Original research

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Bioclimatic modeling of *Avenella flexuosa* (L.) Drejer distribution in connection with its possible polemochoral origin on the territory of Central Russia

For the first time, the method of bioclimatic modeling was used to determine the boundaries of the range of occurrence of a potential polemochoral species *Avenella flexuosa* (L.) Drejer. The simulation was performed by the method of maximum entropy (MaxEnt). It is shown that the conditions for the growth of this species are initially suitable (the probability of finding 0.54 and higher) in the territory of Central Russia. For comparison, the same bioclimatic modeling approach was applied for the occurrence data of *Carex brizoides* L. species, the polemochoral origin of which is not in doubt. It is shown that its growing places are beyond the limits of the climatic optimum (the probability of finding 0.08) in the territory of Central Russia.

Key words: polemochore plants, alien plant species, MaxEnt, biological diversity, WWII

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Оригинальное исследование

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Биоклиматическое моделирование распространения *Avenella flexuosa* (L.) Drejer в связи с ее возможным полемохорным происхождением на территории Центральной России

Впервые использован метод биоклиматического моделирования для определения границ ареала потенциального вида-полемохора *Avenella flexuosa* (L.) Drejer. Моделирование выполнено методом максимальной энтропии (MaxEnt). Показано, что на территории Средней России условия для произрастания этого вида изначально подходящие (вероятность нахождения 0,54 и выше). Для сравнения был взят вид *Carex brizoides* L., полемохорное происхождение которого не вызывает сомнений. Показано, что его места произрастания на территории Средней России находятся за границами климатического оптимума (вероятность нахождения 0,08).

Ключевые слова: растения-полемохоры, заносные виды растений, MaxEnt, биологическое разнообразие, Вторая Мировая война

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Introduction

The polemochoral is the type of invasive plants, penetrated to a particular territory as a result of military actions. For a number of reasons [Shcherbakov et al., 2013] this topic was not the subject of any noticeable attention of botanists in Russia. Only recently, thanks to the efforts of A.N. Sennikov (2012), it attracted the interest of researchers.

Unfortunately, the study of this group of plants is becoming more and more difficult: over 70 years passed since the Second World War, and it is very hard to separate the plants included in the Central Russia as a result of military actions at that time from those who got there earlier (in particular, as a result of appeared parks and gardens) or later (with seed material, exotic species, etc.). Moreover, as we move from North to South, this complexity increases.

The identification of such plants is not so difficult today in the Murmansk region and Karelia, where the front line ran away from the main roads, and the area occupied by agricultural land is extremely small. It is applicable both to species listed by the Wehrmacht and its allies and to the plants listed by the Red Army. Therefore, the lists of the polemochoral plants are quite extensive there [Sennikov, 2009, 2012].

On the contrary, identification of the polemochoral plants is much more complicated in the Russian non-chernozem region. First, there are many manor parks or their remnants with the Western and Central European plants, many of which were used in the landscaping in the XIX century. Secondly, many plants from Southern and South-Eastern Russia, as well as from the Trans-Urals, came there with seed material and forage in the second half of the XX century. Therefore, at present, it is almost impossible to separate the species that entered the non-chernozem region in the post-war period from the drifts associated with the conduct of military operations by the Red Army. Clarification of a “polemochore” nature of a species related to maneuvers of the German troops requires the use of special “filters” [Shcherbakov et al., 2013], a thorough analytical work, including military nature, good knowledge of the history of that period, and sometimes just good luck [Reshetnikova, 2014].

Avenella flexuosa (L.) Drejer. can be found in the most areas of non-tropical Eurasia, North Africa, North America, in the highlands of tropical Africa and Asia and in southern South America. In Europe, it is distributed geographically from Scandinavia to Gibraltar, except for the forest-steppe and steppe parts. In the territory of Russia the species is distributed in the Arctic regions of Europe and Siberia, in the Caucasus, in the North-Western European part, more rarely found in the far East, in Eastern and

Western Siberia [Zhukova, 1980]. It is considered as Holarctic-Alpine species with a very broken distribution [Tsvelev, 1974]. Presumably it could have originated in the pre-glacial era, and live in post-glacial coniferous and birch forests.

