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Analysis of the Eurasian steppe flora – species inventory, species richness and rates of endemism

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Summary. The Eurasian steppe belt extends from the Danube to the Amur River and represents the largest expanse of steppe vegetation in the world. Despite numerous studies of the flora of individual regions, there is no a reliable estimate of the total number of higher plant species characteristic of this biome as a whole. Filling this gap is the aim of this study. Based on an analysis of modern floristic summaries, a count of species associated with steppe ecosystems was conducted, with an emphasis on the Euro-Siberian and Mongol-Chinese subregions. Special attention is paid to the correct assignment of taxa to the steppe flora, taking into account possible errors in taxonomic status and anthropogenic landscape changes. Estimates of the number of steppe species vary: for northern Kazakhstan – 750–850, for Mongolia – 800–900. Our calculations revealed that the species composition of the Pontic steppe ranges from 200 to 400 species, while for the Kazakh, Mongolian, and Chinese steppe regions, it ranges from 700 to 900 species. The rate of endemism in the 'lowland' steppes was extremely low (less than 1 %), which contrasts with the high rates in mountainous provinces such as Anatolia and Altai. This is primarily explained by the history of climate change in the Late Pleistocene, as well as the fact that the cryoarid conditions of glacial periods contributed to the impoverishment of flora and decreased isolation, hindering speciation. The results emphasize the dominant role of paleoclimatic factors in shaping the modern floristic structure of the Eurasian steppes and point to the need for further comprehensive research, particularly in the poorly studied regions of Central Asia.

Анализ флоры степей Евразии: видовой состав, видовое богатство и степень эндемизма

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Ключевые слова: видовой состав, Евразия, ландшафты, палеоклиматы, современное состояние, степи, эндемизм.

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Аннотация. Евразийский степной пояс простирается от Дуная до реки Амур и представляет собой крупнейший в мире участок степной растительности. Несмотря на многочисленные исследования флоры отдельных регионов, до сих пор отсутствует достоверная оценка общего числа видов высших растений, характерных для этого биома в целом. Восполнение данного пробела является целью данной работы. На основе анализа современных флористических сводок осуществлён подсчёт видов, ассоциированных со степными экосистемами, с акцентом на евро-сибирскую и монголо-китайскую подобласти. Особое внимание уделено корректности отнесения таксонов к степной флоре с учётом возможных ошибок в таксономическом статусе и антропогенных изменений ландшафтов. Оценки численности степных видов варьируют: для северного Казахстана – 750–850, для Монголии – 800–900. Наши расчёты показали, что видовой состав понтийских степей составляет от 200 до 400 видов, а для казахских, монгольских и китайских степных регионов – от 700 до 900 видов. Уровень эндемизма в равнинных степях оказался крайне низким (менее 1 %), что контрастирует с высокими показателями в горных провинциях, таких как Анатолия и Алтай. Данный факт объясняется, в первую очередь, историей климатических изменений в позднем плейстоцене, а также тем, что криоаридные условия ледниковых эпох способствовали обеднению флоры и снижению изоляции, препятствуя видообразованию. Результаты подчёркивают доминирующую роль палеоклиматических факторов в формировании современной флористической структуры евразийских степей и указывают на необходимость дальнейших комплексных исследований, особенно в малоизученных районах Средней Азии.

Expanded Summary

There is no reliable inventory of the number of vascular plant species in the Eurasian steppes. We evaluated the current available data and realized a significant lack of concrete data (Table 1). To improve this situation, we calculated the number of steppe species based on relevant floras and recent species checklists. Our calculations resulted in a species pool of 200 to 400 species for the Pontic steppe and 700 to 900 species for the Kazakh, Mongolian and Chinese steppe regions. This is in contrast to the widespread acceptance of much larger species pools in the Eurasian steppe belt. The overall low number of species in the steppe regions and the strikingly smaller species pool of the Pontic steppe compared to the steppe regions further east can be explained in context with the late Pleistocene climatic macrocycles. We also recorded the number of endemics and discovered extremely low endemism rates in the Euro-Siberian and Mongol-Chinese steppe regions compared to significantly higher rates in the Altai Mountain Country (AMC) and in the steppes of Anatolia. The low endemism rate of the 'lowland' steppes can be partially explained by the relatively small species pool, low topographic heterogeneity and low isolation barriers but severe ecological disruption caused by the Late Pleistocene climatic macrocycles had a negative influence on the number of endemics, too. The high rates of endemism in the mountainous AMC and Anatolia are consistent with the findings that mountains generally have higher numbers of endemics, as they exhibit a high degree of environmental heterogeneity. We assume that disturbance events caused by Pleistocene climate cycles also play a role and are more pronounced in the boreal AMC than in the nemoral Anatolia. This together with a Pleistocene immigrant flora could explain the much higher rate of endemism in Anatolia.

Table 1. Number of higher plants in the Eurasian steppe belt as revealed by AI inquiries
We asked: How many species of higher plants in the steppes of …..?

Geographical Region	Estimated Figures (enquiry outputs)	Source AI and access date
Entire Eurasian Steppe belt	2500–5000	ChatGPT, January 2025
	6000–7000	ChatGPT, January 2025
	3000–4000	ChatGPT, 8.4.2025
	2500–3000	Meta AI, 6.4.2025
	ca. 2600	Meta AI, 6.4.2025
	'likely in the thousands'	Gemini AI, 9.4.2025
	ca. 4000–5000	Bing AI, 7.7.2025
	More than 1500	Perplexity, 14.7.2025

Ending Table 1

Geographical Region	Estimated Figures (enquiry outputs)	Source AI and access date
European Steppe region	1500–2000	ChatGPT, January 2025
	several hundred to over a thousand	Perplexity, 14.7.2025
Pontic Steppe, Romania	600–700	ChatGPT, 8.4.2025
Pontic-Caspian (Pannonian) Steppe	ca. 1500–1800	Bing AI, 7.7.2025
Romania	700–800	ChatGPT, 9.4.2025
Hungary	600–700	ChatGPT, 9.4.2025
Bulgaria	500–700	ChatGPT, 9.4.2025
Eastern Europe (Ukraine, Moldavia, southern Russia)	2000–2500	ChatGPT, January 2025
European Russia	800–1000	ChatGPT, 9.4.2025
Ukraine	1700–2000	Meta AI, 9.4.2025
	ca. 1600	Bing AI, 5.7.2025
Asian Steppe region	3000–4000	Meta AI, 9.4.2025
	Several thousand	Perplexity, 14.7.2025
Kazakh Steppe	2500–3000	ChatGPT, January 2025
	1800	ChatGPT, 8.4.2025
	2600	Meta AI, 8.4.2025
	1000–1200	ChatGPT, 9.4.2025
	2000–2500	Bing AI, 5.7.2025
	ca. 1300–1500	Bing AI, 7.7.2025
Southern Siberia	700–1000	ChatGPT, 9.4.2025
Asian Russia	700–1000	ChatGPT, 9.4.2025
Altai Mountain Country	2500–3000	ChatGPT, January 2025
	ca. 1100–1300	Bing AI, 7.7.2025
Central Asia	700–800	ChatGPT, 9.4.2025
	Ca. 2500–3200 (Kazakhstan 2100, Mongolia 1600, Xinjiang, Inner Mongolia 800, Irano-Turkestanian steppe 1200)	
	Bing AI, 7.7.2025	
Central Asia (Mongolia, Xinjiang, western China)	2500–3000	ChatGPT, January 2025
Mongolia	700–1000	ChatGPT, 9.4.2025
	ca. 2900	Meta AI, 9.4.2025
	ca. 2000	Bing AI, 5.7.2025
China (Inner Mongolia)	700–1000	ChatGPT, 9.4.2025
	ca. 2500 (Desert steppes 1200, True steppes 1800, Meadow steppes 2000)	Bing AI, 7.7.2025
Mongolia and Inner Mongolia	1000–1500	ChatGPT, January 2025
Mongolian-Manchurian steppe	1500–2000	ChatGPT, January 2025
	1000–1200	Bing AI, 7.7.2025

