



УДК 575.8:574.42(252.51)(4/5)

## The Eurasian steppe belt: Status quo, origin and evolutionary history

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**Keywords:** Eurasia, landscapes, origin and evolution, paleoclimates, present state, steppes.

**Summary.** We present a comprehensive review of the characteristics and structure of the Eurasian steppe and of its evolutionary history in space and time. During the last decades, tremendous advances in research methods in earth and palaeontological sciences have greatly increased knowledge on palaeoclimates and palaeoenvironments of the Cenozoic era. We discuss well-known facts against the background of the recent progress made in these fields and others related to our topics, and address open questions.

In Part I (Status quo), we deal with steppe classification systems, human impact and present state of the Eurasian steppe. Here, we concentrate on prehistoric times when the first human cultures emerged, and on the last 100 to 200 years when drastic changes occurred and in many regions steppe nearly completely disappeared. In Part II (Origin and evolutionary history of the Eurasian steppe) we attend to the origin and evolution of grasses and grassland in general, and to the evolution and climate/landscape history of the Eurasian steppe belt in particular. Uplift of the Himalayan-Tibet Plateau, changes in land-sea distribution and global climate trends have been invoked as driving forces behind Cenozoic paleoclimate changes, but there is little consensus which one is the most important driver.

We finally identify gaps/challenges in our knowledge about the evolutionary history of the Eurasian steppe and discuss research directions, which might help to unravel the florogenetic and steppe habitat dynamics from the beginning of steppe formation to the present time.

## Евразийский степной пояс: статус-кво, происхождение и эволюция

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**Ключевые слова:** возникновение и эволюция, Евразия, ландшафты, современное состояние, палеоклиматы, степи.

**Аннотация.** В статье представлен всесторонний обзор характеристик и структуры евразийской степи и ее эволюции в пространстве и времени. В течение последних десятилетий огромный прогресс методов исследования в науках о Земле и палеонтологии значительно расширил знания о палеоклиматах и палеоокружении кайнозойской эры. Обсуждаются общеизвестные факты на фоне недавнего прогресса в этих и других областях, связанных с нашими темами, и решаем открытые вопросы.

В части I (Статус-кво) представлены системы классификации степей, влияние на них человека и современное состояние евразийской степи. Здесь наиболее подробно рассматриваются доисторические времена, когда возникли первые человеческие культуры, а также последние 100–200 годах, когда произошли радикальные изменения и во многих регионах степь почти полностью исчезла. В части II (Происхождение и эволюция Евразийской степи) рассматриваются происхождение и эволюция травянистых растений и лугов в целом, а также эволюция и история климата/ландшафта евразийского степного пояса в частности. Подъем Гималайско-Тибетского плато, изменения в распределении суши и моря и глобальные климатические тренды были вызваны изменениями кайнозойского палеоклимата, но нет единого мнения, какое из них является наиболее важным фактором.

И, наконец, в статье выявлены пробелы/проблемы в наших знаниях об эволюции евразийской степи и обсуждаются направления исследований, которые могут помочь распутать динамику флорогенетики и степных сообществ от начала формирования степи до настоящего времени.

