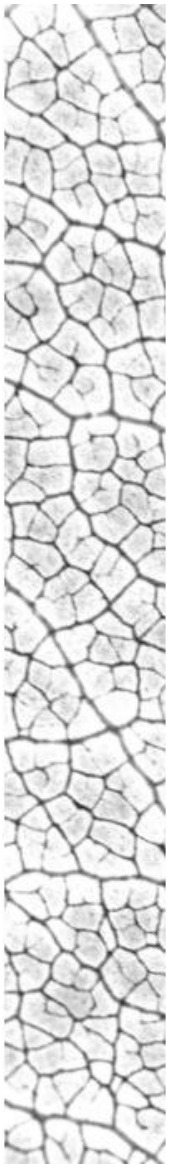

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Can invasive plant species "differentiate" colonized ecotopes?

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Abstract
The article presents the analysis and results of the application of traditional research methods for the distribution of model alien plant species in various habitats, as well as new visualization approaches to data used for these purposes.
The determination of the characteristics of invasion of alien species by traditional research methods is promising in studying the colonization of ecotopes by individual model plant taxa. To identify patterns of conjugate migration of entire groups of plants into various types of macroecotopes, the methods of multivariate statistics as effective analysis tools are proposed and used.
It is established that alien species are able to colonize various habitats, exhibiting a group strategy, depending on the intensity of the action of natural and anthropogenic factors. An analysis of the main groups of invasive species formed in: 1) natural habitats (ravine-gully ecotopes, Cretaceous and steppe territories; 2) anthropogenically transformed ecotopes (railways, parks); alien plants of agrophytocenoses (corn, sunflower, wheat and soy fields) indicates associated migrations of alien species separate groups to specific environmental conditions.
The conducted study established that invasive plant species colonize the natural and anthropogenic ecotopes of the region selectively depending on the ecological and coenotic environmental conditions, which leads to the selection of plants with certain properties and, as a result, to the similarity of the species compositions of different types of ecotopes.

Keywords: invasions, alien species, methods of multivariate statistics, data visualization

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INTRODUCTION

The effect of alien organisms on the flora, fauna and, in general, on society is gaining global significance, since the problems associated with their distribution in the world currently can be addressed only at the international level (Tokhtar and Groshenko, 2016).

Anthropogenous disturbance of habitats accelerates the rate of extinction of species by tens and hundreds of times, which is thousand times higher than the natural rate of their extinction. Recently, the problem of alien and invasive species has come to the forefront of environmental protection. According to some data (Cabral et al., 2010), the loss of biodiversity caused by invasive species is slightly less than the loss due to habitat disturbance.

The biological invasion of alien plant species is global in nature and leads to a reduction in natural biodiversity. In addition, the relevance of the study of alien species is determined by the fact that they are either economically valuable or harmful invasive species, crowding out indigenous native species. Therefore, at present, one of the most important theoretical tasks in the study of alien plant species is to determine the main regularities of their distribution based on the set of existing natural and anthropogenic factors at different types of ecotopes. Using methods of visualization of significant amounts of heterogeneous data can greatly facilitate the solution to this problem.

The successful introduction of alien species into plant communities in the secondary range depends not only on the biological characteristics of the taxon itself, but also on the characteristics of the habitats. Thus, a comparison of the invasive degree of habitat carried out at more than 50 thousand registration sites in the Mediterranean, subcontinental, and oceanic regions of Europe showed that only 8 of 545 alien species were found in all three regions. However, the set of habitats most susceptible to invasion was almost the same in all these regions. Large pools of alien species were found in disturbed habitats with changing nutrient availability - in technogenic areas, as well as in coastal, littoral and

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riverine habitats (Chytry et al., 2008). A comparison of habitats between Europe (Czech Republic) and the temperate zone of North America (Carolina) also showed that both the most and least invasive plant communities are similar on both continents. The authors concluded that the habitat conditions invaded by alien species are a more significant factor than the biological characteristics of the species (Kalusova et al., 2015).

A comparative analysis of the habitats invaded by the most aggressive alien plant species in the Moscow and Kaluga regions, revealed that the most invaded habitats in the anthropogenic group are the roadsides and railroads, nitrogen-rich weed ruderal habitats, and overgrown plant cultures. The least invaded are fields, arable land and man-made wastelands. In the group of semi-natural habitats, the most invaded habitats include manor parks, roadsides of forest and country roads, quarries, deposits, forest parks, and the least abandoned peat extraction, logging and burning. In the group of natural habitats, the most invaded are meadow cenoses and the banks of water bodies; the least invaded are forests and swamps (Vinogradova and Reshetnikova, 2016).