1. Problems and objectives

The Eurasian steppe belt is the world largest steppe region. It stretches 8000 km from the Hungarian basin and the Danube delta in the west to the Amur in the east, and ranges about 800 km to 1000 km from North to South (Lavrenko, Karamysheva, 1993). Steppe exclaves occur in Middle Europe and in northeastern Asia. Investigations into the vascular flora of this huge area have a long history. The steppe flora of Europe, Anatolia and the Asian part of Russia is rather well known ("Flora of USSR" (Komarov, 1934–1964); "Flora Europaea" (Tutin et al., 1964–1980); "Flora of Russia. The European Part and Bordering Regions" (Fedorov, 1988–2007); "Flora of Siberia" (Malyshev, 2000–2008); Peshkova, 2001; Krasnoborov, Artemov, 2012; Sârbu et al., 2013; Namzalov, 2015; Ambarh et al., 2016). The steppe flora of Middle and Central Asia, however, is not yet fully explored. Several recent articles reviewed the history of botanical investigations and floristic works in these regions and brought out major gaps in the floristic information and addressed the limitations of the present knowledge (Du et al., 2020; Li et al., 2020; Wang et al., 2020). Regional plant surveys are still needed, but floristic information on steppe floras of Mongolia and Kazakhstan has much improved in the last years (Kupriyanov, 2020; Baasanmunkh et al., 2022; Alibekov et al., 2025).

Despite the current state of knowledge about the flora of the Eurasian steppes, there is no reliable inventory of the number of species in the steppe belt as a whole and/or in individual regions. Studies on species richness, on the other hand, are very popular. 'Species richness' is defined as the number of species per area (plot, grain) and should not be confused with the total number of species per area ('species inventory' or 'species pool'). Species richness figures are reported mostly for plots from 1 m^2 up to 1 ha (Biurrun et al., 2021), whereas our target area is in the size of hundreds and thousands of square kilometers. A high species richness does not necessarily mean a large regional species pool, and therefore one cannot (or only to a limited extent) infer the size of the species pool from species richness data (and vice versa).

We address the current state of the art and aim to get a realistic estimation of the species pool of higher plants (Pteridophyta, Gymnospermae, Angiospermae) in the Eurasian steppe belt. We searched the literature for figures on species richness and the total number of higher plants in the Eurasian steppe biome. We evaluated the data and emphasized compatibility and discrepancies between the data sets. Significant gaps in knowledge about the steppe species pool were evident. To fill these gaps, we calculated the number of respective steppe species based on relevant floras and recent checklists. Local endemism is particularly significant because it can provide information about effective current and historical factors. The goal of our research is not only an up-to-date recording of the status quo, but also the interpretation of the data against the background of the evolutionary history of the Eurasian steppes.

2. Subdivision of the Eurasian steppe biome

Extensive literature exists on steppe classification systems and nomenclature of steppe formations. Three main classification approaches can be recognized, the physiognomic approach, the dominant species approach, and the floristic approach (Hurka et al., 2019, for a review). The most accepted main division scheme of the Eurasian steppe biome is that of Lavrenko (Lavrenko et al., 1991; Lavrenko, Karamysheva, 1993), which we adopt here. The broad outlines of Lavrenko's steppe classification systems are as follows (Smelansky, Tishkov, 2012).

(1) Latitudinal zoning. In the Eurasian plains, the steppe belt divides into four mostly north to south running latitudinal (zonal) bands reflecting decreasing humidity and changing soil parameters: (a) meadow steppes as a component of the forest steppe – (b) forbs-bunchgrass steppes – (c) dry bunchgrass steppes – (d) desertified (semi-desert steppes) and desert steppes. The two bunchgrass steppes b) and c) are often combined as 'genuine', 'true' or 'typical' steppes. The zonal vegetation pattern can be interrupted or replaced by azonal steppe formations, which are often related to topography and edaphic factors, such as sandy steppe, petrophytic steppe, or halophyte communities.

(2) Altitudinal zoning. All of the latitudinal zones have analogous zones along altitudinal gradients in the mountains, which are classified as (e) mountain steppes. They also include the high mountain cold cryophytic steppes.

(3) Longitudinal zoning. Lavrenko (1969, 1970a, b) divided the Eurasian steppe zone into two meridional subregions: (a) the western Black Sea-Kazakhstan subregion with the east European and west Siberian forest steppes and the Pontic-Kazakh steppes, and (b) eastern Central Asian subregion with the Dauro-Mongolian block and the Manchuro-Northwestern Chinese block. Often, following Schroeder (1998), Lavrenko's western subregion is named the Euro-Siberian steppe, and the eastern

subregion the Mongol-Chinese steppe. The border between the western and eastern subregions runs along the line Yenisei River – Russian Altai – Mongolian Altai along the upper reaches of the Irtysh River.

Sometimes, within the Euro-Siberian steppe region, the Pannonian Steppe is treated as an exclave, separated from the main steppe by the Carpathian Mts. The ‘main steppe’ itself is divided into the Pontic-Caspian Steppe (Western Steppe) and the Kazakh Steppe (Central Steppe), spreading from the Urals to Dzungaria.

The two main subregions, the Euro-Siberian and the Mongol-Chinese steppes, differ in floristic, climatic and edaphic respect. Floristic aspects clearly mirror the subdivision of the steppe belt into a western (Boreal) and an eastern (Ancient Mediterranean) region. Their floras differ notably from one another. The distribution area of many plant species is restricted to only one steppe region. The main differentiating climatic factor is the time of annual rainfall. Maximum precipitation in the Euro-Siberian steppe is in early summer, whereas in the Mongol-Chinese steppe it is in midsummer due to the influence of the eastern Asiatic monsoon. Thus, the western region is rich in spring ephemeroids while late-summer annuals are characteristic for the eastern region. Regarding edaphic aspects, chernozem soils (black earth soils) are the typical zonal soils for the meadow steppe. The more or less continuous forest steppe and black earth steppe belt reaches the Ob, and – interrupted by mountain steppe – the Yenisei. Further east of the Yenisei in the Mongol-Chinese steppe, prevailing soil types are kastanozems, burozems and serozems apart from leptosols in montane areas. Chernozem soils are rare and only locally found, except for the easternmost part of Mongolia and northeastern China. In the Mongol-Chinese steppe, typical steppe and semi-desert and desert steppes prevail over large areas. Meadow steppes are found in a considerable area only in eastern Mongolia and in northeastern China. Desert steppes nearly exclusively occur only in the eastern subregion, and mountain steppes are absent from the western subregion.

The Altai Mountain Country (AMC) is the contact zone between the Euro-Siberian and the Mongol-Chinese steppe subregions. It comprises the mountains of the Altai, southwestern Tuva and main parts of the western Sayan ridges. In the south, the mountains bordering Dzungaria, the Baitak Bogdo and the Adz Bogdo mark the boundary of the AMC area (Kamelin, 2005). The flora of the AMC is very heterogeneous. It comprises species of diverse floras of different biogeographical origin (Boreal Euro-Siberian, contact zone Boreal-Ancient Mediterranean, and Ancient Mediterranean), and environmental differences between the areas of the AMC are tremendous. Taiga prevails in the northeast and forest steppe in the northwest, whereas steppes, semi-deserts and deserts are characteristic for the eastern and southern parts (Kamelin, 2005; Pyak et al., 2008).