This type of plant is characterized by the following type of soil: coarse sandstones, poor acidic soils, gravel, sandy shale, rarely found on clay soils and completely absent on calcareous soil [Larin et al., 1950]. Most often, *Avenella flexuosa* is found on poor, leached sandy loam and sandy soils of mainland meadows, upper transitional swamps, and pine forests. It is worth noting that nitrates are almost absent and the level of calcium carbonate is very low in such soils.

This type of plant prefers a soil with an average level of humidity, such as forest zone, highlands, forest tundra, etc. Places with a high degree of moisture can adversely affect it. It calmly reacts to a decrease in the level of humidity in the soil, can not tolerate long-term drought, which is why this plant can be found on the slopes and developed peat bogs with a high probability.

A. flexuosa is also common in cuttings, in high-altitude and continental meadows where it grows, flowers and fruits during the period of maximum illumination [Zhukova, 1980]. The meadow has the ability to resist the wind, so it can safely occupy small-to-medium sized hills, such as tree stumps, boulders, slopes. Also, these types of habitat contribute to faster development due to the absence of a forest litter and a blackening. The species is able to withstand relatively long extremely low temperatures (up to –50°).

We often found *A. flexuosa* next to other species introduced by the German army in the territory of Central Russia [Shcherbakov et al., 2017; Reshetnikova et al., 2018, 2019]. At the same time, after a careful analysis, some of the finds can be attributed to location of an old manor (https://plant.depo.msu.ru/module/itempublic?d=P&openparams=%5Bopen-id%3D140984645%5D). Thus, we set our goal to find out whether the points of this species found by us are located within the boundaries of the natural areal or outside of it.

Materials and methods

Georeferenced occurrence data for *A. flexuosa* were accessed from the online database GBIF.org: all finds of this species with coordinates, total 461 617 records (GBIF Occurrence Download https://doi.org/10.15468/dl.3j9zv0 on 28th October 2019), preserved specimen only, total 4736 records (GBIF Occurrence Download https://doi.org/10.15468/dl.ywqlg8 on 28th October 2019). Georeferenced occurrence data for *Carex brizoides* L. were accessed from online database GBIF.org: all finds of this species with coordinates, total 53 837 records (GBIF Occurrence Download https://doi.org/10.15468/dl.kyv2wz on 31th October 2019), preserved specimen only, total 508 records (GBIF Occurrence Download https://doi.org/10.15468/dl.acq19w on 31th October 2019).

These datasets were used to identify the actual and potential areas of distribution of *Avenella flexuosa*. That was done in order to understand whether this species findings in non-chernozem regions are related to its possible polemochoral origin or it is rather the natural process of the species distribution to a new suitable habitats. As a reference we used presence data of *Carex brizoides* which is a polemochoral plant without a reasonable doubt [Sennikov, 2009; Reshetnikova et al., 2019].

We built a model of a probable area distribution using MaxEnt v3.4.1 which is a program for modeling a species distributions from presence-only records. The approach of modeling used in MaxEnt is based on minimizing the relative entropy between probability densities of presence data and environmental characteristics of presence sites in covariate space which is equivalent to maximizing entropy in geographical space [Elith et al., 2010]. This approach works well when presence-only data is available (no absence data) and the potential distribution area can be modeled with a limited number of points of registered species findings.

The distribution of suitable habitats of the species was evaluated by MaxEnt according to the principles of maximum entropy [Phillips et al., 2006; Phillips, Dudik, 2008]. The software can be downloaded at http://biodiversityinformatics.amnh.org/open_source/maxent/. A detailed description of the principles and procedures is available online in Russian https://gis-lab.info/qa/maxent.html.

The parameters selected were: ‘Auto features’, percentage of test sample = 25%, maximum number of iterations = 50 000, cross-validation procedure, background at random in the entire study area. We considered the model runs to be accurate based on AUC statistic value achieved (0.973 for *Avenella flexuosa* and 0.988 for *Carex brizoides*), which represents capability of a model to distinguish between classes, habitat suitability of geographical point in our case.

