Dependence of diversity of floras on climate in the Middle Volga region

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Abstract. Links with climate of richness of species (Ns), genera (Ng) and families (Nf) for 28 polygons each 400 km2 in Middle Volga were studied. Negative correlations with temperatures T and positive with precipitation P of the warm period were revealed, and T and P most strongly affected diversity. Closest links with climate were for Nf, and the least for Ns. We estimated gradients of T and P in four geographic directions. The most pronounced are northern cold-humid and southeastern thermo-arid trends. The northern trend is characterized by a decrease in T by 0.34°C and an increase in P by 17 mm per 100 km; southeast – with an increase in T by 0.27°C and a decrease in P by 15 mm. The cold-humid trend provides the most favorable conditions for the growth of diversity in the region. In it, Ns increased by 36, Ng – by 17, Nf – by 6 per 100 km. For floras with highest Nf and Ng, closer links with T, P and directions are revealed; in contrast to Ns. This indicates the ecological plasticity of the diversity, with different responses to climate variations for different taxonomic levels, which contribute to the preservation of diversity in a heterogeneous climate.

1. Introduction
Global and continental studies of plant diversity (resolution 50–200 km) have shown that diversity is closely related to climate [1–6]. However, due to the difficulties in calculating the number of species Ns, the diversity of vegetation in drylands was characterized by the number of families Nf [7]. Largest Nf are observed in the equatorial zone [8]. It was noted that plant families show smaller endemism than species [9]. Reviews include [10–12]. On a regional scale (resolution 5–20 km), links between Ns and climate were mostly studied; links at this scale were weaker, but depend on groups or life forms of plants [13–15].

A certain problem is the dependence of Ns on the area S of the observation sites. It is known that Ns increases with S, and for Ns values to be comparable, it is necessary, at least, that S of sites be the same (e.g., 100 km² on a regional scale [16]) and each should be well studied in terms of species richness. However, this is not enough since the representativeness of the site description suggests that Ns should change little with an increase in S, for example, by 20% with double increase in S. To take this into account, the concept of concrete floras was suggested with S varying from 100 to 500 km² depending on region specifics [17]. In the conditions of the Middle Volga region, the minimum S for determining concrete flora that was studied in detail here in the period 2004–2014 was estimated as 400 km² [18].
The study of the relationships between the number of genera $N_g$ or the number of families $N_f$ and climate on a regional scale was carried out less frequently than for $N_s$ [17, 19]. Despite the general tendencies for the closeness of the link between $N_s$, $N_g$, $N_f$ and climate, their distributions may not coincide in space. In North America, the largest $N_s$ and $N_g$ were found in the southwest, and $N_f$ in the southeast [4]; in Eastern Europe, it has been shown that the maximum rate of variation of $N_f$ with latitude lies 3.5–4.4° farther north than for $N_g$ and $N_s$ [20]. In general, the patterns of differences in the relationship between $N_s$, $N_g$, and $N_f$ with climate are not yet fully understood [19].

The aim of this paper is to study links between $N_s$, $N_g$, and $N_f$ of vascular vegetation and climate in the Middle Volga region at 28 sites, each with an area of 400 km$^2$, to determine the difference and similarity of these relationships and assess their impact on ecological relationships with the climate in this region.

2. Materials and methods

2.1. Vegetation baseline data
The size of the study area in the Middle Volga region is 5.4° × 3.0°. The study sites are distributed over the territory of Samara, Ulyanovsk, Penza regions, the Republic of Mordovia and the Republic of Chuvashia. Forest coverage in the region is low. Soils vary from chernozems in the south to sod-podzolic in the north. The study area is characterized by three types of soils: chernozems, gray forest and sod-podzolic soils; their registration was carried out using a soil map at the scale of 1: 2.5 million. The lists of vascular plant species used in this paper correspond to the minimum range of flora in a particular area. Such samples of the floristic composition of regional floras for the territory, for example, the forest-steppe zone of the Middle Volga, include 600–800 species and correspond to 400 km$^2$ [21]. In total, 28 plots of the indicated area were selected for research (figure 1). For 9 sites, the area of which did not exceed 400 km$^2$, published lists of species were used [22–29]. For the rest of the sites, lists of species available in the FD SUR database [30] were combined according to 163 floristic descriptions. Source lists of species were established during field research from 2004 to 2020. Each list was compiled on the ground for a separate geographical point using the route method (5–10 km) and subsequently supplemented with a certain herbarium material. Some of these floristic data have been published [31–40]. Each of the 19 sites of area 400 km$^2$ is represented by a unified list of vascular plant species and includes from 5 to 15 floristic descriptions.