3. Species richness in the Eurasian steppe belt

Worldwide, there are numerous publications on species richness for areas (plots, grains) from 1 m^2 up to 1 ha. Very high species richness at any spatial grain is found only in temperate grasslands and in tropical rain forests. Maxima at smaller plot sizes (up to 100 m^2) were from temperate grasslands (e. g. 89 plant species on 1 m^2), and at larger plot sizes from tropical rain forests (e. g. 942 plant species on 1 ha) (Wilson et al., 2012). Meanwhile, a lot of plot-based data of species richness across regions, vegetation types and biomes have become available. Secondary (semi-natural) grasslands are the richest vegetation types with maxima in the temperate mid-latitudes (Biurrun et al., 2021). The highest species richness for vascular plants was recorded in the western part of the Eurasian steppe belt, in the Peri-Carpathian Forest steppe grasslands (110–120 species per 10–16 m^2, Roleček et al., 2025), in the Central Chernozem Steppe Reserve, Kursk Region, Russia (110–130 species in 100 m^2, cited in van der Maarel, Titlyanova, 1989 and Vasilevich, 2009), and in the typical steppes of Ukraine (107 species per 100 m^2, Borovyk et al., 2024). High species richness is also recorded for the steppes of Khakassia, Russia (94 higher plant species on 100 m^2 plots, Polyakova et al., 2016). The emphasis given on ‘richness hotspots’ (Biurrun et al., 2021) on ‘extreme species richness’ (Roleček et al., 2025), on ‘species richness records’ (Borovyk et al., 2024), or even on ‘world records’ (Wilson et al., 2012), however, should not be taken too seriously. Mean values of species richness data and their standard deviations, in our view, are much more meaningful as are the ranges of the data, because they lessen the influence of random variables in species counts and protect against over interpretation. Mean values are more suitable than maximum data to compare number of species between areas and between different steppe types.

We searched the literature for figures on species richness in the Euro-Siberian and in the Mongol-Chinese steppe regions. There are more reports for the Euro-Siberian steppe (Table 2) than for the Mongol-Chinese (Table 3). Data for 1 m^2 plot sizes are predominant for the Mongol-Chinese data set whereas for the Euro-Siberian steppe region, 16, 10 and 100 m^2 plot size data are the majority. Nevertheless, taking all the uncertainties in species counting into account, it would appear that the Euro-Siberian steppe region houses more species per area than the Mongol-Chinese steppe. It is also obvious from both data sets that forest steppes (including the meadow steppes), compared to typical steppes, are species richer, which was to be expected. (There are no mountain steppes in the Euro-Siberian steppe, and semi-desert and desert steppes are rare and not covered by the present Euro-Siberian data set.)

Table 2. Species richness in the Euro-Siberian Steppe. Indicated are recorded numbers, ranges (minimum – maximum) or mean values and standard deviation, if available. n, number of samples

No.	Country (study area)	Forest Steppe, Meadow Steppe	Typical Steppe	References
1	**Czech Republic** (Southwest White Carpathians)	93.8 (n = 20)		Hajek et al (2020) 16 m^2 plots
2	**Romania** (Transylvania, Cluj County)	89 (n = 4)		Hajek et al. (2020) 16 m^2 plots
3	**Romania** (Transylvania, Covasna County)	93 (n = 1)		Hajek et al. (2020) 16 m^2 plots
4	**Ukraine** (West Ukraine, Chernivtsi Oblast)	108 (n = 3)		Hajek et al. (2020) 16 m^2 plots
5	**Ukraine** (West Ukraine, Iwano-Frankivsk Oblast)	93 (n = 1)		Hajek et al. (2020) 16 m^2 plots
6	**Hungary** (North Hungary, Mátra Mountain Range)	90 (n = 2)		Hajek et al. (2020) 16 m^2 plots
7	**Peri-Carpathian** (Total data set No. 1–6)	95.3 (n = 31)		Hajek et al. (2020) 16 m^2 plots
8	**Czech Republic** (White Carpathians)	70 – 133 106.6 ± 8.4 (n = 35)		Merunková et al. (2012) 100 m^2 plots
9	**Western Carpathians** (Czech Rep., Slovakia, Poland)	13 – 105 36 (n = 3868)		Divíšek et al. (2020) Plot sizes 4 m^2 – 25 m^2
10	**Romania** (Transylvania)	57.2 ± 17.4 (10 m^2 plots; n = 40) 83.3 ± 24.2 (100 m^2 plots; n = 20)		Turtureanu et al. (2014) 10 m^2 and 100 m^2 plots
11	**Ukraine** (Southwestern Ukraine, Podolian Upland)	37.2 (10 m^2 plots; n = 226) 66.8 (100 m^2 plots; n = 21)		Kuzemko et al. (2016) 10 m^2 and 100 m^2 plots
12	**Ukraine** (Southern Ukraine, steppe zone with 3 subzones)		30.1 (n = 455) 28.0 (n = 240) 26.9 (n = 569)	Borovyk et al. (2024) 10 m^2 plots
13	**Bulgaria and Romania** Lowlands and mountains south of the Danube	52.2 ± 17.6 (n = 156) (Total data set)		Palpurina et al. (2015) 100 m^2 plots

Ending Table 2

No.	Country (study area)	Forest Steppe, Meadow Steppe	Typical Steppe	References
14	**Bulgaria and Rumania** Lowlands south of the Danube	70.7 ± 13.3 (n = 41) (Submediterranean areas)	35.0 ± 12.4 (n = 31) 38.6 ± 8.3 (n = 13) 47.8 ± 10.3 (n = 50) (Subcontinental areas)	Palpurina et al. (2015) 100 m^2 plots
15	**Bulgaria and Rumania** Mountains south of the Danube	60.1 ± 9.8 (n = 21) (Mountains and foothills)		Palpurina et al. (2015) 100 m^2 plots
16	**Russia** (Asian part; Rep. Khakassia)	43.9 ± 10.8 (10 m^2 plots; n = 132) 65.3 ± 14.8 (100 m^2 plots; n = 39)		Polyakova et al. (2016) 10 m^2 and 100 m^2 plots

Table 3. Species richness in the Mongol-Chinese Steppe

No.	Country (study area)	Mountain Steppe	Meadow Steppe	Typical Steppe	Desertified and Desert Steppe	Reference
1	**Mongolia** (West to East, Mongolian Altai to Greater Khingan)	25 – 40	25 – 55	15 – 30	6–15	Tuvshintogtokh (2014) (100 m^2 plots, number of plots not indicated)
2	**Mongolia** (Khentei and Middle Khalkha regions)*		26.9 ± 0.41 (n = 108)	17.1 ± 0.30 (n = 108)	9.09 ± 0.2 (n = 108)	Liu et al. (2013) (1 m^2 plots)
3	**China** (Eastern part of Inner Mongolian Plateau)		10 – 35 19.7 ± 4.9 (n = 53)	5 – 25 11.6 ± 3.7 (n = 84)	4 – 23 10.4 ± 2.7 (n = 70)	Ma, Ren (2007) (1 m^2 plots)
4	**China** (Northeastern Inner Mongolia)		5 – 35	5 – 25		Wang et al. (2024) (31 m^2 plots in 235 sample sites)
5	**China** (Southeastern Inner Mongolia)		24 – 55 34.2 (n = 15)	8 – 41 (n = 53)		Liu, Cui (2009) (plot sizes not indicated)
6	**China** (Ningxia, Mu Us Sand land)				5 – 18	Luo et al. (2016) (4200 m × 200 m plots with 397 nebkhas = vegetated dunes)
7	**China** (Eastern Inner Mongolia)				7 – 9 (n = 40)	Li et al. (2022) (1 m^2 plots)

Ending Table 3

No.	Country (study area)	Mountain Steppe	Meadow Steppe	Typical Steppe	Desertified and Desert Steppe	Reference
8	**China** (Northeastern Inner Mongolia)		15 – 30 (n = 12) 3 – 7 (n = 360)			Wang et al. (2015) (50 m × 50 m plots and 1 m^2 plots)
9	**China** (Northeastern Inner Mongolia)		19 ± 3 24 ± 1 31 ± 2	8 ± 1 9 ± 1 9 ± 2		Liu et al. (2022) (1 m^2 plots, n = 3 per site)

Note: *, Phytogeographical Regions after Grubov (1982). Numbers in the Steppe columns indicate Range (min. – max.) and/or Mean ± Standard Deviation; n, number of samples.

4. Species inventories of higher plants in the Euro-Siberian steppe

Many data on species richness are available but a reliable inventory of the total vascular species pool of the Eurasian steppe or main parts of it is missing. To improve this situation, we searched the floristic literature for species' habitat descriptions, and divided the species occurrences up into two categories, 'steppe' and 'non-steppe' plants. Assignment of a species to one of the two categories, 'steppe' and 'non-steppe', is not always unambiguous, and we have adopted a rather generous approach in favor of the 'steppe' category. In terms of the number of steppe plants, a high level of reliability is achieved by this approach.

