodic response of samples.

6. A comparative study of the variability of anatomical features. A series of works was performed with a view to studying the stomatal apparatus in alien and closely related native species and determining the transpiration area. The relative transpiration area (relative transpiration index, Iot) was calculated as the ratio of the total average transpiration area to the total area of the leaf blade, according to the formula, where L is the average length of the stoma polar axis, D is the average equatorial diameter of a stoma, n - the number of stomata, ΣS - total area of all microscopic fields examined:

$$Iot = \frac{\sum n\pi LD}{\sum S} 100\%$$

The study of the stomatal apparatus in *Solidago* species revealed various strategies used by plants to expand the total transpiration area (Vinogradova, 2019). At the cellular level, an increase in stomata size (*S. sempervirens* L., *S. altissima* L., *S. juncea* Aiton) and number (*S. altissima*) takes place until amphistomatic leaves develop (*S. lepida* DC., *S. graminifolia* (L.) Salisb.). At the organismic level, there are either larger leaf blades (especially in rosellate leaves of *S. sempervirens, S. juncea, S. uliginosa* Nutt.), or more leaves per shoot (*S. lepida*) or more shoots (*S. serotinoides* A. Love & D. Love, *S. graminifolia* (L.) Salisb.).

When studying *Symphyotrichum* species, it was found that the most well-adapted invasive ones had the maximum relative transpiration area (12–14% in *S .novae-angliae* (L.) G.L. Nesom, *S. novi-belgii* (L.) G.L. Nesom and *S.×salignum* (Willd.) G.L. Nesom). In alien species not escaping cultivation, this index achieved less than 2% (*S. chilense* (Nees) G.L. Nesom, *S. cordifolium* (L.) G.L. Nesom and *S. tradescantii* (L.) G.L. Nesom) (Vinogradova et al., 2021a).

We found that the indigenous *Impatiens noli-tangere* L. had hypostomatic leaves with small stomata and a small transpiration area (815 μ^2). Invasive alien species *I. glandulifera* and *I. parviflora* had amphystomatic leaves, while their transpiration area was 1.5–2.0 times larger (Vinogradova, 2021).

Thus, we suggested a hypothesis stating that a high value of the transpiration area index testified to a better adaptability of alien plants. Along with other features, it may be used for forecasting the secondary range expansion dynamics and the possibility of a species developing into an invasive one.

7. Comparing the amplitude and type of variability in the primary and secondary distribution ranges. Considering the second distribution range in Europe, two *Solidago* species of the *Triplinervae* subsection may be expressly singled out (especially on experimental plots): *S. canadensis* L. and *S. gigantea* Ait. They differ in the complex of morphological characteristics. *S. canadensis* has pubescent shoots (A), short rhizomes (B), a spreading panicle (C), small heads (D) and leaves with serrated margins (E), whereas *S. gigantea* has glabrous shoots (except the panicle axis) (a), long rhizomes (b), contracted panicles (c), large heads (d) and denticulate or entire leaf margins (e). However, in North America, the polymorphism of taxa within the *Triplinervae* subsection is much higher. It represents a variety of microspecies which can coexist in the same habitat. During our field work in 2017–2018, we found seven varieties in the north of the USA: ABCDE, abCDe, aBcdE, ABcdE, aBcdE, ABCdE and abcde, whereas only one specimen had the ABCDE feature set typical of *S. canadensis* in Europe (Vinogradova, 2020). In North America, populations most frequently consist of plants with long rhizomes (AbCDE). We did not come across any plants with *S. gigantea* characteristics (abcde) in the natural communities. They only occur in cultivation in the vicinity of gas stations or stores. On the experimental plot in the Moscow region, North American samples of *S. canadensis* grown from rhizome fragments bloom en masse. Compared to European samples, they have longer rhizomes, smaller heads (3.1±0.1 vs.

4.4±0.1 mm) with many staminate flowers, and differ in height, being shorter (101.4±1.5 vs. 136.1±1.5 cm).

Thus, only one of the many *S. canadensis* morphotypes occurring in natural habitats has disseminated widely in the secondary distribution range in Europe and become invasive. It should be stressed that this morphotype occurs least frequently in its native habitat, in North America. It is a vivid example of the bottleneck effect described in the studies of other invasive taxa as well (in *Epilobium* and *Bidens* etc.). However, the competitive advantages of the genotype which provides an intensive expansion are not clear. Probably, a comprehensive comparative study of morphotypes on experimental plots will give us a clue.