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## 1. Introduction

Steppe is generally characterized as a grassland formation of the Earth's semiarid regions. The Eurasian steppe is the largest steppe region worldwide. In view of its ecological importance, studies on the evolutionary and biogeographical history of Eurasian steppe plants are largely missing. This contrasts conspicuously to other vegetation formations. Species histories of the large mountain system in Europe and North America and the circumpolar habitats of the Northern Hemisphere are in the focus of molecular phylogeographic studies but are generally rare for steppe plants. Some recent studies focus on genetic structure of central vs. marginal populations of certain steppe taxa and discuss possible explanations for the observed patterns including colonization histories (Wróblewska, 2008; Wagner et al., 2011; Durka et al., 2013; Hirsch et al., 2015). However, only few studies evaluate historical influences on contemporary genotypic patterns within a phylogeographical framework (Franzke et al., 2004; Hurka et al., 2012; Seregin et al., 2015; Friesen et al., 2016; Kajtoch et al. 2016; Meindl et al., 2016). Unfortunately, information on the climate/landscape history of the Eurasian steppe, its origin and evolution, is not only rather scattered throughout the literature but also often centred around the view and problems of a special scientific discipline (e.g., biogeography, biodiversity, climatology, palaeontology). The lack of an up-to-date comprehensive overall view of the evolutionary history of the Eurasian steppe belt makes it more difficult to test the congruence of species phylogenies and landscape evolution. Recent reviews on Eurasian grasslands, including steppes, focus either on regional scales like Central Europe (Poschlođ et al., 2009; Hejman et al., 2013) or primarily on biodiversity and phytosociological aspects (Dengler et al., 2014; Willner et al., 2016). Review articles on the origin of grasslands on a broader perspective are of older date (Jacobs et al., 1999; Bredenkamp et al., 2002), but recently Strömberg (2011) summarized the state of knowledge of the evolution of grasses and grassland ecosystems. Development of grassland ecosystems on most continents was a multistage process, and the timing of these events varied between regions. The latter reviews focus on the origin of grassland-dominated ecosystems on a worldwide perspective and seem to indicate a knowledge gap for the Eurasian steppe belt compared to other geographical regions. However, a great amount of Russian literature on the origin of the Eurasian steppe belt is available but not considered by Jacobs et al. (1999), Bredenkamp et al. (2002) and Strömberg (2011) as, for instance, the summary on climatic and environmental changes in Russia from the Palaeocene to the Holocene edited by Velichko and Nechaev (1999). This standard work has even been translated into English (Wright et al., 2005). The past decade has witnessed a rapid development of quantitative approaches for palaeoclimate reconstructions using fossil plants (e.g., Bruch et al., 2007; Utescher et al., 2011) and the interaction between palaeogeography, vegetation and climate is of special interest for the history of the steppe.

Advances in research methods, intensive field research over the last years and interdisciplinary as well as international cooperation have greatly increased knowledge on palaeoclimates and palaeoenvironments of the Cenozoic era. This is especially true for the Pleistocene landscapes of the Northern Hemisphere. Topics with particular relevance for the palaeogeographical history of the Eurasian steppe include (i) species migration, area dislocation, extension, contraction and reorganization of terrestrial biomes; (ii) interactions between herbivores and grassland and the impacts of megafaunal extinction, many of which were herbivores; (iii) steppe refuge centres during periods of unfavourable conditions. We will also address the present state of the Eurasian steppe, since it currently faces severe ecological problems and threats (Werger, van Staalduinen, 2012). Important issues in this context are (iv) the recent history (Holocene to present) of the Eurasian steppe; (v) human impacts on the steppe biome; and (vi) actual challenges and conservation actions.

The goal of our study is an up-to-date review of the characteristics, structure and composition of the Eurasian steppe, and of its historical development and dynamics in space and time. We will discuss well-known facts against the background of recent progress made in various disciplines related to this topic, and address open questions.

In Part I (Status quo), we deal with steppe classification systems in general as well as zonal patterns, human impact and present state of the Eurasian steppe. In Part II (Climate/landscape history), we attend to the origin and evolution of grasses and grasslands in general, and to the evolutionary history of the Eurasian steppe belt in particular.

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### Part I: The Eurasian steppe: Status quo

## 2. Steppe characterization

### 2.1 General aspects

To define the term 'grassland' turns out to be "a tautological problem" as Gibson (2009) put it ('a

habitat dominated by grasses’). To find an all-encompassing definition of the term grassland is elusive. Main points that all definitions have in common are the dominance of grasses, infrequent or low abundance of woody vegetation, and a generally arid climate (Gibson, 2009). The world grasslands comprise the tundra as a treeless grass-dominated ecosystem beyond the temperature-related forest line, and the grass-dominated ecosystems in the semi-arid and arid regions of the tropical, subtropical and temperate climatic zones. These regions are more or less treeless not because of temperature but of too low water supply to support tree growth. Climate in these latter grassland regions is seasonal with a dry and a wet season. Main precipitation is either in summer or winter times. The tropical and subtropical ‘savannas’ – a term, which obviously lacks conceptual clarity – exhibit an array of physiognomic forms between desert, grass savanna, dry woodland and dry forests. Similar to the savannas, the temperate grasslands – steppe, prairie and pampas – vary in physiognomy and species composition depending on variations in climate, soil, topography, and land use. (For detailed expositions see, e.g., Walter, 1962, 1968; chapters in Coupland, 1992, 1993; Gibson, 2009). Here, we concentrate on the steppes.