4a. Number of higher plants in the Kazakh steppe region

Surprisingly, data on Kazakhstan are nearly missing despite the fact, that the Kazakh steppe is one of the largest dry steppe regions worldwide, where the entire spectrum of zonal steppe types is observed. We tried to fill this gap.

Kazakhstan has an area of ca. 2.75 million km^2 and is the ninth largest country in the world. It stretches about 3000 km from the Caspian Sea and the Volga plains in the west to the Altai mountains in the east, and about 1700 km from the foothills of the Tien Shan in the south and southeast to the West Siberian lowland in the north. In the western and northern parts, 60 % of the total territory are composed of plains, and in its central part the plains alternate with hills and low mountains ('melkosopochnik', 30 % of the territory). 10 % of the country's territory is covered by mountain areas, the Altai and Saur – Tarbagatai in the northeast and the northern and western Tien Shan mountain systems in the south (Rachkovskaya, Bragina, 2012).

Phytogeographically, Kazakhstan is divided into two main zonal regions, the Eurasian steppe zone, which is in our focus, with the cold-temperate and temperate regions of northern Kazakhstan (Black Sea – Kazakhstan steppe subzone), and the Sahara-Gobian desert zone with the warm regions with a Mediterranean-like type of climate in the southern part of Kazakhstan (Irano-Turanian subzone). The demarcation line runs approximately along 48°N latitude (Rachkovskaya, Bragina, 2012). Following Takhtajan (1986), the northern zone belongs to the Western Siberian Province of the Boreal Subkingdom, and the southern zone to the Turanian or Aralo-Caspian Province of the Tethyan Subkingdom. Semideserts are a transition zone between steppes and deserts stretching from the banks of the river Zhaiykh (Oral) to the Altai Mountains. Pavlov (1956) divided the flora of Kazakhstan into 29 floristic divisions. In the following, if appropriate, we refer to these floristic divisions. A significant part of the natural steppes in the northern Kazakh zonal steppe region has been destroyed by plowing, and in the southern part of the steppe zone, large parts are occupied by pastures often suffering from overgrazing (see for instance, Rachkovskaya, Bragina, 2012; Kamp et al., 2016; Hurka et al., 2019).

The remarkable diversity of natural conditions in Kazakhstan contributes to the exceptional richness of its flora, its notable originality and a significant number of endemic plant species in Kazakhstan. According to the latest inventory, 5658 vascular plant species, representing 159 families and 1067 genera, occur in the country (Abdulina, 1999). This checklist includes all vascular plants reported for the territory of Kazakhstan up to the end of 1998 and is mainly based on the "Flora of Kazakhstan" (Pavlov, 1956–1966) and thus, may not be up to date. Many reasons, such as new findings, significant changes in nomenclature and taxonomic reassessments, including synonymy issues, may limit the actuality of this checklist, but up to now, it is the only complete checklist of vascular plants for Kazakhstan. Very recently, however, floristic information and biogeographical knowledge of Kazakhstan increased considerably. Of special relevance for our aims are the publications by Kupriyanov (2020) and Alibekov et al. (2025). (i) Kupriyanov (2020) compiled an outline of the flora of the Kazakh Uplands covering the floristic regions Ulutau, Western Upland, Eastern Upland, and Karkaraly, and documented 2105 vascular plants. 351 of them were new findings for the region. This checklist gives details about habitats but the full number of steppe taxa cannot be gathered from this list alone. (ii) Alibekov et al. (2025) presented a checklist of vascular plants for the Akmola Oblast. This Oblast is situated in the central northern Kazakhstan steppe zone and represents quite a remarkable diversity of steppe types. It covers parts of the floristic regions Irtysh and Kokchatev in the north, Western Upland in the south, and Turgay in the west. Alibekov et al. (2025) documented 1164 species of vascular plants in the Akmola Oblast including 112 introduced and naturalized species. Seven species were new records for Akmola. For each of the species the authors report on life form and ecology (basically hygrophyte, mesophyte, xerophyte) but the specific habitat cannot be deduced from this information.

To identify the steppe taxa from the Alibekov et al. (2025) checklist, we mainly consulted following floras: “Flora of USSR” (Komarov, 1934–1964); “Flora of Russia. European Part and Bordering Regions” (Fedorov, 1988–2007); “Flora of Siberia” (Malyshev, 2000–2008); “Key to the Vascular Plants of Mongolia” (1982); “Flora of China” (Wu et al., 1994–2013). All of them indicate habitat occurrences for each species. We thus identified 352 steppe taxa for the Akmola Oblast (out of the 1164 listed). From the 2105 taxa listed by Kupriyanov (2020) for the Kazakh Uplands, we identified 653 steppe taxa based on the habitat description given by Kupriyanov himself and additionally based on the floras cited above. Whereas the central Kazakh Uplands are fully covered by Kupriyanov, the Akmola Oblast covers only part of the total planar steppe biome and may not be representative of the whole Kazakh lowland steppe. There is, however, a survey of steppe species within the framework of phytosociological studies covering lowland zonal steppe communities. The most important study is the publication by Isachenko and Rachkovskaya from 1961 (cited in Korolyuk, 2017). Data were ascertained from 199 relevés located in the oblasts Kostany, Akmola including Kokchatev, North Kazakhstan and Pavlodar. The field studies were done from May to September during the years 1954–1958. At that time, the relevant Flora was Komarov’s “Flora of USSR” (Komarov, 1934–1964). Pavlov’s “Flora of Kazakhstan” started not until 1956. We checked the plant lists of Isachenko and Rachkovskaya (as presented in Korolyuk, 2017) and recorded 255 species. Together with the steppe species characteristic for the forest steppe, lowland steppe, and Altai and Tarbagatai steppes mentioned by Rachkovskaya and Bragina (2012), the number of steppe plants by these two literature sources sums up to 290 (Table 4). 198 of them are shared with the Akmola steppe taxa, 47 with the Kazakh Upland taxa, and 45 taxa are unique. Akmola (352) and Kazakh Upland (653) share 215 taxa. Double and triple references are adjusted as outlined in Table 4, and the number of steppe taxa sums up 788. Taking possible errors as discussed below and missing data into account, we tentatively estimate the number of steppe taxa in the north Kazakhstan Eurasian steppe zone at 750 – 788 – 850 (Table 4).

4b. Number of higher plants in the Euro-Siberian steppe

There are some literature reports on the number of higher plants in the Euro-Siberian steppe. They cover the Western Carpathians, and parts of Romania, Ukraine, European Russia and Turkey. We added new data for Ukraine, European Russia, and Kazakhstan (Table 5).

5. Species inventory of higher plants in the Mongol-Chinese steppe biome

Mongolia can stand in place of the Mongol-Chinese steppe in total due to its geographical situation and its size, i. e. 1.6 million square kilometers which is roughly equivalent to the size of western and central Europe. Mongolia embraces the largest area of intact steppe in the world. 66 % of the Mongolian territory are covered by steppe vegetation including nearly all steppe classification types: High-cold Mountain steppe (2.6 % of the Mongolian territory), Mountain steppe (13 %), Meadow steppe (3 %), True steppe (22 %), Desertified steppe (5.4 %), and Desert steppe (20 %) (Tuvshintogtokh, 2014). Floristic information on Mongolia is advanced. Grubov (1982) reported 2239 vascular plants, and Gubanov (1996) published a checklist of 2823 higher plants. Urgamal et al. (2014) updated the checklist