We should note that alien species change their confinement to a particular habitat both in space and in time. Thus, as naturalization proceeds, the species first develop the disturbed territories of the secondary range, and then invade into natural communities, thus changing the state of the native habitats over time. Moreover, an alien species can have a wide ecological amplitude and occupy different types of habitats. A change in the habitat types of alien species in space can be demonstrated, for example, by analyzing the secondary range of ragweed *Ambrosia artemisiifolia*: in the chernozem zone this species grows along roadsides and in river floodplains, and to the north - along railway embankments and housing. *Hippophae rhamnoides* in Kaluga region grows on limestone quarries, in Belgorod - on open slopes in chalk, in Ivanovo - on the open slope of the Volga Valley, and in the north of the Moscow Region - along the edges of highways (Reshetnikova and Vinogradova, 2016; Adjanke et al, 2017).

The objective of research was to identify the distribution patterns of alien plants at the level of individual model taxa and at the level of groups of species that colonize various natural and man-made habitats.

MATERIALS AND METHODS

The study of the characteristics of the distribution of alien species into natural and anthropogenically transformed ecotopes applied both traditional methods of analysis and methods of multivariate statistics, in particular, analysis of the main components.

In the course of studies of alien species, extensive original, literature, and herbarium material was generalized on the distribution of model species of the genus *Bidens* L., *Conyza* L., *Erigeron* L., *Oenothera* L. and *Solidago* L. in Western and Eastern Europe.

The lists of alien plant species colonizing local habitats were evaluated based on the results obtained from a floristic study of natural and anthropogenically transformed ecotopes in the southwest of the Central Russian Upland, which we consider within the administrative borders of the Belgorod Region (Russia).

We studied the species composition of groups of invasive species growing in various ecotopes of the region: in steppe areas (c3), within ravine-gully complexes (ob1-ob9), cretaceous outcrops (m1-m3), areas of agrophytocenoses that form on corn (k1-k3), wheat (ps1-ps3), sunflower (po1-po3), and soybean fields (s1-s2), in parks (p1-p3) and on railways (z1-z4).

To study the similarity of plant groups colonizing different ecotopes, 2025 Jacquard coefficients were calculated for each pair of lists of invasive species. Based on the correlation matrix obtained during the study, the data were analyzed by placing them in the factor space (Chibrik, 1991; Tokhtar, Vinogradova, 2009; Tokhtar, Fomina, 2011; Tokhtar, 2018; Tokhtar et al., 2011; Tokhtar, Kurskoy, 2019). For analysis, we used the Microsoft Exceel XP, Statistica 4.7, and Statistica 6.0.

RESULTS AND DISCUSSIONS

Currently, a significant number of approaches and methods have been developed in the world to assess the processes of adventisation of plant cover and the invasive success of alien species. Some of them are based on traditional empirical approaches, while others are based on statistical data analysis.

The distribution features of invasive plant species are studied mainly at two levels: species and floristic (according to the structure of flora complexes and analysis of the species composition of habitats).

The main objectives of the study of migrations and invasions of individual taxa are usually the identification of the invasive potential of species, quantitative analysis of the presence of species in various habitats, prediction of their distribution, and also analysis of the invasive activity of hybrids of alien species (Wittig, Tokhtar, 2003). For example, when studying various species of the genera *Bidens, Conyza, Erigeron, Oenothera, Solidago*, the colonization features of these species of various ecotopes depending on environmental and climatic factors were revealed (Tokhtar and Groshenko, 2014; Vinogradova and Galkina, 2019). A number of authors study and predict the rate of introduction of hybrids into natural ecotopes, since the success of their distribution depends on hybridization processes (Wittig and Tokhtar, 2003; Tokhtar et al., 2011; Vinogradova and Galkina, 2019). A considerable number of publications are devoted to the study of ecological and

climatic niches and the geographical area of alien and hybridogenic plant species (Olonova et al. 2018).