The term “steppe” is of ambiguous meaning. It was and sometimes still is applied to many treeless predominantly grassy vegetation formations caused by hygric and/or anthropogenic reasons. Allan (1946) named more than fifty diverse types of vegetation, which have been brought under the ample mantle of ‘steppe’, and he proposed that ‘steppe’ as an ecological term, “should be sent to rest in peace”. Today, in vegetation science and plant geography, the term “steppe” has a much more narrow meaning to which we refer here (Walter, 1968, 1974). It characterizes a naturally treeless extra-tropical climatic vegetation formation dominated by drought-resistant xeromorphic grasses, perennial herbs and low shrubs as well as geophytes and therophytes. Steppe is the characteristic climax formation of the semiarid regions within the nemoral (= cool temperate) vegetation zones (Northern Hemisphere Eurasian steppe and prairie, and Southern Hemisphere pampas). However, the ‘treeless steppe’ may also depend on various kinds of physical disturbances like grazing and fire. Steppes are associated with semi-permanent areas of high atmospheric pressure systems and with great solar radiation characterized by a climate with cold winters, hot summers with a drought period, and summer rain (Walter, 1968, 1974; Ripley, 1992; Lavrenko, Karamysheva, 1993).

There are many attempts to fit the steppes into a global vegetation classification system. Well known are the systems based on zonal vegetation (climax vegetation) of Schmithüsen (1976) and many textbooks on plant geography like Schroeder (1998), the Zonobiomes of Walter (Walter, Box, 1976), the Ecozones of Schultz (Schultz, 2008), and the FAO Ecozones (FAO, 2001, 2012). They have in common that they are primarily based on climate parameters as temperature and rainfall and corresponding climate zones. Olson et al. (2001) on behalf of the WWF introduced a new global map of terrestrial ecoregions that are built on the foundations of classical biogeography. Within 14 major habitat types, which more or less correspond to climax vegetation formations, and eight biogeographic realms 867 ecoregions are categorized (for detailed description of the ecoregions see <http://www.worldwildlife.org/biome-categories/terrestrial-ecoregions>). The WWF Ecoregions are primarily intended as units for conservation action but also offer very valuable information for ecologists, systematists and biogeographers. Another classification system now frequently used by the European Union member states as a basis for designating conservation areas is EUNIS (European Nature Information System). It is a standardized habitat classification and integrates environmental factors with predominant vegetation. Eight habitats are classified at Level 1. The distinction between categories at Level 2 is based on the presence or absence of trees, climate zones, and soil moisture (<http://eunis.eea.int/index.jsp>).

In the system of Walter, steppes belong to the “Zonobiome VII” (Walter, Box, 1976; Walter, Breckle, 1999), i.e. the ‘arid-temperate (continental)’ zonobiome with the subzonobiomes semi-arid steppe, semi-desert and arid-desert. Forest-steppe is listed under the zono-ecotone VI/VII (‘forest-steppe or grove-belt mosaic’). In the system of Schultz (2008) steppes are part of the “Dry Mid-Latitudes Ecozone”, and in the FAO Ecozone System, steppes are listed under the “Temperate Domain” as the ecological zone ‘Temperate steppes’, and pro parte within the ecological zones ‘Temperate deserts’, ‘Temperate continental forest’ and ‘Temperate mountain systems’ (FAO codes TeBSk, TeBWk, TeM). Of relevance is also the “Subtropical Domain” with the ecological zone ‘Subtropical steppes’ (FAO code SBSH). In the WWF Ecoregions system, the Eurasian steppe belt belongs to the Palearctic realm within the ‘Temperate grasslands, savannas and shrublands’ habitat, and comprises 14 ecoregions including mountain steppes and forest-steppe (WWF

codes PA0801 to PA0818, with four omissions). In the EUNIS classification, steppes belong to Level 1 habitat code E (grasslands and lands dominated by forbs, mosses or lichens), and are listed under Level 2 codes E1 (Dry grasslands) and E6 (Inland salt steppes) with several ecological units (habitats) each.

In the context of this review, we will not refer to these categories further, except where it appears appropriate. For our purpose, the steppe characterisation as outlined above is sufficient.

## 2.2 The Eurasian Steppe

It seems appropriate to refer to the terms ‘Central Asia’ and ‘Middle Asia’ first. The geographical area described by ‘Central Asia’ has been and still is differently used in the literature (Cowan, 2007). Often, ‘Central Asia’ refers to Asian areas of the former Soviet Union and to areas of Mongolia and China. This broad interpretation includes Kazakhstan, Turkmenistan, Uzbekistan, Tajikistan and Kirghizia. In the relevant Russian literature, these latter countries, however, are traditionally referred to as ‘Middle Asia’, and ‘Central Asia’ is confined to Mongolia, to large parts of northern China adjoining southern Mongolia, to the most eastern parts of Kazakhstan and to small parts of southwest Siberia adjoining northern Mongolia. This is approximately the area between longitude 80° and 120°E, and latitude 40° to 50°N, also referred to as ‘Russian Central Asia’. In this review, we use the terms ‘Middle Asia’ and ‘Central Asia’ in the sense of the Russian biogeographical and geobotanical literature.