8. Revealing the differences between the species under study in primary and secondary distribution ranges, using molecular genetic techniques (Galkina et al., 2021). Analysis of nucleotide sequences of nuclear (ITS 1–2) and chloroplast (trnL-trnF, rpl32-trnL) DNA has shown that *Bidens connata* Muhl. ex Willd. specimens from North America are not hybrids. Despite the fact that European blackjack is frequently referred to as the North American invasive *B. connata* species, it was described by C. Warnstorf as *B. decipiens* Warnst as early as 1895. This species disseminating in Eastern Europe is of hybrid origin (=*B. frondosa* × *B. cernua* L.).

9. Comparing the competitive ability of closely related indigenous and alien species. A higher competitive ability has been experimentally proven in the invasive *Bidens frondosa* as compared to the indigenous *B. tripartita* L. The *B. frondosa* species develops faster and has a higher seed productivity both on fertile and infertile soils, with excessive and insufficient moistening (Vinogradova, 2003, 2010).

A correlation of the competitive abilities of alien and indigenous species may differ in various communities. As a rule, alien plants have a higher seed productivity, faster germination and development rate, a substantial ecological plasticity, efficient use of resources and the absence of dangerous phytophages and parasites in the new habitat (Mirkin & Naumova, 2002, Vinogradova et al., 2010). Still, the advantages of alien species are rarely unambiguous. The result of their competition with indigenous plants largely depends on the circumstances. Works by V.V. Akatov and his colleagues prove that the competitive potential of alien species differs in various communities (Akatov & Akatova, 2012). In the Western Caucasus, xenophytes are more competitive in the plant communities on rock outcrops, fields and point bars than indigenous species. Their advantages become subtle on steppified meadows and glades. On low-mountain banks, native species display a higher competitive ability than xenophytes. Ergasiophytes are most active on rock outcrops, frequently becoming dominant. However, in seedings of annual plants they are evidently inferior to indigenous explerents.

The study of the variability of alien species will result in revealing major patterns of their microevolution which accompanies plant invasion, as well as factors determining the microevolution processes. Of equal interest is the analysis of characteristics which facilitate intensive naturalization. These will make it possible to forecast the secondary range expansion dynamics. Such comprehensive and detailed research will not be able to encompass all alien species at once. Priority should be given to the study of target species (Alien species..., 2004–2021), as their introduction evidently harms ecosystems and the economy.

4.5. Detection and study of polemochore plants

The term *polemochores* (denoting alien plants spreading beyond their natural habitat as a result of hostilities) was suggested by Finnish scholars who recorded the emergence of alien plants in the areas of Finland where the Soviet Army units were deployed. Later, alien plant seeds penetrated into Russia, as Nazi soldiers brought fodder from Central Europe to the occupied territories. The latter was needed to feed horses used in the cavalry and horse-drawn carts (Reshetnikova, 2016, Reshetnikova et al., 2021).

Summarizing the data concerning the first polemochore finds in Central Russia, scholars suggested a specific algorithm for their search. They also developed the criteria enabling species to be referred to as polemochores (Shcherbakov & Reshetnikova, 2017). The major criteria include: 1) occurrence only within the occupied areas and detection only in the postwar period; 2) location at a significant distance from the main distribution range and absence of the species in some habitats under study, though conditions may be suitable; 3) frequent association of the finds with natural, or low-disturbed, habitats where alien species do not usually invade; 4) detection of several species which meet the above criteria in the same habitat at one time.

The efficiency of this approach was confirmed by focused research conducted in some regions of Central Russia between 2018–2020 (Reshetnikova

ET AL., 2021). Biologists found over 45 species of polemochores. The most intensive naturalization of polemochores was recorded in the Tver region. Within the placement of the Germans troops between the towns of Rzhev and Vyazma during WWII (a key strategic object of the war), some polemochores became dominant in meadow and ruderal communities. Special research enabled their invasion status to be assessed. The approach described is used in further studies of polemochores. More detailed research in the north-west of European Russia is of immediate importance.