Table 4. Estimation of the number of steppe plants in Kazakhstan

No.	Literature source	Number of steppe taxa (explaining remarks)	Geographical region (Steppe classification)
1	Isachenko, Rachkovskaya (1961)	255 (extracted from syntaxonomic tables presented in Korolyuk, 2017)	Kostany, Akmola, North Kazakhstan, Pavlodar oblasts (mainly lowland zonal steppe biomes)
2	Rachkovskaya, Bragina (2012)	115 (characteristic species from all steppe types)	Eurasian steppe zone of northern Kazakhstan (forest steppe, lowland steppes, Melkosopochnik steppes, Altai and Tarbagatai steppes)
3	No. 1 and No. 2 summed up and cleared from double references	290 (198 are shared with No. 4, 47 with No. 5 only, 45 are single references)	Eurasian steppe zone of northern Kazakhstan (forest steppe, lowland steppes, Melkosopochnik steppes, Altai and Tarbagatai steppes)
4	Alibekov et al. (2025)	352 (out of 1164)	Akmola Oblast (steppes of the floristic regions Irtysh, Kokchatev, Western Uplands and Turgay)
5	Kupriyanov (2020)	653 (out of 2105)	Central Kazakhstan Uphill region (droughty forb-feather grass steppes; dry steppes, deserted steppes; shrub steppes)
6	No. 4 and No. 5 summed up and cleared from double references	790 (352 plus 653 minus 215)	Akmola Oblast and Central Uphill region (lowland steppes, Melkosopochnik steppes)
7	No. 3 and No. 6 summed up and cleared from double references plus single references from No. 3	788 (790 minus 47 plus 45)	Eurasian steppe zone of northern Kazakhstan (forest steppe, lowland steppes, Melkosopochnik steppes, Altai and Tarbagatai steppes)
8	Estimation adjusted to possible errors and missing data as e. g. regional underrepresentation	750–850	Eurasian steppe zone of northern Kazakhstan (West Siberian forest steppe, Trans Volga – Kazakhstanian steppe, South Altai mountain steppe)

and reported 3127 taxa comprising native and non-native taxa. The latest revised checklist is from Baasanmunkh et al. (2022). The authors reviewed the species status and made critical changes by adding, synonymizing, and excluding non-native taxa compared to Urgamal et al. (2014), and ended up with 3041 native vascular plant taxa (2835 species and 206 infraspecific taxa).

The checklist of Baasanmunkh et al. (2022) serves as a reference for our species inventory of the steppe biome. Occurrence of each taxon in Grubov's 16 phytogeographic regions is specified by Baasanmunkh et al., but, in contrast to Grubov (1982), Baasanmunkh et al. (2022) do not report on the representative habitats of the taxa. Thus, the number of steppe and non-steppe taxa cannot be seen from this list. We, therefore, checked for each of the 3041 taxa the site types by intensive literature surveys and split them up into two categories, 'steppe' and 'non-steppe' taxa. Two thousand eighty-two taxa of the Baasanmunkh et al. list are also covered by Grubov, who characterized the habitats. For the remaining 3041 – 2082 = 959 taxa, however, we had to go through other literature sources ("Flora of USSR" (Komarov, 1934–1964); "Flora of China" (Wu et al., 1994–2013); "Flora of Siberia" (Malyshev, 2000–2008); "Flora Altaica" (2005); Krasnoborov, Artemov, 2012). Our search for Mongolian 'steppe' taxa revealed 657 steppe taxa based on Grubov and additional 191 steppe taxa based on the other literature cited above, summing up to 848 steppe taxa in Mongolia, which is within the magnitude/size of order reported for China (Table 6). For 72 taxa out of the 3041, we could not find habitat descriptions. Tuvshintogtokh (2014) reported 614 species for the Mongolian steppe biome, probably relying on Grubov (1982). Our estimation is partly also based on Grubov, and this 'Grubov-part' resulted in 657

Table 5. Number of vascular steppe plants in the Euro-Siberian steppe

No.	Country (Geographical Region)	Steppe classification	Reported number of steppe plant species	Reference
1	**Czechia, Slovakia, Poland** (Western Carpathians and Peri-Carpathians)	Steppe and steppe-like grasslands	1759 (4–25 m^2 plot data, n = 3868)	Divíšek et al. (2020)
2	**Romania** (Cluj County, Botanical Reserve 'Cluj Hayfields', Fanatele Clujului)	Meadow steppe	'More than 450'	Cluj Tourism Homepage https://clujtourism.ro>de>naturschutzgebiete (In German. Retrieved January 2025)
3	**Ukraine** (Central Podolia, Podolian Upland)	'Dry and steppic grassland', Forest steppe zone	581 (10 m^2 plot data, n = 226)	Kuzemko et al. (2016)
4	**Ukraine** (Kherson Oblast, Askania Nova Reserve)	Meadow steppe	200 – **216** – 250 (out of 521)	Calculations by the authors based on Shapoval (2012)
5	**Russia** (Kursk Region)	Meadow steppe	200 – **211** – 250 (out of 1409)	Calculations by the authors based on Polujanov (2005)
6	**Russia** (Belgorod Region, Belogorye Nature Reserve, Ostrasevy sector)	Meadow steppe, Gullies and ravines	100 – **146** – 200 (out of 585)	Zolotukhin, Reshetnikova (2023)
7	**Russia** (Astrakhan Region, Bogdo-Baskunchak Nature Reserve)		100 – **142** – 200 (out of 507)	Calculations by the authors based on Laktionov et al. (2008)
8	**Russia** (Orenburg Region, Orenburg Steppe Reserve	*Stipa* steppes	250 – **282** – 350 (out of 574)	Calculations by the authors based on Rjabinina (2000)

registered steppe taxa, a plus of ca. 7 % compared with Tuvshintogtokh (2014, Supplement, Table 2). Tuvshintogtokh's records of the total number of steppe taxa mirrors the state of floristic knowledge ca. 10 years ago. Based on the latest information on the total number of species, we recorded 848 steppe plant taxa (2014, Supplement, Table 2), an increase of ca. 230 taxa compared to Tuvshintogtokh. Taking possible errors into account, we think it is realistic to estimate the number of steppe taxa in Mongolia within the range of 800 – 848 – 900.

We summarize present knowledge about the number of species in the Mongol-Chinese steppes in Table 6.

6. Possible sources of error, error analysis

Reported data on species numbers of steppe taxa are primarily related to regional biogeographical histories and affiliation to floristic regions. But the number of recorded species in a given site, whether it concerns 'species richness' or the 'total number of species', is highly influenced by 'objective' and 'subjective' parameters. These include: (1) In general, reported data on species numbers depend on the level of exploration of a region and on sampling strategy. The number of species per area increases with exploratory plot sizes but only up to a certain saturation level, which inter alia depends on the local overall species pool. Data may also be influenced by differences between estimates of individual observers. – (2) Habitat site conditions strongly influence the number of species per area, e. g. relief, soil properties, microclimate conditions like precipitation and temperature, water availability, and heat load. – (3) Natural disturbances such as wild fires and herbivory as well as vegetation successional stages are modifying factors. – (4) Recorded species numbers also depend on the time of data collection. Differences in the composition of species may be explained both, by real changes in the flora and by year-to-year dynamics in the abundance of species. – (5) Human impact does exert great influence on species numbers, e. g. by agricultural management practices such as mowing or pasturing which may