The largest steppe region in the world is the Eurasian steppe belt followed by the North American prairie. The Eurasian steppe stretches from the Hungarian basin and the Danube delta in the west to the Amur in the east, situated between 48° and 57° northern latitude, and between 27° and 128° eastern longitude. It ranges from 800 to 1000 km from North to South, and about 8000 km from East to West (Lavrenko, Karamysheva, 1993), and includes the world’s largest dry steppe region from the Ural River in the West to the Altai foothills in the East, approximately along 48° to 50°N. To the North, the Eurasian steppe belt borders on deciduous forests in the West and boreal needle forest in the East; in the South, it borders on semi-deserts and deserts. Steppe exclaves occur in middle Europe and in northern Asia. The “prairie” of North America is the equivalent to the Eurasian steppe, thus prairie and steppe are synonyms. However, the Eurasian steppe spreads out along latitudinal gradients, whereas the

North American prairie along longitudinal gradients. It is interesting to note that in the North American steppes C<sub>4</sub>-grasses are common and partly dominating in the southern prairie whereas in the Eurasian steppes they are a minority as, e.g., the widely distributed *Bothriochloa ischaemum* and *Cleistogenes squarrosa*. A few other C<sub>4</sub>-grass species from the genera *Arundinella*, *Bothriochloa*, *Pennisetum* and *Themeda* occur in the Chinese northern subtropical and tropical shrubby tussock grasslands (Hu, Zhang, 2003).

For the Eurasian steppe belt, an intense anticyclone causes the characteristic semi-permanent high atmospheric pressure system of the steppe regions. It develops over Mongolia during the winter and extends from Siberia and China into east Europe. The Mongolian anticyclone begins to disappear as continental temperatures rise in the spring and is gradually replaced by a depression by midsummer. Cyclonic activity is much more frequent over Central Asia during the summer (Ripley, 1992). Annual mean precipitation lies mostly within the 200–400 mm range. In the inner part of the Eurasian continent, increasing continentality towards the East favours the development of the steppe, whereas oceanic conditions to the West favours the development of forest.

## 3. Steppe classification systems and latitudinal zonation

### 3.1 Introductory remarks, use of terms

Extensive literature on vegetation classification has accumulated, with different approaches emphasizing different characteristics and often adopting different classification procedures. There is urgent need for common concepts and terminology to overcome this confusing and awkward situation as a consortium of experts point out in a recent article (De Cáceres et al., 2015). Steppe is no exception from this general situation. Classification and nomenclature of steppe formations is rather vague and far from being standardized and coherent. Three main classification approaches can be recognized, the physiognomic approach, the dominant species approach and the floristic approach. In the plant-geographical and geobotanical literature, a physiognomy-based division is traditionally preferred, whereas in vegetation science/ecology quite understandably the floristic composition is the leading guideline for division and nomenclature of the steppe formations. The dominant species approach, most successfully applied in Russia, is somehow in between.

With regard to soil terminology, we use the traditional and familiar steppe-soil classification and nomenclature that is still mostly used in the steppe literature but we also refer to the corresponding soil groups of the World Reference Base for Soil Resources, WRB, in its latest/current version (FAO, 2015).

### 3.2 Physiognomic approach

Ellenberg and Mueller-Dombois (1967a, b) presented a physiognomic-ecological classification of plant formations of the earth, which is mirrored in many physiognomic steppe classification systems. We concentrate on three exemplary examples, which are widely used. They refer to zonal (latitudinal) vegetation types. Altitudinal zonality will be dealt with later.