2.2. Climatic data
Average data on monthly precipitation and temperatures, precipitation amounts by seasons, as well as values of 19 bioclimatic variables, for example, the average annual precipitation amount and its coefficient of variation, were taken from the WorldClim database [41]. In WorldClim, monthly climatic variables are averaged over 50 years (1950–2000) and are presented with a spatial resolution of 900 m. To characterize the research sites of 400 km$^2$, we used climatic grids at the resolution of 600 m, average, minimum and maximum values of climatic features, their range and standard deviation.

2.3. Calculation of spatial climatic trends, analysis of relationships between the richness of species, genera and families with climate
Spatial climatic trends, as well as their gradients, were determined by analyzing the relationships of the main climatic indicators with geographic directions in the Analytical GIS Eco program [42]. The severity of the trend was characterized by the closeness of the links between them, and the rate of change in the trend or its spatial gradient was the coefficient of linear regression. The analysis of relationships between the richness of species, genera, and families with climate was carried out in Analytical GIS Eco and Excel programs.
3. Results and Discussion

Variation coefficients for $N_s$, $N_g$, and $N_f$ are as follows: 11.3%, 10.4%, and 11.2%, respectively. The ratios of mean values are as follows: density of species in a genus ($N_s/N_g$)$_{AV}$ = 1.94, density of genera in a family ($N_g/N_f$)$_{AV}$ = 3.97, and density of species in a family ($N_s/N_f$)$_{AV}$ = 7.72.

In the study area, monthly average temperatures $T$ and precipitation $P$ are closely negatively related in the warm period, but practically independent in the cold one (figure 2b). For this reason, there are difficulties in determining what affects the diversity of vegetation during the warm season: precipitation or temperature. According to figure 2b, we can conclude that with a decrease in precipitation in summer, the temperature may increase, that is, there is a dry period, especially in July.

![Figure 2](image_url)

**Figure 2.** Monthly distribution of (a) temperature $T$ and precipitation $P$, (b) the strength of the link between $T$ and $P$ (determination coefficient with the sign of the link)
The curves of links $N_s$, $N_g$, and $N_f$ with average monthly temperature $T$ (figure 3a) show that when the temperature changes its sign, the links also change signs. The curves of relations with precipitation $P$ (figure 3b) are similar to temperature ones, but they are a mirror image of them. A change in the signs of the $N_s$, $N_g$, and $N_f$ links with precipitation occurs together with a change in the signs of the temperatures of the months.

**Figure 3.** Relationships between the number of $N_s$ species, $N_g$ genera, and $N_f$ families with (a) average monthly precipitation and (b) temperatures. Values of $R^2$ are given with signs of links

Diversity indices $N_s$, $N_g$, and $N_f$ are positively associated with negative $T$ months during the cold period and negatively with positive $T$ months during the warm period (figure 3a). This indicates that species richness $N_s$ (as well as $N_g$ and $N_f$) is positively affected by the increased $T$ in the cold period and negatively by the high $T$ in the warm period. In other words, moderate $T$ of cold and warm periods contribute to higher diversity at all the three taxonomic levels. The result corresponds to the known facts that severe frosts and summer heat are unfavorable for vegetation in the temperate zone (e.g., [43, 44]).

The link with $P$ has the opposite character (figure 3b) – the curves are mirrored curves of the relationships with $T$ (figure 3a). Low $P$ values during the warm season diminish diversity, as do low $P$ values during the cold season. This corresponds to the fact that, in the temperate zone, summer droughts adversely affect vegetation, as does a small snow cover (e.g., [43]).

The relative influence of $P$ and $T$ on the diversity could be assessed by the closeness of links, but this requires independence of $P$ and $T$. In the study area, $P$ and $T$ are significantly dependent (figure 2b), as is often observed for climatic variables, and this leads to the known problem of their use. In some cases, regions with a weak connection between $P$ and $T$ on the planet are even chosen for research to obtain a clear interpretation [45]. Note that the number of families $N_f$ is more closely related to both precipitation and temperatures during the warm period than $N_g$ or $N_s$ (figure 3).