4.6. Invasion pathway analysis

The significance of botanical gardens as plant invasion pathways may be exemplified by the Main Botanical Garden of the Russian Academy of Sciences (VINOGRADOVA ET AL., 2020b).

The role of railways in plant invasion has been examined based on the data collected from the Trans-Siberian Railway (TSR). Its capacity allows for the transportation of over 50% of Russia's commercial and transit cargoes. Two approaches to studying the TSR role as a plant invasion pathway are used: A) analysis of the invasive flora fraction in the Far Eastern Federal district based on the time of invasion, by inspecting herbaria; B) making an inventory of contemporary railway flora in various natural biomes. Characteristics of the latter are provided in "The biomes of Russia" map (OGUREEVA, 2018).

A. A large team of Far Eastern botanists has prepared "The Black book of flora of the Far Eastern Federal district" for publication (VINOGRADOVA ET AL., 2020a). It contains data on 117 invasive alien species representing 99 genera and 32 families. They fall within four groups of species in compliance with the dates when they were first found.

1. Species found in the 19th century before TSR was constructed (47 species). They are mainly represented by segetal plants typical of European Russia and introduced into the Far Eastern Federal district unintentionally, as weeds. Today they are widespread (in 9–10 out of 11 administrative subjects, on average). Despite having a low competitive ability, they have filled all possible ecological niches throughout many decades and are not perceived as alien ones. We believe it makes no sense to take any special measures to control their populations, except using traditional methods to combat weed plants.

2. Those collected before WWII, between 1900–1940 (30 species). The number of invasive diaspores increased significantly during TSR construction and the majority of finds were primarily associated with this railway.

3. Those found before the boom in alien species research, between 1941–1980. After WWII, the anthropogenic disruption in the area increased rapidly, resulting in the emergence of 29 new alien species. The majority of such plants were first found along the railway. Today they are locally distributed in the Far Eastern Federal district (in 4–5 out of 11 administrative subjects, on average), though some highly aggressive invasive species may be singled out, in particular, *Ambrosia artemisiifolia* L..

4. Species recorded in recent decades, between 1980–2020, with the beginning of an intensive and purposeful search for alien plants and research into plant invasion. This group includes 11 alien species locally distributed in the Far Eastern Federal district (in 3–4 out of 11 administrative subjects, on average). They are very aggressive and require the implementation of special control measures.

Thus, an unintentional introduction of alien weed plant diaspores became the invasion pathway of the first stage of the invasive flora fraction formation in the Far Eastern Federal district. At the second stage, a new invasion pathway emerged, and it was associated with the large volume of cargoes and workforce brought into the area for TSR construction. At the third stage, TSR became the main invasion pathway. Today, ornamental species which have escaped cultivation become a strong feature of plant invasion.

B. In 2020, we began to make the inventory of contemporary railway flora in areas crossing three natural biomes of the East European Plain. We have already studied the northern branch (Kirov – Kostroma – Yaroslavl – Moscow) and the central branch (Kirov – Nizhny Novgorod – Vladimir – Moscow). Quadrants were selected in three different ecotopes: alongside the railway tracks, on the railway slopes and at the railway right of way.

As many as 265 plant species were found along the European parts of TSR, with invasive ones representing 11% of this number. Only 6 species were recorded in all three biomes: *Acer negundo*, *Amaranthus albus*, *A. retroflexus* L., *Erigeron canadensis*, *Epilobium adenocaulon* and *Lepidium densiflorum* Schrad. All of them are invasive alien species, while four are included in the TOP-100 of the most dangerous invasive species of Russia (DGEBUADZE ET AL., 2018).

First, the railway became a recipient of alien plants. Species which have escaped cultivation in residential areas and garden plots and considered as weed plants invade the railway flora (*Heracleum sosnowskyi* Manden., *Erigeron annuus* (L.) Pers.).

Plants used in landscape design may have been another source of invasion (*Oenothera glazioviana* Micheli and *Solidago* species). Subsequently, the railway became the main pathway of alien species distribution. Intensive dissemination of Asian *Artemisia sieversiana* Willd. along the railways in European Russia confirmed the crucial role of TSR in unintentional transfer of plant species from Asia to Europe (TOKHTAR ET AL., 2020a).