*Example 1 (“Long grass – Short grass steppe”):* A strict physiognomic classification reflecting zonal climatic sequences along aridity gradients is the sequence forest-steppe – long (or tall) grass steppe – mixed steppe – short grass steppe – desert steppe. (1) Forest-steppe characterizes the transition zone between steppe and closed forest, and grows on chernozems, Lessivé chernozems or phaeozems (WRB Reference Soil Groups: Chernozems, Luvisols and Phaeozems; FAO, 2015). It is a macro-mosaic of meadow steppe and contrasting forest (or tree) islands. One should not confuse the term “forest-steppe” with “steppe forest”, which means forests with undergrowth of steppe elements (Wendelberger, 1956; Walter, 1974). (2) Long-grass steppe (also referred to as wet steppe) develops as meadow steppe on black earth soils (typical and common chernozem, known as eu-chernozem), and as herb-rich feather grass steppe on carbonat-chernozem (southern chernozem; WRB Reference Soil Group: Chernozems and their principal qualifiers; FAO, 2015). The transition zone between wet and dry steppes is sometimes named (3) mixed steppe and covers large areas in North America. (4) Short-grass steppe (also referred to as dry steppe) is typical for kastanozem soils (WRB Reference Soil Group: Kastanozems and their principal qualifiers; FAO, 2015) and appears as herb-poor dry feather grass steppe on weakly saline kastanozems, or as wormwood – feather grass steppe on strongly saline kastanozems. With increasing aridity, the kastanozem soils turn into burozems with semi-desert vegetation, and into serozems with desert vegetation (WRB Reference Soil Groups: Calcisols, Gypsisols, Arenosols, Regosols; FAO, 2015). (5) Desert steppe has only sparse grass cover and dwarf shrub and

subshrubs prevail. The desert steppes are often assigned to the semi-deserts and deserts, and “true” steppes are then only the grass- and herb-rich steppe formations of the semi-arid regions, except for the forest-steppe.

*Example 2 (“Stipa and Artemisia steppe”):* Another primarily physiognomic steppe-classification system widely used in the European literature (following Kleopov, 1941 as outlined in Walter, 1968, 1974) is the differentiation between (1) Forest-steppe zone, a macro mosaic of meadow steppe and more or less sharply contrasting forest (or tree) islands (Walter, 1968). The meadow steppes comprise hygrophilous herb-rich variants, and, under less moist climates, the “typical” meadow steppe. Sometimes, the meadow steppes are treated as an independent category. (2) Feather grass steppes (*Stipa* steppes) constitute the true steppe-zone with herb-rich variants on chernozems under moist conditions, and herb-poor variants on kastanozems under more dry conditions. (3) Wormwood (or sagebrush) steppes (*Artemisia* steppes) occur in the transition zone from feather grass steppes to semi-deserts on halophytic soils and comprise many variants with varying amounts of subshrubs and grasses, depending on aridity and salinity of soils.

*Example 3 (“Bunch-grass steppe”):* Russian geobotanists traditionally used still another terminology to characterize the zonal steppe types (Lavrenko et al., 1991; Lavrenko, Karamysheva, 1993). (1) Meadow steppes (= forest steppe) in semi-humid climates; (2) True or typical steppes classified into bunch-grass steppes (syn. tuft-grass steppes) with many forbs in semi-arid climates, and into bunch-grass steppes with few forbs in arid climates; (3) Desertified bunch-grass and dwarf half-shrub-bunch-grass steppes (semi-desert steppe) in very arid climates; (4) Desert dwarf half-shrub-bunch-grass steppes in hypoarid climates.

The zonal vegetation pattern can be interrupted or replaced by interzonal and azonal steppe formations, which are often related to topography and edaphic properties, as for instance mountain steppe, valley steppe, sandy steppe, stony or petrophytic steppe, or halophyte communities. Saline soils develop on water-logged ground (solonchak, “white alkali” with halophytic vegetation) and on periodically wet ground (solonetz, strongly alkaline soils with natrophilous vegetation) (WRB Reference Soil Groups: Solonchaks and Solonetz; FAO, 2015).

An example of a recent application of a physiognomic approach is the Map of the Natural Vegetation of Europe, Scale 1:2.5 Mill. (Bohn et al., 2003).

The classification system corresponds at the highest hierarchical level to the physiognomic-ecological system of Ellenberg and Mueller-Dombois (1967a, b). Fourteen zonal and extrazonal main plant formations (description A to O), and five azonal main plant formations (description P to U) are recognized. Formation L (Forest-steppe and dry grassland) and Formation M (Steppes) refer to steppe grasslands. At the second level, a subdivision is undertaken into (sub)zonal and geographical subgroups (Subformations) or into higher vegetation types with dominant species or characteristic species combinations in the main vegetation layer. The assignment of the vegetation types to ecological climate types follows the Zonobiome concept of Walter et al. (1975).