Consider now links of ratios $N_s/N_g$, $N_g/N_f$ and $N_s/N_f$ with temperatures and precipitation. The closest links with climate are observed for the average density of genera in families $N_g/N_f$ during the warm period, especially with July precipitation (figure 4). The decrease in $N_g/N_f$ with a lack of precipitation by almost 40% can be explained by summer droughts (figure 4b). The genus density of families in a certain trend corresponds to the antiquity of plants [44]; then, according to the data in figure 4, diversity of ancient families shows the greatest sensitivity to summer droughts decreasing with them and to the availability of summer heat increasing with it. At the same time, droughts affect the density more strongly (figure 4). In contrast, the species density of genera $N_s/N_g$ is practically independent of
the conditions of the warm period and is negatively, albeit weakly, related to winter temperatures (figure 4). It is believed that the species density of genera in a certain trend is associated with the later stages of evolution – the younger is vegetation, the higher is the density [44]. The obtained result may reflect the lesser dependence of this vegetation on the modern climate, which is described by the shown relatively weak relationship.

Figure 4. Monthly distribution of (a) relationships of the densities $N_s/N_g$, $N_g/N_f$, and $N_s/N_f$ with temperatures $T$ and (b) precipitation $P$. Values of $R^2$ are given with the sign of the relationship.

To understand the patterns in the Middle Volga region, the richness of species, genera and families of vascular plants, spatial climatic trends were considered, temperature and precipitation gradients were estimated in different geographic directions.

Identified by us spatial climatic trends for the base period (1950–2000) are shown in table 1 and figure 5. The severity of trends was judged according to the closeness of the identified relationships – the correlation coefficient between climatic indicators and geographical directions.

For the identified spatial climatic trends in geographic directions, the following characteristics have been determined. The most pronounced for the annual temperature, averaging the indicators of periods, seasons and individual months, is the cold trend to the north and less pronounced to the northeast (figure 5a). The northern cold trend is characterized by an average decrease in annual temperature by 0.28 °C per 100 km, and the northeastern cold trend – by 0.14 °C per 100 km. No noticeable changes in annual precipitation in these directions were observed (figure 5b). For the indicators of the warm period (April-October), the northern direction is characterized by a cold-humid trend with gradients of $-0.34$ °C per 100 km per month and +17 mm per 100 km per period (figures 5a, b), as well as somewhat less pronounced for summer ($-0.34$ °C and +9 mm). The north-east direction is characterized by a cold trend for the winter season ($-0.42$ °C per 100 km) and the cold period as a whole ($-0.33$ °C per 100 km). In the easterly direction, there is a noticeable decrease in winter temperature ($-0.39$ °C per 100 km).

The thermo-arid trend is characteristic of the southeastern direction for the summer season (+0.33 °C and −9 mm per 100 km) and for the entire warm period (+0.27 °C and −15 mm per 100 km). For winter, the southeast trend is also one of the coldest (−0.40 °C / 100 km). The indicators of the spring season do not have pronounced climatic trends in the directions.
Summarizing the results of the analysis, we emphasize that the northern cold-humid trend is most relevant for the climatic indicators of the middle and end of the growing season – summer and autumn. The summer months are also characterized by a pronounced thermo-arid trend to the southeast. At the beginning of the growing season, obvious climatic trends are not relevant; only weakly expressed humid trends to the east and arid ones to the southeast can be noted. In the winter season of “dormancy” of plant communities, cold trends to the northeast, east, and southeast are most noticeable, but not to the north. For annual indicators that integrate annual cycle averages, only the northern cold trend is important.

Links for richness of species, genera and families with geographical directions are shown in table 1.
Table 1. Links between the number of species \( N_s \), genera \( N_g \) and families \( N_f \) with geographic directions

| Geographic direction | Correlation coefficient \( N_s \) | Correlation coefficient \( N_g \) | Correlation coefficient \( N_f \) |
|----------------------|----------------------------------|----------------------------------|----------------------------------|
| Eastern              | \(-0.063\)                       | \(-0.101\)                       | \(-0.168\)                       |
| Northern             | \(0.557\)                        | \(0.574\)                        | \(0.668\)                        |
| North-eastern        | \(0.270\)                        | \(0.251\)                        | \(0.253\)                        |
| South-eastern        | \(-0.402\)                       | \(-0.444\)                       | \(-0.560\)                       |

\( N_s, N_g \) and \( N_f \) have the same character of dependences on directions: they synchronously change the signs of connections with them (figure 6). The tightness of connections with geographic directions for all taxonomic levels diminishes in the order north – southeast – northeast – east. The closeness of the relationship between diversity and directions increases in the \( N_s – N_g – N_f \) series. That is, the most sensitive to changes in directions is the number of families, the least is the number of species.