The study of plants at the species level of analysis makes it possible to clarify the species status of individual species and their hybrids, based on the features of their distribution and the assessment of the volume of ecological niches they occupy, to identify patterns of their distribution in natural and man-made habitats, and to forecast their distribution. However, most of the results of the studies of the distribution features of phylogenetically close taxa make it possible to identify particular patterns that concern only the analyzed model plants. In addition, such studies are most informative if analyzing the distribution of species along a wide geographical gradient, assessing their occurrence in different regions, climatic zones in relation to the action of various climatic factors (Tokhtar and Groshenko, 2014; Morozova, 2018), and are rarely associated with the study influence on the processes of local plant migrations within the framework of ecologically unique ecotopes of different territories. This is explained by the complexity of the quantitative assessment of the resulting response of plants to the action of these factors and the still insufficient development and unification of the methodological apparatus for solving these problems. Therefore, identifying patterns of distribution of plant groups under various environmental conditions by traditional methods is a quit difficult task.

The study of the distribution of alien species at the level of floral complexes, elements and fractions is mostly devoted to an analysis of the similarity of their species composition in various natural and anthropogenic habitats of different regions. The objective of most of the studies is to identify the species composition of invasive plant species, establish their status and provide a comparative analysis of flora complexes (Borisova, 2010; Baranova and Bralgina, 2015; Vladimirov and Grigorievskaia, 2015; Morozova, 2018; Pismarkina and Silaeva, 2018).

A study of the role of specific plant habitats in the Czech Republic (Pysek et al., 1998) indicates the uneven distribution of alien species. They most often grow in settlements, including large cities, towns, villages (25.6%). Coastal-aquatic habitats: rivers, lakes, etc. are the second most important for their role in the distribution of adventitious plants (22.4%). The contribution of other types of habitats never exceeds 10%. However, the share of forests, relatively less disturbed habitats, is quite high (9.2%). Changing the value of habitats over time and their number is also important in their distribution (Pysek et al., 1998).

Great opportunities for solving the problems of invasive biology are provided by the use of statistical methods. They can be successfully solved using multivariate statistics methods. For example, a study by a group of authors (Alahuhta et al., 2020) showed that environmental factors explain the greatest variability of both species richness and the presence of species in different environmental conditions. Variation-related variables (i.e., spatial and dispersion) were also significant, but less important than environmental factors.

Thus, an analysis of our earlier research results shows that the mechanisms of invasion of alien species can be identified with a combination of traditional and statistical research methods that visualize the complex and multilateral relationships of the ecological and biological characteristics of the species, climatic and environmental factors of colonized ecotopes.

Much more complex problems than the task of determining the patterns of distribution of certain closely related alien species include identification of distribution patterns of entire groups of heterogeneous species that conjugate migrate to different types of natural (in the case of naturalization) and anthropogenically transformed ecotopes.