China after Australia and Russia has the third largest grassland areas in the world (White et al., 2000). Grassland and steppe classification in China differs slightly from the three examples given above. Nine grassland classes with varying numbers of subclasses and types are recognized. Steppe grasslands are listed in three classes. (a) Temperate Steppe Class with the three subclasses Temperate Meadow-Steppe, Temperate Typical Steppe and Temperate Desert-Steppe and 69 types. (b) Temperate Desert Class with the two subclasses Temperate Typical Desert and Temperate Desert Steppe and 39 types. (c) Alpine Steppe Class with the three subclasses Alpine Meadow Steppe, Alpine Typical Steppe and Alpine Desert Steppe and 17 types (Hu, Zhang, 2003).

Looking closer, these three physiognomic exemplary classification systems have in common (and this applies also to other systems not referred to here as, e. g., Sochava, 1979) that they reflect decreasing humidity and changing soil parameters along a North to South gradient in Eurasia (East to West gradient in North America). They differ in terminology, in the breadth of their categories (meadow steppe, for instance, is mostly included in the forest-steppe zone but sometimes classified as a separate category), and in their reference to characteristic plant taxa. In this latter respect, they lead up to a floristic steppe classification system.

### 3.3 Dominant species approach

In the Russian geobotanical literature, a more taxon-based classification system of steppe communities is common, which refers to the dominant plant taxa of the major stratum but includes also physiognomic characteristics. The classification is hierarchical using syntaxonomic units, a terminology that partly coincides with those

of the Braun-Blanquet system but differ in their contents (Alexandrova, 1973; Safronova, 2005). The lowest unit is the association. Associations with similar dominants and codominants are united into groups of associations, which with regard to their life forms are joined to classes. The classes are grouped into formations characterized by similar dominants in the dominant vegetation layer. To give some examples for steppe characterization: *Stipa* steppe, *Cleistogenes* steppe, *Agropyrum cristatum* steppe, *Filifolium sibiricum* steppe, etc. Often, the subdominant taxa are also named and are put before the dominant taxa, as e. g. *Carex duriuscula-Stipa* steppe, *Artemisia frigida-Cleistogenes-Stipa* steppe, *Stipa-Caragana* steppe. Steppes without clear dominance of certain taxa are often referred to as “diverse steppe” as, for instance the classic polydominant ‘four-grass-steppes’ *Festuca lenensis-Stipa krylovii-Cleistogenes squarrosa-Koeleria cristata* steppe (e.g., Lavrenko et al., 1991; Karamysheva, Khramtsov, 1995; Kamelin, 2005). As regards content, the association rank within the dominant species approach often corresponds to the association-rank of the Braun-Blanquet approach (see below).

The classification of desert and steppe vegetation on the European Vegetation Map follows the Russian dominant-determinant concept (Safronova, 2005) and corresponds to the Russian classification of arid vegetation outlined by Gribova et al. (1988).

### 3.4 Floristic approach

The floristic approach defines all vegetation types (called ‘syntaxa’) by their floristic composition. The traditional and best-known approach is the Braun-Blanquet method. It aims at producing a universal classification system with four main hierarchical levels. These are in ascending ranking order: association, alliance, order and class. The Plant Sociological Code of Nomenclature (latest edition: Weber et al., 2000) rules the naming of the ranks. The Braun-Blanquet method is extensively applied in Europe but has followers worldwide.

With regard to the European steppe region (“Steppe Biome in the Temperate Grassland Biome”), Mucina (2013) identifies three classes: (i) Class *Festuco-Brometea* Br.-Bl. et R.Tx. 1943 with 11 orders and 49 alliances (typical for dry grassland and steppe vegetation of mostly base-rich soils of the submediterranean to the hemiboreal zones of Europe). (ii) Class *Festucetea vaginatae* Soó ex Vicherek 1972 with one order and six alliances (intrazonal vegetation in European continental steppes and



dry grasslands on sandy soils). (iii) Class *Festuco-Puccinellietea* Soó ex Vicherek 1973 with six orders and 29 alliances (intrazonal vegetation type in saline steppes and secondary steppic grasslands of the continental regions of eastern and southern Europe). The European “Continental semi-desert Biome” has one class *Artemisietea lerchianae* Golub 1994 with two orders and five alliances.