Eleven climactic variables with 30 arc-min resolution from IPCC were utilized as environmental layers in MaxEnt 3.4.1. [Phillips et al., 2006]:
– diurnal temperature range, annual (dtr6190_ann);
– frost frequency, annual (frs6190_ann);
– precipitation, annual (pre6190_ann);
– precipitation, January (pre6190_I1);
– precipitation, April (pre6190_I4);

– precipitation, July (pre6190_I7);
– precipitation, October (pre6190_I10);
– mean temperature, annual (tmn6190_ann);
– minimum temperature, annual (tmp6190_ann);
– maximum temperature, annual (tmx6190_ann);
– vapour pressure, annual (vap6190_ann).

The modeling outcome is presented as heat maps which display a probability of species distribution across the globe. Warmer colors represent better conditions for a species which can be interpreted as a higher probability of presence. The colors display the calculated probabilities according to the scale: warmer colors show areas with better predicted conditions; from 0.69 (yellow) to 0.92 and more (orange and red); green represents conditions similar to those in which the species was collected on the territory of Central Russia (~0.5–0.6); blue shades indicate unlikely conditions.

Results and discussion

The relative contribution of environmental variables to the MaxEnt model was estimated as a result of the modeling process (Table 1). To determine the percentage of contribution, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable or subtracted from it if the change to the absolute value of lambda is negative. For the permutation importance, for each environmental variable, in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. So, the most influential variables (with correction on the permutation importance) are “mean temperature, annual” (tmn6190_ann) and “maximum temperature, annual” (tmx6190_ann).

To determine the importance of environmental variables on *Avenella flexuosa* potential distribution, another statistical approach was used. The following picture (Figure 1) shows the results of the jackknife test of variable importance [Efron, Stein, 1981].

The environmental variable with the highest gain, when used in isolation, is “mean temperature, annual” (tmn6190_ann), which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is “maximum temperature, annual” (tmx6190_ann), which therefore appears to have the most information that isn't present in the other variables. These results on variable importance should be interpreted with caution though since these variables are correlated.

Table 1

Analysis of variable contributions for *Avenella flexuosa* models, showing: Percent contribution (PC) and Permutation importance (PI), discussed in the text

Variable	Percent contribution	Permutation importance
pre6190_l1	19.3	2.9
frs6190_ann	18.9	6.7
tmn6190_ann	**18.1**	**42.3**
pre6190_l10	15.1	7.2
tmx6190_ann	**12.9**	**19.6**
pre6190_l7	5.4	4.7
tmp6190_ann	4.1	4.5
dtr6190_ann	3	7
pre6190_l4	2.6	1
vap6190_ann	0.3	1.5
pre6190_ann	0.2	2.8