At the same time, similar research was conducted along the Siberian section of TSR connecting Tayshet and Ulan-Ude. Only 4 of the 266 plants recorded there represent the TOP-100 of the most dangerous invasive species of Russia (DGEBUADZE ET AL., 2018): *Acer negundo*, *Amaranthus retroflexus*, *Erigeron canadensis* and *Hordeum jubatum* L.. However, the invasion process is intensifying. In the last 10–15 years, *Acer negundo* has been actively disseminating in Ulan Ude, while *Hordeum jubatum*, *Tussilago farfara* L., *Acer negundo* and *Pimpinella saxifraga* L. have spread in Tayshet. Only a third of the railway-associated species occur both in near-Baikal Siberia and European Russia. Alien plants represent almost half of them (41%). So far, the invasion activity of alien species in Siberia has been lower than that in Europe.

4.7. Studying the invasibility of plant communities

Alien plant invasion has already become a global issue. Moreover, there has been sufficient evidence of its acceleration in recent decades (BORISOVA, 2011). It is connected with the intensive destruction of natural landscapes, the continuing introduction of new alien plants, as well as with the end of the lag phase of previously introduced species, a rapid expansion of their secondary distribution ranges and adaptation to new habitats (MIRKIN & NAUMOVA, 2002, VINOGRADOVA ET AL., 2010, AKATOV & AKATOVA, 2012). Lately, scholars have also focused on global warming as a factor contributing to alien plant dissemination (MIRKIN & NAUMOVA, 2002, VINOGRADOVA ET AL., 2010). In view of this, research into the mechanisms of plant community sustainability or insustainability against invasion (invasibility) has been intensified. These are mainly aimed at determining invasibility indicators (AKATOV & AKATOVA, 2012).

The invasibilty of plant communities most frequently depends on the correlation between species richness and the resources available (ELTON, 1958, MIRKIN & NAUMOVA, 2002).

The hypothesis of fluctuating resources was suggested, stating that "a plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources" (DAVIS ET AL., 2000). It may be confirmed with a substantial abundance of alien species in habitats which are frequently disrupted – segetal and ruderal communities, outcrops, paths and road sides (MIRKIN & NAUMOVA, 2002, AKATOV & AKATOVA, 2012). However, this factor is not unique. Coenoses which are less exposed to disruption are also invasible (STARODUBTSEVA, 2011).

A number of scholars believe that pioneer species are more likely to invade new areas, as they have more transcontinental transfer opportunities. Therefore, in recipient areas they mainly occur within coenoses which are disrupted on a regular basis (AKATOV ET AL., 2011, AKATOV & AKATOVA, 2012). Sometimes invasion is not accompanied by the disappearance of indigenous species. It enables us to suggest that the species richness of the initial plant community was not very high, providing available resources for new species development (AKATOV ET AL., 2009). The species pool is increasingly described as an invasibility factor (AKATOV ET AL., 2009, AKATOV & AKATOVA, 2010). According to AKATOV ET AL. (2005, 2010), the species pool depends on the local environment and regional specifics (species formation rate, the history of plant communities and their degree of isolation). Still, the example of *Bidens frondosa* shows that phytocoenosis structure matters much more than species richness. Alien species do not invade coenoses with 1–3 dominant and several codominant plants (VINOGRADOVA, 2010).

The degree of alien invasion depends on many factors. At the same time, only a few of them are predictable and subject to quantitative assessment (AKATOV & AKATOVA, 2012).

5. Conclusions

The majority of the approaches reviewed are aimed at solving general issues of invasion biology. Their development and the promotion of activities to prevent the consequences of bioinvasion are of importance in all countries and regions. The Russian experience in developing Black books and maintaining records may facilitate the emergence and consolidation of an international tradition to compile unifying works on invasive species which would be more detailed than Black books. This will make it possible to prepare a unified legal framework for their use. Of special significance is the exchange of experience in the study of the most dangerous transformers. The emerging ecological-and-phytocoenotic approach to transformer population analysis requires further development. The study of plant community invasibility also deserves scientific attention. More detailed research into invasive plants is of equal importance. It may be based on comprehensive approaches using contemporary information sources and mathematical analysis methods.

We hope the discussion of our findings will enable scholars worldwide to collaborate for joint research and the implementation of international projects.

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