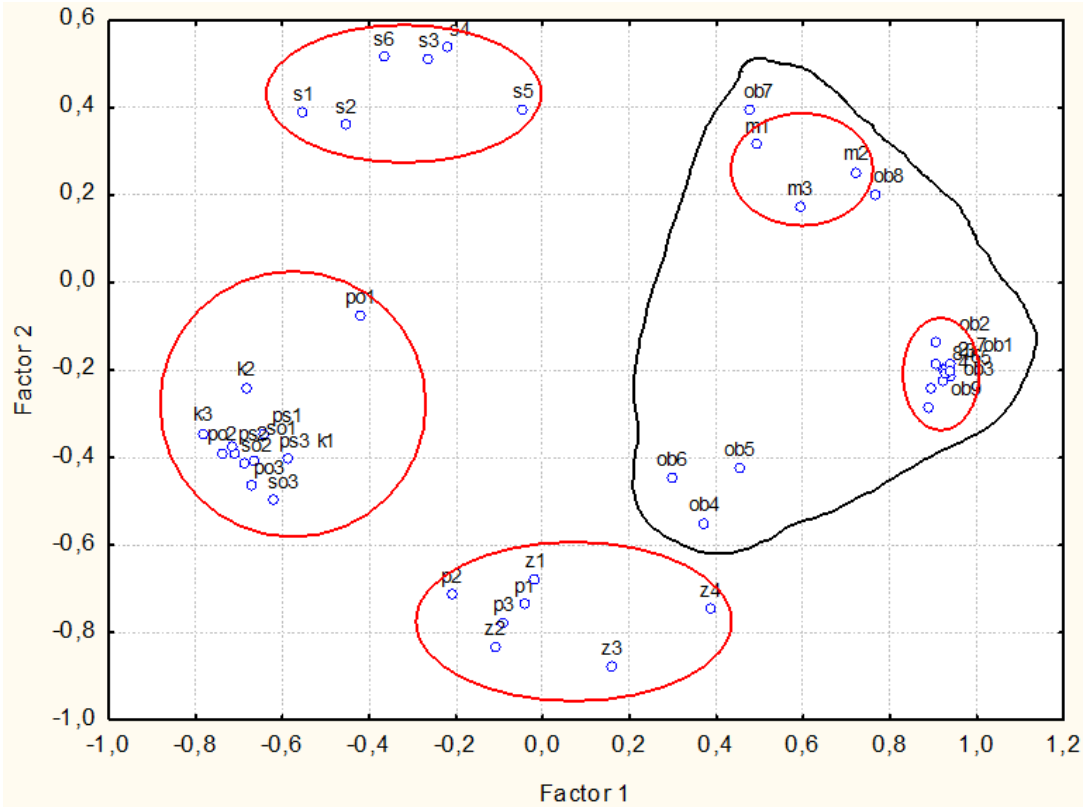
We have studied groups of invasive species that have been forming in the southwest of the Central Russian Upland in various natural and anthropogenic habitats along the gradient of a decrease in the anthropogenic factor: on railways, in parks, agrophytocenoses, forests, within steppe plots, ravine-beam habitats, and cretaceous outcrops. The studied correlation matrices obtained by calculating the Jacquard coefficients were placed in the factor space, which made it possible to visualize the distribution features of invasive species in various habitats.

Fig. 1a and **1b** shows quite clear distribution of the invasive species into separate groups in the diagram. The most isolated groups of plants were those colonizing the steppe habitats. The similarity of species composition between these groups of alien plants growing in these ecotopes is determined by the generality of species that are marked on the diagram community of plotted species (**Fig. 1a** and 1**b**). Within the steppe habitats, these are: *Amaranthus retroflexus, Cyclachaena xanthiifolia, Conyza canadensis, Alcea rosea* etc.

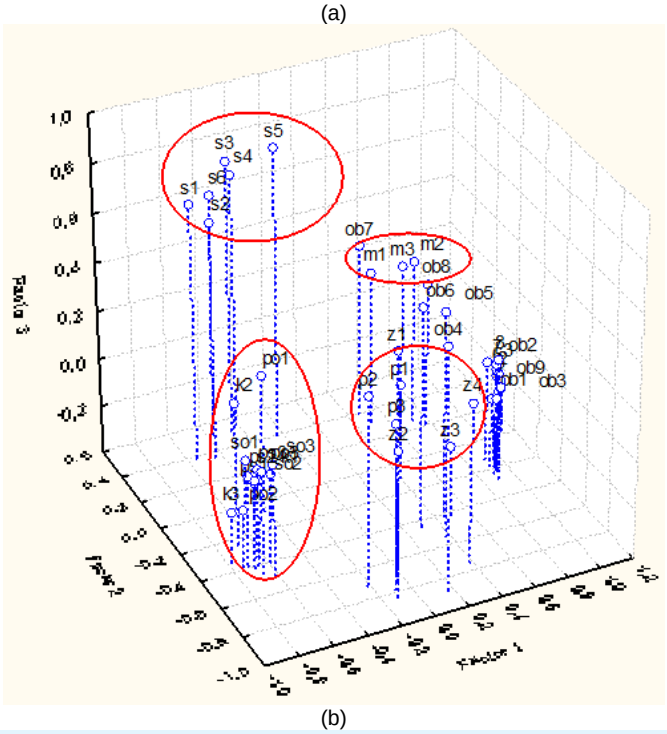
Groups of invasive species of cretaceous habitats are located separately in the factor space. The proximity of the species composition of invasive plants colonizing cretaceous habitats (**Fig. 2b**) is determined by the presence of *Elaeagnus angustifolia, Hippophaë rhamnoides, Crataegus monogyna, Caragana arborescens* and other species.