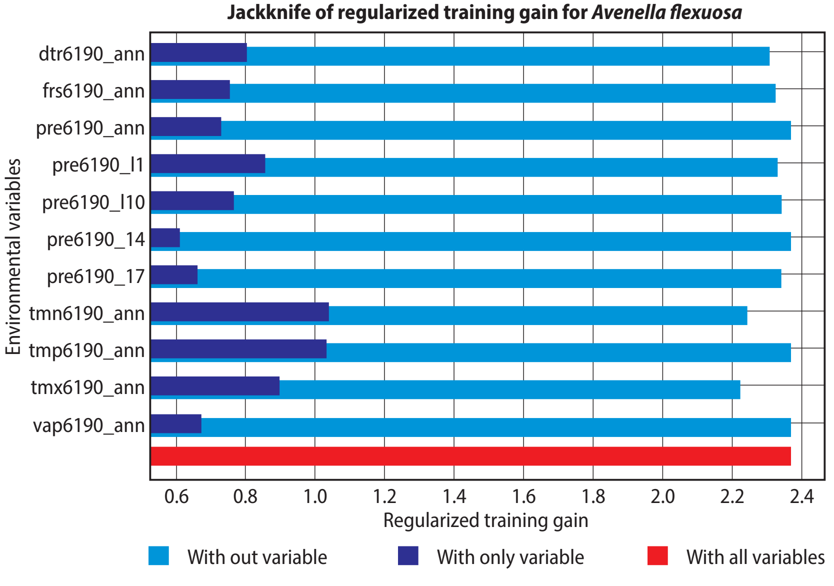

Fig. 1. The results of the jackknife test of variable importance

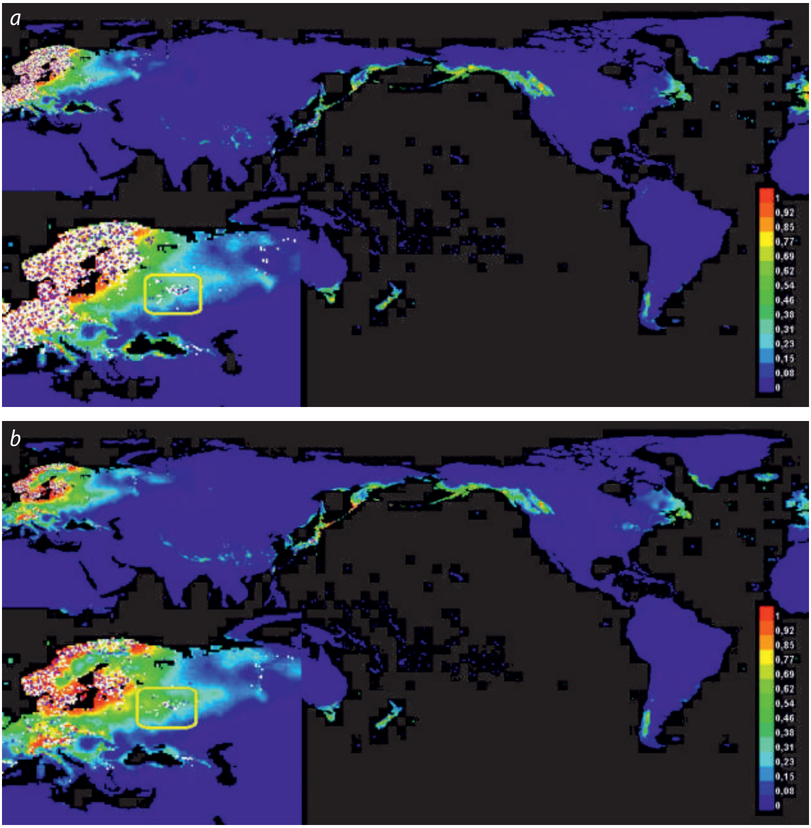

Fig 2. MaxEnt modeling of *Avenella flexuosa* (L.) Drejer. for datasets with a different volume:

a – dataset of worldwide distribution (total 461617 records with coordinates);
b – dataset of worldwide distribution by preserved specimen (total 4736 records with coordinates).

White dots show the presence locations, purple dots show the records which used for program training. The probability of the species presence is reflected by logarithmic color scale, see lower right corner. On the inset in the lower left corner, a yellow rectangle indicates the area of finds in Central Russia.

The results of bioclimatic modeling for *Avenella flexuosa* are presented in the figure 2, and for *Carex brizoides* in the figure 3. It is shown that the conditions for the growth of *Avenella flexuosa* are initially suitable in the territory of Central Russia (the probability of finding 0.54 and higher). For *Carex brizoides* it is shown that its growing places are beyond the limits of the climatic optimum in the same territory (the probability of finding 0.08).