Figure 6. Relationships of \( N_s \) (a) and \( N_f \) (b) with the minimum (Tmin) and maximum (Tmax) temperatures within the study sites

A noticeable decrease in diversity in the southeastern direction is expressed on average by the following gradients: every 100 km, the number of species decreases by 26, genera – by 16, and families – by 5. This may be associated with the thermo-arid trend of spring and summer revealed for this direction, as well as the winter cold-humid trend. In the direction to the north, on the contrary, an increase in the number of species (by 41/100 km), genera (by 20/100 km) and families (by 6/100 km) is observed.

The growth of diversity towards the north is consistent with the cold-humid spatial trend of the warm period, and separately – summer and autumn, as well as with the winter arid trend (see figure 5). The eastern direction is characterized by a weaker decrease in species diversity (by 10 species per 100 km), genera (by 8 per 100 km) and families (by 3 per 100 km), which is apparently caused by the summer thermo-arid trend and a fairly cold winter trend with little snow. The direction to the northeast, which corresponds to well-pronounced cold winter and spring arid trends, has practically no effect on biodiversity (figure 6).

The result of a pronounced increase in diversity to the north, in the direction of which the cold-humid trend intensifies during the growing season, is consistent with the results of the analysis of pair-
wise relationships of diversity with monthly average indicators: a decrease in temperature and an increase in precipitation leads to an increase in diversity. Agreement with pairwise correlations is also present for the southeastern thermo-arid trend.

Analysis using linear pairwise correlations showed that there is some spatial differentiation in temperature at the studied sites. Figure 6 shows, firstly, that the tightness of connections for $N_s$ with extreme temperatures is noticeably less than for $N_f$. Secondly, the dependence of the number of species on the minimum temperatures during the warm period is more pronounced than on the maximum; and, on the contrary, for the number of families, the relationship with the maximum temperatures in the same period is closer. For a cold period with negative temperatures, connections with maximum temperatures are more relevant for both taxonomic levels. This result may indicate both the differences in responses to climatic indicators, and a certain trend of possible spatial differentiation at the sites between $N_s$ and $N_f$. The latter can be expressed in the confinement of taxonomic levels to different areas of the plots. For example, $N_s$, less dependent on maximum temperatures, occupy areas with temperatures close to these temperatures, and more dependent on $N_f$ maximum temperatures occupy areas with close to minimum temperatures.

4. Conclusion
With the existing features of similarity, different taxonomic levels of diversity of a particular flora of vascular vegetation react differently to climate variations in the Middle Volga region.

The similarity consists in negative links of $N_s$, $N_g$, and $N_f$ with temperatures and a positive link with precipitation of the warm period when these links are the closest. At the same time, the generic density of families $N_g/N_f$ is more closely related to climate than $N_s/N_g$ or $N_s/N_f$. Assuming that $N_g/N_f$ corresponds to the antiquity of the families [44], the oldest families are most sensitive to summer droughts decreasing with them and the availability of summer heat increasing with it, while droughts play somewhat greater role. The species density of genera $N_s/N_g$ is presumably related to later stages of evolution [44] and this indicator reflects the lesser dependence of evolutionarily younger vegetation on modern climate, which corresponds to the weak link between $N_s/N_g$ and climate. Although these assumptions are still unsubstantiated, they are consistent with the results obtained (figure 4).

The distinction consists in that for floras with the highest $N_f$ and $N_g$, closer links with temperatures, precipitation, and climate gradients in directions have been revealed. For the flora with the highest $N_s$, the situation is opposite: relatively weak links and low gradients. Differences in the links of different taxonomic levels with extreme temperatures are shown. In general, the results substantiate that the relationships of $N_s$, $N_g$, and $N_f$ with climate are not the same and indicate the ecological plasticity of plant communities in the Middle Volga region, with different responses to climate variations for different taxonomic levels. Our opinion is that this contributes to the preservation of diversity in a heterogeneous climate.

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