Species of the genus *Oenothera, Robinia pseudoacacia, Acer negundo, Fraxinus pennsylvanica, Ulmus pumila*, and broadleaf forests have *Impatiens parviflora, Arrhenatherum elatius*, *Parthenocissus inserta* are distributed within most ecotopes of coniferous forests.

The group of invasive species of ravine-gully ecotopes is most widely presented in the factor space



(a)



(b)

Fig. 1. Jacquard coefficient-based distribution diagram of groups of alien species colonizing various natural and anthropogenically transformed ecotopes: a) in the two-factor space, b) in the three-factor space, c3 - steppe plot, z1-z4 - railways, k1- k3 - corn fields, ob1-ob9 - ravine-gully habitats, m1-m3 – cretaceous outcrops, p1-p3 - parks, po1-po3 - sunflower fields, ps1-ps3 - wheat fields, s1-s2 - soybean fields.

(**Fig. 1**). The occupied area of factor space covers groups of invasive plants growing in forest and cretaceous habitats. This is explained by the presence in their species composition of a number of woody plants which are common to these groups (**Fig. 1a**).

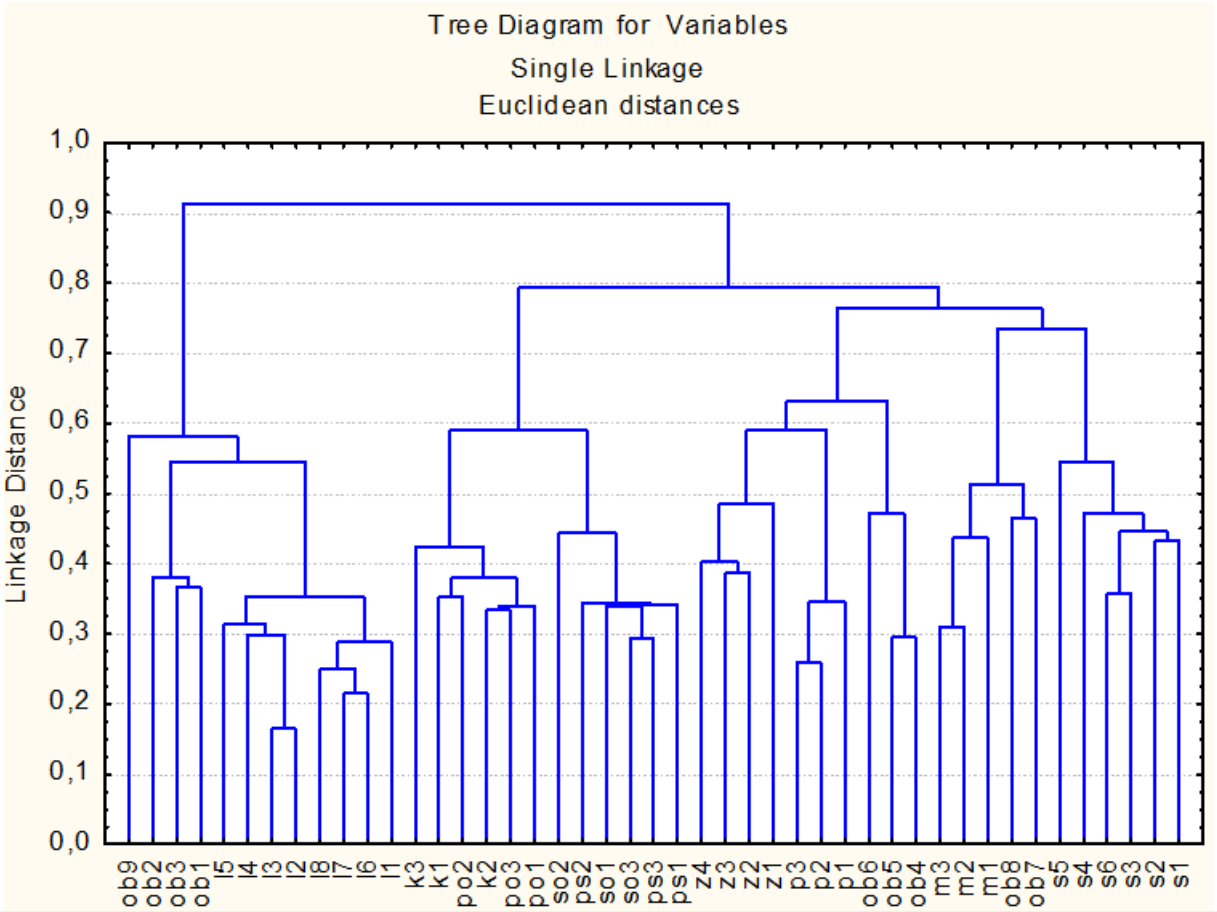


Fig. 2. Visualization of data reflecting Euclidean distances between groups of alien plants colonizing various habitats: c3 - steppe plot, z1-z4 - railways, k1- k3 - corn fields, ob1-ob9 - ravine-gully habitats, m1-m3 - cretaceous outcrops, p1-p3 - parks, po1-po3 - sunflower fields, ps1-ps3 - wheat fields, s1-s2 - soybean fields

Anthropogenically transformed ecotopes (parks, railways) are located near to each other in the factor space due to the similarity in the species composition of alien plants (**Fig. 1a** and **1b**).

Visualization of data using cluster analysis confirms the results of factor analysis. The results presented in **Fig. 2** clearly shows differences among the isolated groups of invasive species that colonize various natural and anthropogenically transformed ecotopes. Complexes of species that have invaded the communities of ravine-girder habitats are rather widely and evenly distributed throughout the diagram in various clusters. They are presented in groups of clusters with invasive species of forest habitats and cretaceous outcrops, which indicates not only the proximity of the species composition of alien species in these ecotopes, but also, apparently, the similarity of ecological habitats, since in ravine-gully ecotopes groupings with a high proportion of woody species, as well as present cretaceous outcrops.