Table 6. Number of vascular plant species in the Mongol-Chinese steppe regions

No.	Country (Geographical Region)	Steppe Classification	Reported number of species	Reference
1	**Russia** (Tuva and southeastern Altai)	Mountain steppe, True steppe, Desertified steppe	671	Namzalov (2015)
2	**Russia** (Rep. Altai, Krasnojarski Krai, Rep. Tuva, Rep. Buryatia)	Mountain steppe	1014	Peshkova (2001)
3	**Mongolia** (Khovd, Mongolian Altai, Khangai)*	High-cold Mountain steppe (2.6 % of Mongolian territory)	89	Tuvshintogtokh (2014)
4	**Mongolia** (Khovd, Mongolian Altai, Gobi Altai, Khangai, Khentei, Mongolian Dauria, East Mongolia, Foothills of Great Khingan)*	Mountain steppe (13 % of Mongolian territory)	260	Tuvshintogtokh (2014)
5	**Mongolia** (Khangai, Mongolian Dauria, Foothills of Great Khingan)*	Meadow steppe (3% of Mongolian territory)	307	Tuvshintogtokh (2014)
6	**Mongolia** (Mongolian Altai, Depression of Great Lakes, Valley of Lakes, Middle Khalkh, East Mongolia, Mongolian Dauria)*	True steppe (22 % of Mongolian territory)	250	Tuvshintogtokh (2014)
7	**Mongolia** (Depression of Great Lakes, Valley of Lakes, East Gobi, Gobi Altai)*	Desertified steppe (5.4 % of Mongolian territory)	157	Tuvshintogtokh (2014)
8	**Mongolia** (Dzungarian Gobi, Depression of Great Lakes, Valley of Lakes, Gobi Altai, Alashan Gobi, East Gobi)*	Desert steppe (20 % of Mongolian territory)	142	Tuvshintogtokh (2014)
9	**Mongolia** (Mongolian Altai in the West to Greater Khingan Range in the East)	All Steppe types (66 % of Mongolian territory)	614	Tuvshintogtokh (2014)
10	**Mongolia** (Mongolian Altai in the West to Greater Khingan Range in the East)	All Steppe types	800 – **848** – 900 (out of 3041)	Calculations by the authors based on Baasanmunkh et al. (2022)
11	**China** (Nature Reserves in Inner Mongolia, Gansu, Ningxia, Xinjiang)	Mountain steppe, True steppe, Desertified and Desert steppe	200 – 933 564 ± 217 (n = 18)	Zhao, Fang (2006), Appendix 1
12	**China** (Nature Reserves in Gansu, Ningxia, Xinjiang)	Mountain steppe	670 – 933 795 ± 100 (n = 6)	Zhao, Fang (2006), Appendix 1
13	**China** (Nature Reserves in Inner Mongolia, Gansu, Ningxia)	True steppe, Desertified and Desert steppes	200 – 690 449 ± 157 (n = 12)	Zhao, Fang (2006), Appendix 1
14	**China** (Hulun Buir Steppe, foothills of western Greater Khingan Mountains)	Meadow steppe, True steppe, Desertified and Desert steppe	765	Zhu Y. et al. (2019)

Ending Table 6

No.	Country (Geographical Region)	Steppe Classification	Reported number of species	Reference
15	**China** (Inner Mongolian Plateau, Loess Plateau, Xinjiang Mountains, Tibetan Plateau)	*Stipa* steppes in total	893 (1 m^2 plot data, n = 1306)	Liu C. et al. (2022) Liu C. et al. (2022)
16	**China** (northeastern Inner Mongolia, Dauria)	Meadow and True steppe	411 (1 m^2 plots, n = 188)	Liu C. et al. (2022)
17	**China** (Inner Mongolian Plateau)	True steppe, Desertified and Desert steppes	510 (1 m^2 plots, n = 439)	Liu C. et al. (2022)
18	**China** (Loess Plateau)	True steppe, Desertified and Desert steppes	303 (1 m^2 plots, n = 231)	Liu C. et al. (2022)
19	**China** (Xinjiang)	Mountain steppe	511 (1 m^2 plots, n = 276)	Liu C. et al. (2022)
20	**China** (Tibetan Plateau)	Mountain steppe, High-cold steppe	251 (1 m^2 plots, n = 172)	Liu C. et al. (2022)

cause grazing pressure. Disturbed habitats are often colonized by weedy species, and steppe degradation and colonization by neophytes are presently often regarded as main drivers of species composition changes. Zolotukhin and Reshetnikova (2023), for instance, demonstrated a significant change in species numbers and species composition in the Belogorye State Nature Reserve (Russia) since 2002, whereby naturalized alien plants play a most significant role and are thought to be the main danger for the natural communities of the forest-steppe zone. – (6) The ecological amplitude of many species is rather high indicated by assigning different habitat types to the same species. In these cases, the decision whether a taxon is a representative or just an 'occasional' steppe plant is often difficult and subjective. For instance, should plants with habitat descriptions like 'alkaline areas of steppe', 'sayrs in steppe' or 'bottom of sayrs', 'steppe debries', 'chee-grass stands' or 'steppified meadows' and 'meadowy steppes' classified as 'non-steppe' or 'steppe' plants? – (7) Should 'weedy' species on disturbed steppe habitats be regarded as 'non-steppe' or as 'steppe' species? – (8) The number of species listed depends heavily on the authors' species concept, e.g. 'lumpers' versus 'splitters'. – (9) Finally, local botanists tend to overestimate the number of local endemics.

Whereas no. (1) to (5) are rather 'objective' parameters, (6) to (9) strongly depend on the attitude of the person dealing with the issue. It follows that published data on steppe species numbers are not fixed values but are time-, environment- and person-dependent and consequently quite flawed. It is advisable to treat the recorded numbers as estimated values and to indicate 'confidence intervals' by fluctuating ranges. The validity of the estimated values depends on the size of the fluctuating ranges. The greater the ranges, the greater the probability space for the likely value but the less meaningful is its significance. One has to find a balanced decision, which, after all, will be subjective.

7. Species inventory of higher plants in the entire Eurasian steppe belt

Taking the possible sources of error discussed above into consideration, we summarize the presently most reliable data about the number of higher plants in the Eurasian steppe biome in Table 7. Data on the Western Carpathians (Divisek et al., 2020: Tab. 4, No. 1) are not included. The same applies to the Central Podolian Upland, where the meaning of 'dry and steppic grassland' remains unclear (Kuzemko et al., 2016; Table 4, No. 3). We also omitted the vague data on the Botanical Reserve 'Cluj Hayfields'

Table 7. Summary of species inventory of the Eurasian steppe, most reliable data are shown

No.	Steppe subregion Geographical region	Numbers of steppe species	Steppe classification	Reference to Tables
	Euro-Siberian Steppe			
1	**Ukraine** (Kherson Oblast, Askania Nova Reserve)	200–250	Meadow steppe	Tab. 4, No. 4
2	**Russia** (Kursk Region)	200–250	Meadow steppe	Tab. 4, No. 5
3	**Russia** (Belgorod Region, Belogorye Nature Reserve, Ostrasevy sector)	100–200	Meadow steppe, Gullies and ravines	Tab. 4, No. 6
4	**Russia** (Astrakhan Region, Bogdo-Baskunchak Nature Reserve)	100–200	True steppe, Desertified steppe	Tab. 4, No. 7
5	**Russia** (Orenburg Steppe Reserve, Orenburg Region)	250–350	*Stipa* steppes	Tab. 4, No. 8
6	**Kazakhstan** (Kostany, North Kazakhstan, Akmola, Karagandy, Pavlodar, East Kazakhstan)	750–850	West Siberian Forest steppe, Trans Volga-Kazakh steppe, South Altai Mountain steppe	Tab. 4, No. 10
7	**Turkey** (Nature Reserves and Nat. Parks, Central Anatolian plateau, Eastern Anatolian highlands, Southeastern Anatolian plateau)	1027	Forest steppe, True steppe, Desertified steppe	Tab. 4, No. 11
	Altai Mountain Country			
8	**Russia** (Tuva and southeastern Altai)	671	Mountain steppe, True steppe, Desertified steppe	Tab. 5, No. 1
9	**Russia** (Rep. Altai, Krasnojarsk Territory, Rep. Tuva, Rep. Buryatia)	1014	Mountain steppe	Tab. 5, No. 2
	Mongol-Chinese Steppe			
10	**Mongolia** (Mongolian Altai in the west to Great Khingan in the east)	800–900	Mountain steppes, Forest steppe, Meadow steppe, True steppe, Desertified and Desert steppe	Tab. 5, No. 10
11	**China** (Steppe Nature Reserves in Inner Mongolia, Gansu, Ningxia, Xinjiang)	350–850	Mountain steppe, True steppe, Desertified and Desert steppe	Tab. 5, No. 11
12	**China** (Hulun Buir Steppe, western foothills of Greater Khingan Mts.)	765	Meadow steppe, True steppe, Desertified and Desert steppe	Tab. 5, No. 14
13	**China** (Inner Mongolian Plateau, Loess Plateau, Xinjiang Mts., Tibetan Plateau)	893	*Stipa* steppes	Tab. 5, No. 15

(Romania; Table 4, No. 2). The number of 1759 species indicated by Divíšek et al. (2020) is related to the vegetation class Festuco-Brometea. Since this vegetation unit also includes non-steppe species, this number cannot be taken as an appropriate estimate for the pool of steppe species. Furthermore, the data of Divíšek et al. (2020) is based on species richness data ("Number of vascular species at individual sites across the study area"). It is unclear whether this number has been adjusted for multiple nominations or not. Given the Festuco-Brometea numbers for the Balkans (ca. 1300 species, Aćić et al., 2015) and North Caucasus (365, Vynokurov et al., 2021), we assume that the number includes multiple entries. We therefore omitted the numerical data from Divíšek et al. (2020).