In central Asia, publishing on the vegetation according to the Braun-Blanquet system started in the 1970ies in Mongolia (Hilbig, 1995, 2006). In his book on “The Vegetation of Mongolia”, Hilbig (1995) brought together extensive data on the vegetation of Mongolia, and he classified and ranked plant communities at the association rank-level. Later, he published an annotated outline of the plant communities and added the higher ranks of the plant-sociological system: alliances, orders and classes (Hilbig, 2000). The steppe vegetation of Mongolia is classified into three classes: (i) Class *Agropyreteea cristati* Hilbig et Korolyuk 2000 with two orders, three alliance and 14 associations (these plant communities occur in dry steppes and meadow steppes). (ii) Class *Brometea korotkyi* Hilbig et Korolyuk 2000 with one order, one alliance, one association and four plant communities not ranked (typical habitats are dune-sands). (iii) Class *Stipetea glareosae-gobicae* Hilbig 2000 with three orders, four alliances and 14 associations (these communities are typical for semi-desert and desert steppes with shrubs, half-shrubs, dwarf half-shrubs and low bunch grasses). Von Wehrden et al. (2009) present an updated inventory and classification of the plant communities of the Gobi region with some newly described communities at the association level.

Gadghiev et al. (2002) published a prodromus of a phytosociological classification after Braun-Blanquet for the Central Asian steppe belt, covering Mongolia and adjacent Russian regions north of Mongolia as well as Chinese regions south and east of Mongolia. The authors recognize three classes each with orders, alliances and associations. (i) Class *Ajanio-Cleistogenetea songoricae* Mirkin et al. 1988 (syn. *Stipetea glareosae-gobicae* Hilbig 2000) with two orders, two alliances and nine associations. Compared to Hilbig (2000), the number of orders, alliances and associations is reduced. Some of the ranks correspond to Hilbig (2000), others are new. (ii) Class *Cleistogenetea squarrosae* Mirkin et al. ex Korolyuk 2002 (syn. *Agropyreteea cristati* Hilbig et Korolyuk 2000) with four orders, seven alliances and 29 associations. From the four orders, only one

corresponds to one of Hilbig’s (2000) two orders. Two of the seven alliances correspond to two of Hilbig’s (2000) three alliances, and 12 associations correspond to Hilbig’s (2000) 14 associations. Gadghiev et al. (2002) reduce the class *Brometea korotkyi* from Hilbig (2000) to the association level. (iii) Class *Festuco-Brometea* Br.-Bl. et R.Tx. 1943 is not referred to in Hilbig (2000) because, according to Gadghiev et al. (2002), these plant communities are confined to the mountain meadow steppes in the north-eastern Altai and western Sayan ridges outside Mongolia.

It is obvious, that compatibility between the Hilbig (2000) and Gadghiev et al. (2002) classification systems is limited although, for the most part, they cover identical geographic regions, use the same vegetation analyses methods and rely largely on the same stock of literature and relevés. This applies not only to nomenclature but also to the delimitation of the phytosociological ranks. Scientists not firmly familiar with phytosociological vegetation analyses, might be confused. In addition, the rather complicated taxonomy and phytosociological working procedures involved as well as the lack of a reliable and widely accepted standardization of the vegetation units, are not helpful to promote the use of the Braun-Blanquet method in steppe research as fruitful as this might possibly be. One should admit, however, that some of the problems are certainly due to the still limited floristic knowledge of these vast steppe regions. Our reserved attitude is in line with the critical comments of De Cáceres et al. (2015).

### 3.5 Concluding remarks

Summarizing this chapter on steppe classifications, we would like to stress that both classification systems – the physiognomic and the floristic systems – reflect environmental parameters like climatic gradients along latitude, longitude and altitude, edaphic factors, and anthropogenic influences like deforestation and grazing pressure as well as differences between floristic regions. Whereas a physiognomic classification may have its strength in comparing steppe formations on a broader, macro-geographic scale, a floristic classification is much more sensible to narrow-scale, micro-geographic changes, and can better take differences between floristic regions into account. In essence, both classification principles have their advantages and disadvantages, and none of them alone is sufficient to cope with the steppe conditions. It would appear that the dominant species approach is a practicable compromise for communication.

#### 4. Longitudinal and altitudinal zonation of the Eurasian steppe region

##### 4.1 Longitudinal subdivision and classification

In view of the enormous longitudinal direction of the Eurasian steppe belt spanning ca. 8000 km, climatic and floristic differences within the steppe belt are to be expected and may be expressed in a meridional zonation pattern. It was Lavrenko (1969, 1970a, b) who proposed to divide the Eurasian steppe zone into two meridional subregions, the Black Sea-Kazakhstan subregion and the Central Asian (Dauro-Mongolian) subregion. Each subregion consists of five provinces.