Fig. 2 clearly distinguishes several clusters of invasive species that grow in anthropogenically transformed ecotopes: on the railways, in parks, and groups of plants presented in agrophytocenoses located somewhat separately (**Fig. 2**). Within the most agrophytocenoses there are species: *Acer negundo* L., *Ambrosia artemisiifolia* L., *Bidens frondosa* L., *Cyclachaena xanthiifolia* (Nutt.) Fresen., *Erigeron annuus* (L.) Desf., *Erígeron canadénsis* L., *Heliánthus tuberósus* L., *Xanthium albinum* L., *Robínia pseudoacácia* L., *Fraxinus pennsylvanica* Marsh.,*Oenothera biennis* L., *Prunus cerasus* L., *Parthenocíssus quinquefolia* Planch.

The cluster of invasive plants of agrophytocenoses is also heterogeneous. It identifies close groups of species in row crops: corn and sunflower, which grow under similar environmental conditions. Under these conditions, the distance between rows of cultivated crops is quite large in comparison with wheat and soybean field because of the applied agricultural technologies for growing these crops. Other groups of species which grow in soybean and wheat crops united at the same cluster because they are also formed under similar environmental conditions (**Fig. 2**). The closeness of soybean and wheat crops contributes to the formation of several other modes of lighting and moisture than in crops of sunflower and corn. These differences in environmental conditions, apparently, determine some

differences in the species composition of invasive species in the groups of this cluster.

Thus, it is established that groups of invasive species conjugately migrate to various types of ecotopes. In the upper left part of the diagram (**Fig. 1a** and **1b**) a group of alien plants colonizing the steppe habitats is located somewhat separately. Their similarity is due to the high values of the Jacquard coefficients between the compared species compositions of plants. In the southwest of the Central Russian Upland, the most active invasive species that can invade these phytocenoses are widespread in the steppe habitats. Sufficiently difficult conditions for colonization by alien species developed under the conditions of the cretaceous outcrops of the region. Groups of invasive plants exhibiting expansion in relation to the phytobiota of cretaceous outcrops were located nearby in the factor space. They occupy a rather narrow isolated zone in the same way as a group of plants of steppe habitats, which indicates the difficulty of overcoming natural barriers by invasive species under these conditions. This fact is also explained by the formation of specific, species-similar composition, plant groups similar to each other. Due to such similar ecological and biological characteristics, they can "differentiate" specific natural and anthropogenic ecotopes, since they undergo selection for compliance with specific environmental conditions.