An unexpected result we found is the low number of higher plants throughout the Eurasian steppe biome, below 500 for the Pontic steppe regions (Table 7, No. 1–5), and between 500 and 1000 for the steppes of Kazakhstan, Turkey, the Altai Mountain Country, Mongolia and China (Table 7, No. 6–13). It would appear that the number of higher plants declines from east to west. The species pool of the Pontic steppe appears to be significantly smaller.

The reasons for this may be historical (see below). Actually, one would expect a higher number of species, since the Pontic Steppe is primarily located in the forest-steppe zone, and meadow steppes, as a component of the forest-steppe, are, as a general rule, species-richer than the other steppe types.

8. Regional plant endemism in the Eurasian steppe regions

Our data provide a unique opportunity to determine and compare the rates of endemism, i. e. the rate of species unique to a specific geographic area. Such a compilation has not yet been made. Studying the rate of endemism can help to understand evolutionary and biogeographical processes. It can provide clues about how changes in the environment influence speciation and how isolation and historical events shape biodiversity patterns over time.

Before going into detail, a few general remarks first. (i) Quantitative statements about endemism are strongly influenced by the applied species concept. The number of endemics is much higher with a 'splitter' approach than is the case with a 'lumper' approach. (ii) Regional endemism may be quantified by the absolute number of endemic taxa and/or by the ratio of endemic taxa to the total number of taxa. A high percentage may result from either high number of endemic species or low total species numbers. (iii) Great care must be taken when comparing endemism rates of regions with areas of varying sizes (see Bruchmann, 2011). Furthermore, the meaning of the terms 'endemic' and 'subendemic' is sometimes not clearly distinguished. One must be aware of these uncertainties.

8a. Europe

The most comprehensive study on plant endemism in Europe is from Bruchmann (2011), on which we rely. Based on the database EvaplantE (Endemic vascular plants in Europe) Bruchmann (2011) distinguished eight habitat categories: rocky habitats and screes, grassland ecosystems, scrubs and heaths, forest, coastal and saline habitats, arable land and other man-made habitats, inland water bodies, and mires. Steppe habitats are not shown separately but are included in the grassland ecosystems. The reported numbers of local endemics per region and grassland habitat are 2 (out of 2411) for Hungary; 25 (out of 3580) for Bulgaria; 9 (out of 3400) for Romania; 5 (out of at least 3000) for the former Soviet Union south-western division, which includes the Ukraine; and 4 (out of at least 3000) for former Soviet Union south-eastern division (Lower Don, Lower Volga, Transvolga, European part of Kazakhstan). The endemism ratios in all these regions are less than 0.01 % for the grassland ecosystems and – since steppes are included in the grasslands – even less for the steppe habitats. The proportion of endemic species in the Pannonian and Pontic-Caspian steppes is extremely low (Table 8).

8b. Kazakhstan

Various sources estimated the number of endemic species in Kazakhstan between 700–800 species. However, a rigorous revision revealed only 451 endemic vascular plant taxa (species or subspecies belonging to 139 genera and 34 families) for Kazakhstan (Kubentayev et al., 2024), which account for ca. 8 % of the total number of vascular plants (5658 as listed by Abdulina, 1999). The largest number of endemic taxa is concentrated in mountainous areas, specifically in the southern and south-eastern parts of Kazakhstan. The northern lowland steppe areas contain only 1–2 % of the endemic plants, the northern mountain areas 3–6 %, but the southern mountains 10–27 %. The share of endemic taxa in the total number of species is insignificant for the Eurasian lowland steppe areas (ca. 0.2 %), few for the northern mountain areas, which also belong to the Eurasian steppe belt (ca. 0.6 %), and ca. 1–2.5 % for the southern mountains (Irano-Turanian region). Endemism rate in the Kazakh steppes is very low, less than one percent.

8c. Mongolia

Baasanmunkh et al. (2022) listed 102 endemic taxa for Mongolia (95 species, 5 subspecies, and 2 interspecies hybrids), and 275 taxa are subendemic. The Mongolian Altai and the Khangai regions alone harbor ca. 70 % of the total endemic and subendemic flora. The share of endemic taxa in the total number of species (as of 2021, approximately 3200 vascular plant species) is very low. The strictly endemic flora (102 taxa) account for only 0.03 % of Mongolia's total higher plant flora. Out of the 848 steppe taxa estimated by us, 25 are endemic to Mongolia (ca. 0.01 %), and 62 (ca. 0.02 %) are subendemic. It is obvious that the degree of endemism in the Mongolian steppe relative to the total number is very low, less than 0.05 %.

8d. Anatolia

The endemism rate of the Turkish native vascular plant flora is generally very high and amounts to ca. 30 % (3035 species out of 9753; Ambarh et al., 2016), which is unique for the whole western Irano-Turanian Region (sensu Takhtajan, 1986). Many of these endemics occur in the Anatolian steppes, which may explain the rather high number of 1027 steppe species reported for the Anatolian steppes (Ambarh et al., 2016). Characteristic of the Anatolian steppes are various types of grass steppes (including typical *Stipa* steppes) and *Artemisia* tragacanthic (thorn-cushion) steppes with dwarf, spiny, cushion like shrublets.

Anatolia represents the evolutionary and main center of diversity for many Irano-Turanian genera, especially cushion-forming species, whose distribution extends eastwards to Mongolia and Afghanistan, such as *Astragalus*, *Verbascum*, *Acantholimon*, *Centaurea* s. l., *Cousinia* and others. Other genera with a high number of endemic species are, e. g. *Achillea*, *Aethionema*, *Onosma*, *Salvia*, *Silene*, and *Thymus* (Kürschner, Parolly, 2012). Unfortunately, there are no estimates of the endemic rate for the Anatolian steppes as a whole. However, endemism in the Anatolian steppes apparently is very high. Ambarh et al. (2016) quote literature with information on gypseous steppes of Sivas (36 % endemism rate) and saline steppes reach an endemism rate of 22 %.

8e. Altai Mountain Country

In contrast to the Anatolian mountains, mountain formation in the AMC is rather old and began in the Triassic period, more than 200 million years ago. Orogenetic events have occurred several times creating uplifted surfaces which have subsequently become dissected by erosion processes and were transformed into peneplains. Tectonic activities especially since the mid-Tertiary period, led to fragmentation of the peneplains, and some parts have been uplifted or downthrust and became high plateaus or large depressions. The modern relief of the AMC is a result of such block movements (Pyak et al., 2008). Climate of the AMC is strongly continental but the complicated relief modifies climatic conditions in different parts considerably. This is clearly mirrored in the vegetation cover. Forest, meadow and forest-steppe prevail in the humid north-western sector ("Forest sector"), and in the rain shadow of the highly elevated plains dry steppes, semi-desert and desert steppes and deserts are characteristic for the south-eastern sector ("Forestless sector") (Kamelin, 2005). In the light of the geological history of the AMC, the climate differences and the flora as a contact flora of Boreal and Irano-Turanian floristic regions, it is not surprising that the number of endemic vascular plants is rather high. Pyak et al. (2008) estimated ca. 2800 higher plant species and subspecies for the AMC. (The area of the AMC in Pyak et al. (2008) is smaller than in Kamelin (2005), as the border lines are different to the south and east.) 182 species are

Table 8. Vascular plant endemism in Eurasian steppe regions

No.	Geographic Steppe region	Endemic rate (%)	Reference
1	Eastern Europe	< 0.01	Based on Bruchmann (2011); see Chap. 8a
2	Kazakhstan	< 0.08	Calculations by the authors based on references cited in Chap. 8b
3	Mongolia	< 0.05	Calculations by the authors based on Baasanmunkh et al. (2021); see Chap. 8c
4	Anatolia	> 20.00	Based on Ambarh et al. (2016); see Chap. 8d
5	Altai Mountain Country	ca. 1.5	Based on Pyak et al. (2008); see Chap. 8e

listed as endemic and 106 species as subendemic, together 288 taxa. 42 taxa are regarded as palaeo-endemic and 246 taxa as neo-endemic. Endemism rate for the endemic and subendemic together thus is ca. 10 % relative to the total number of species, and 6.5 % for the endemic species only. From the 288 endemic and subendemic taxa listed by Pyak et al. (2008), 67 (ca. 2 %) have their main habitats in steppes (36 endemics, 31 subendemic). Endemism in the steppe habitats is relative to the total number amounts to ca. 1.5 % (36 out of 2800).