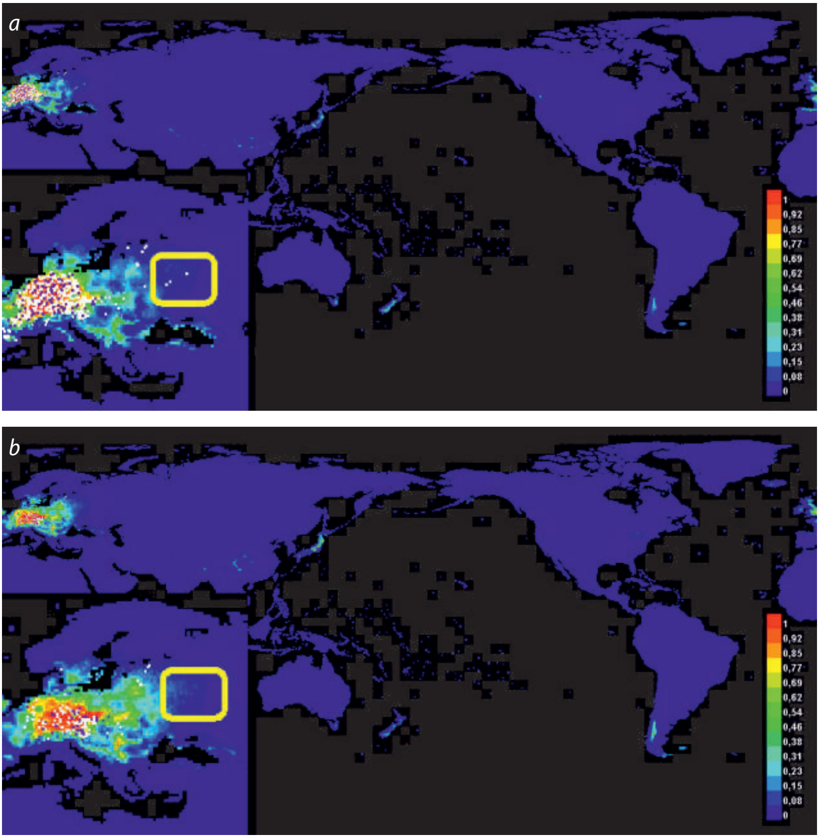

Fig 3. MaxEnt modeling of *Carex brizoides* L. for datasets with a different volume:

a – dataset of worldwide distribution (total 53837 records with coordinates);
b – dataset of worldwide distribution by preserved specimen (total 508 records with coordinates).

White dots show the presence locations, purple dots show the records which used for program training. The probability of the species presence is reflected by logarithmic color scale, see lower right corner. On the inset in the lower left corner, a yellow rectangle indicates the area of finds in Central Russia.

There is a number of indications that currently *Avenella flexuosa* can be attributed to progressive species that are expanding their natural areal [Seregin, 2015]. The same can be attributed to the growth of this species outside the boundaries of the areal, taken as natural, where it can be introduced in various ways, including polemochoral. For example, during the work on the compilation of the floral check-list in the National

Park "Orlovskoe poles'e", *Avenella flexuosa* was fixed only at one point (https://plant.depo.msu.ru/module/itempublic?d=P&openparams=%5Bopen-id%3D140984661%5D). In 2001, only one small group grew on the sandy side of a forest road. In the summer of 2019, we re-examined this place, and found that not only the roadside, but also the nearby hillfort of the Verkhneoksky Balts Radovishche (https://orlpolesie.ru/sokhranyat/unikalnye-ob-ekty/istoriko-kulturnoe-nasledie) covered with *A. flexuosa* almost entirely, and the total population area was about 0.5 hectares (E.O. Korolkova, L.L. Kiseleva, observation). The most dense plants were located on the top, where regular archaeological excavations were carried out in the late 2000s. During which the living ground cover was removed, surfacing the sand from the excavations. All this is in good agreement with the previously described [Zhukova, 1980] ecological preferences of this species: poor sandy acidified soils, and also confirms its role as a plant of the initial stages of succession.

Thus, the conducted bioclimatic modeling confirms that the conditions for the growth of *A. flexuosa* are initially suitable (the probability of finding 0.54 and higher) in the territory of Central Russia, including the places of occurrence with alleged polemochoral origin.

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Я.Е. Васильчиков – построение биоклиматических моделей, интерпретация полученных данных, участие в подготовке текста статьи

Contribution of the authors

E.O. Korolkova – general direction of the research, planning of the research, selection of model species, participation in the preparation of the text of the article
Ya.E. Vasilkov – bioclimatic modeling, results interpretation, participation in the preparation of the text of the article

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All authors have read and approved the final manuscript