Groups of species typical of ravine-gully ecotopes are characterized by their wide distribution in factor space (**Fig. 1**), which indicates the diversity of species that colonize these ecotopes. This is apparently due to the variety of conditions under these conditions, as well as to the presence in them of ecotopes of cretaceous outcrops and ravine-gully habitats, in which many tree species grow. Habitats formed within the forest flora complexes of the region belong to the same type of ecotopes. In **Fig. 1a**, they occupy the local zone on the *right side of the diagram. The most difficult to invade ecotopes are forest, cretaceous outcrops and steppe habitats. Over a long period of evolution of the vegetation cover, local phytocenoses that are stable in species composition and resistant to the invasion by alien species have been formed.

Thus, the study of the distribution characteristics of invasive species using the analysis of the main components established that invasive plant species colonize the natural and anthropogenic ecotopes of the region selectively depending on the ecological and coenotic environmental conditions, which leads to the selection of plants with certain properties and, as a result, to the similarity of the species compositions of different natural and man-made ecotopes.

CONCLUSION

One of the pressing tasks of modern invasive botany is to find answer to the question of whether there is a group strategy for the distribution of alien species invading various types of ecotopes and what it consists of.

The use of traditional methods for analyzing the distribution of model alien plant species is promising in studying the colonization of habitats by individual model plant taxa. To identify patterns of conjugate migration of entire groups of plants into various types of macroecotopes, the methods of multivariate statistics as effective analysis tools are used. They can reflect current statistical distances and relationships between different objects of research, which makes it possible to determine the features of the group strategy of colonization by alien species of various habitats.

Determination of the distribution patterns of alien species using multivariate statistics methods that consider the quantitative characteristics of flora makes it possible to identify isolated groups of plants that conjugately migrate to various macroecotopes. It is almost impossible to do this by assessing the vegetation cover by traditional methods, clearly distinguishing between groups of species and characterizing the main factors that explain their formation in different habitats due to the significant visual similarity of the flora of synanthropized territories.

The understanding of the processes of the distribution of alien species into various natural and anthropogenic habitats requires using complex empirical and statistical approaches based on both the use of traditional methods of analysis and multidimensional statistics to visualize large volumes of data.

The use of these methods makes it possible to come close to understanding the process of interaction of the ecological and biological characteristics of alien plants with specific environmental conditions, which determines their successful invasion. The promise of multivariate statistics methods lies in the fact that they can be used to study any correlation matrices and any coefficients characterizing biodiversity and environmental parameters. Therefore, the results of species distribution analysis using statistical methods are the resulting function, which reflects many formalized variables: ecological and biological characteristics of the species, their competitive capabilities when introduced into local communities, the relationship of environmental components and phytobiotics. This allows us to simulate the processes of the distribution of alien species in various habitats and to predict the appearance of groups of species in specific ecotopes.

The mechanisms of invasion of alien species can be identified with a combination of traditional and statistical research methods that visualize the complex multiple and multilateral relationships of the ecological and biological characteristics of the species, climatic and environmental factors.

The research fulfilled allows to find that alien species colonize various habitats, exhibit a specific group strategy for the colonization of natural and anthropogenic ecotopes depending on the characteristics of the environment. An analysis of correlation matrices using the principal component method revealed groups of invasive species that are separately formed in: 1) natural habitats (ravine-gully ecotopes, cretaceous and steppe plots; 2) anthropogenically transformed ecotopes (railways, parks); 3) agrophytocenoses (fields of corn, sunflower, wheat, soy).

Visualization of the invasion processes by alien species of various natural and anthropogenic habitats indicates: 1. The conjugate migration of plants to different ecotopes; 2. The originality of the studied ecotopes in relation to the ability of alien plants to colonize them. The plant communities of these ecotopes have varying degrees of invasiveness for alien plants due to the complex of ecological and coenotic conditions and the presence of free ecological niches in them. 3. The study of plant migration to anthropogenic habitats indicates the similarity of the species compositions of plants which invade the plant communities of these ecotopes. However, it should be noted that the group of species common in parks and on railways has significant similarities and is located nearby in the factor space (**Fig. 1**). The groups of plants colonizing agrophytocenoses are isolated on the diagram, despite their attribution to ecotopes of anthropogenic origin.

The most difficult to invade ecotopes are forest, cretaceous outcrops and steppe habitats. Thus, the study with the statistical analysis of the main components made it possible to establish that invasive plant species colonize the region's natural and anthropogenic ecotopes selectively depending on the ecological and coenotic environmental conditions, which leads to the selection of plants with certain properties and, as a consequence, to the similarity of species compositions of various colonized ecotopes.

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