(Such a rather high rate seems to contradict the results shown above for Mongolia. Pyak et al. (2008) recorded 131 AMC-endemic species for Mongolia. However, only three of them are limited to Mongolia only and thus are endemic for Mongolia (two are subendemic). The resulting endemism rate of 0.001 % is consistent with the low endemism rate for Mongolian steppes as estimated above).

9. Discussion of regional endemism in the Eurasian steppe regions

Many studies suggest that geographic patterns of endemism worldwide can be explained by a combination of geographical, ecological, and historical factors (e. g. Bruchmann, Hobohm, 2014; Sandel et al., 2020; Qian et al., 2024). It is hypothesized that the main drivers are the degree of isolation, the size of the species pool, environmental heterogeneity (climate, substrates, topography), and historical disturbance events. Past climate changes (e. g. glaciation cycles of the Pleistocene) had a significant impact on the current distribution pattern of species. Regression analyses by Bruchmann (2011) showed that the local pattern of endemism in Europe can be explained essentially by the 'size of the species pool' (non-endemics), 'habitat diversity' and 'degree of isolation'. These parameters are positively correlated with the local endemism rate. The Pleistocene ice-sheet cover had a negative influence on the number of endemic taxa. The ten regions with the highest endemism in Europe were largely unaffected by the ice sheets or had large ice-free refugia.

It is reasonable to assume that these parameters can also be used to understand endemism in the Eurasian steppe zone. The very low endemism rate of the 'lowland' parts of the Eurasian steppe belt can be explained by the relatively small species pool, low topographic diversity and, at least for the Euro-Siberian steppe region, by low isolation barriers both geographically and ecologically. The Mongol-Chinese steppe also has low isolation barriers within its territory and a low number of species, but soil types and the annual distribution of precipitation are different from the Euro-Siberian steppe. Additionally, the two subregions are separated from each other by the Altai Mountain Country and belong to different floristic regions. All of this may represent a certain isolation barrier between the two steppe subregions. And yet, also in the Mongolian-Chinese steppe, the rate of endemism is very low. The presence of many species in both subregions shows, however, that the isolation barrier is not an overly strong one. Nonetheless, to fully explain the low rate of endemism in both subregions, we hypothesize that the Ice Ages had a significant impact on the number of endemics in both subregions. Interglacial periods were characterized by a forest belt stretching from the Atlantic coast in the West to the coast of the Okhotsk and Japanese seas in the East. Glacial periods were characterized by maximum distribution of various steppe communities. During the last interglacial (MIS 3), steppes were only found near the Black and Caspian seas. In Kazakhstan and Mongolia, the southern boundaries of steppe vegetation lay far to the South of its present position. During the last glaciation (MIS 2), the southern limits of permafrost extended southwards to ca. 50° latitude and in Mongolia to ca. 40° latitude. Severity of cryo-arid conditions reached a maximum. Periglacial steppes spread over most of eastern Europe, west Siberian lowlands, northern Kazakhstan and central Yakutia, and hypo-arid open vegetation like semi-deserts and deserts were prevalent in Mongolia and northern China except for the higher mountains, where a mountain steppe prevailed (Hurka et al., 2019 and references therein). Steppe landscape zones shifted to south up to 10° latitude but not in eastern Europe because geomorphological boundaries prevented a shift to the south (Caucasus, Black and Caspian Sea). The steppe flora probably became impoverished, but many species survived the cold phases in situ (Hurka et al., 2019; Molnár et al., 2023).

The flora of the present Holocene steppes in southeastern Europe thus is composed of periglacial steppe elements and post-glacial immigrants from ice age steppe refugia. This could explain the notably smaller species pool of the Pontic steppes compared to the West Siberian, Kazakh, and Mongolian steppes (Tab. 6). The drastic late Pleistocene climate changes and the associated geographic displacement processes can explain the generally low number of species in the eastern steppe regions. Thus, the landscape and climate history of the Eurasian steppe belt is characterized by severe ecological disruptions.

The resulting low habitat continuity can explain the relatively small species pool and the low number of endemics.

Despite the vastness of the territory of the European, Kazakh, and Mongolian steppes, species endemism is very low. This contrasts with the Anatolian and Altai-Tuva-Buryatia steppes. On a global scale, local endemism shows a robust positive correlation with high mountain zones explained mainly by high environmental heterogeneity and habitat diversity. Anatolia and the Altai Mountain Country are no exception. But why does Anatolia have an endemism rate of 20 % or more, compared to only about 1.5 % in the mountain steppes of the AMC? (i) One reason may be the great topographical diversity which is thought to promote the rate of endemism. Turkey is a very mountainous country, has a highly diversified climate, great edaphic diversity and a complicated 'patchy' geological structure. These are factors that may lead to high environmental heterogeneity and a large habitat diversity and thus create favorable conditions for species formation processes. (ii) Another reason, perhaps even the key factor, lies in the different vegetation histories during the glacial macrocycles. Both steppe areas are of the same age (Miocene origin; e. g. Akgün et al., 2007; Strömberg et al., 2007; Yavuz-Işık, Toprak, 2010 [for Anatolia]; Hurka et al., 2019 [for AMC]), but their Pleistocene vegetation history is different. In the cold periods of the late Pleistocene, the AMC, unlike Anatolia, was in the permafrost zone and the mountains were more heavily glaciated, while in Anatolia there were only a few local mountain glaciers. The vegetation was correspondingly different. Periglacial steppes and alpine vegetation dominated the AMC, while mountainous Anatolia featured Mediterranean to sub-Mediterranean steppes and nemoral forest communities (Frenzel, 1992; Grichuk, 1992; Velichko, Isayeva, 1992). This is also clearly evident in mammal assemblages. Mammoth tundra-steppes assemblages are proven for the AMC, and Mediterranean mountain open woodland assemblages, which included inhabitants of xeric shrub and montane forests, are proven for Anatolia (Baryshnikov, Markova, 1992). During the last Interglacial (warm period), the AMC was largely covered by various boreal coniferous forest formations and locally high mountain tundra and alpine vegetation. Steppe formations were displaced to the south. In Anatolia, however, steppe formations were able to persist amongst broad-leaved and evergreen nemoral forest formations (Grichuk, 1992). Climate differences between warm and cold periods were less severe in Anatolia, and steppe vegetation was able to spread from in situ interglacial refugia into the areas opened up by retreating forests. Thus, the 'ecological disruption' (historical disturbance events) of the steppe vegetation was significantly less in Anatolia than in the AMC. Continuity of climate and ecological conditions throughout evolutionary history and the age of a landscape (geomorphology and general composition of habitat-groups) is discussed as one of the main essential drivers of species composition and endemism at regional scales. (iii) Pils (2013) argues that towards the end of the Neogene, Anatolia was invaded by the ancestors of the recent Irano-Turanian plant genera, which experienced explosive radiation. It seems probable, therefore, that Anatolia is not the primary center of evolution for most of its Irano-Turanian genera but a center for secondary adaptive radiation, giving rise to numerous closely related neo-endemic species. This would significantly increase the number of endemics.

Conclusion

The Late Pleistocene has a key position in understanding present-day geographical distribution, structure and floristic composition of the Eurasian steppe belt. Analyzing our data in this context can explain both the overall low number of species in the steppe regions and the strikingly smaller species pool of the Pontic steppe compared to the steppe regions further east.

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