A) Black Sea-Kazakhstan steppe Subregion:

A1) Eastern European Block with Balkano-Mesian forest-steppe province, East European forest-steppe province, and Black Sea (Pontic) steppe province;

A2) West Siberian-Kazakhstan Block with West Siberian forest-steppe province and Transvolga-Kazakhstan steppe province.

B) Central Asian steppe Subregion:

B1) Dauro-Mongolian Block with Hangay-Daurian mountain forest-steppe province, Mongolian steppe province, and North Gobi desert-steppe province;

B2) Manchuro-North-western Chinese Block with Manchurian forest-steppe province, Shanxi-Gansuian forest-steppe and steppe province.

Different from Lavrenko is the division of Sochava (1979). He proposed a subdivision into three meridional sectors: European sector, Volga-Siberian-Kazakhstan sector, and Chino-Mongolian sector. This applies to his 'Forb-grass and forb steppes' (forest-steppe and northern steppe provinces) and to the "Tuft-grass steppes". His third steppe type, the 'Sagebrush-grass steppes' (semi-deserts) is distributed from the Black Sea to the foothills of the Altai Mountains and thus borders in the North to the European sector and to the Volga-Siberian-Kazakhstan sector. Each sector has many associations as defined by the Russian dominant species approach (see above). Regarding content the division of Sochava is not far away from Lavrenko, it differs mainly in nomenclature and ranking orders. The division of Lavrenko, however, is mostly followed in the literature, and is adopted here by us.

##### 4.2 Eurasian steppe belt and its floristic regions

It is the aim of phytogeography to delimit areas with floristic inventory as uniform as possible.

Boundaries of plant distributions, floral contrast and floral gradients are basic tools to divide the Earth's flora into kingdoms, regions and provinces. The Eurasian steppe belt belongs to the Holarctic Plant Kingdom (Holarctis), but several floristic regions have part in its floristic composition. Since the subdivisions of the Holarctis into Floristic Regions in general and with regard to the steppe in particular, is rather diverse and varying from author to author, we shortly comment on the different phytogeographical treatments. The western part of the Eurasian steppe belt is assigned by Meusel et al. (1965) to the Pontic-Southern Siberian Floristic Region extending to the North and West into the Middle European Region (especially Sarmatic and Central European Provinces), and to the South into the Macaronesian-Mediterranean Floristic Region (e. g. Macedonian-Thracian Province). The eastern part of the Eurasian steppe belt is put to the Central Siberian-Mongolian-Daurian Floristic Region with isolated steppe islands in the Circum Arctic and the Circum Boreal Regions. The eastern steppe belt has contact zones with the Oriental-Turanic Region and the Central Asiatic Region in the South, and borders the Sino-Japanic Region in the East (Northwestern Chinese-West Mandshurian Subregion).

The floristic divisions of Meusel et al. (1965) are more or less shared by Lavrenko (1969), by Kleopov (1941; cited in Walter, 1974), by Schmithüsen (1968), and by Walter (1974). Takhtajan (1986) and Schroeder (1998) present different classifications. Takhtajan (1986) assigned most parts of the Eurasian steppe belt to his Boreal Subkingdom of the Holarctis, namely the Circumboreal and the Eastern Asiatic Region, whereas the Mongolian Province with its steppe, semi-deserts and deserts belong to the Irano-Turanian Floristic Region of the Tethyan (Ancient Mediterranean) Subkingdom. Lavrenko (1969), however, considered the steppe and forest-steppe areas as a special region and assigned this region as a whole to a Mediterranean (Ancient Mediterranean) subdominion of the Holarctic dominion.

In Schroeder's system (1998), the Eurasian steppe region is subdivided into the Eurosiberian Subregion (belonging to his Southeurosiberian Floristic Region), and the Mongolian-Chinese Subregion (belonging to the Irano-Turanian Floristic Region).

##### 4.3 Euro-Siberian and Mongol-Chinese Steppe

For clarity in use of terms and to avoid confusion with floristic terminology outlined above, following on the whole Lavrenko (1969) and Schroeder (1998)

we use the geographical terms Euro-Siberian Steppe for the western part of the Eurasian steppe belt, and Mongol-Chinese Steppe for the eastern part. The border between the Euro-Siberian Steppe and the Mongol-Chinese Steppe approximately runs along the line Yenisei River – Russian Altai – Mongolian Altai along the upper reaches of the Irtysh River. The Euro-Siberian and Mongol-Chinese Steppe regions differ in many respects.

*Floristic composition* – Floristic aspects clearly mirror the subdivision of the steppe belt into a western and eastern region. The distribution area of many plant taxa is restricted to only one steppe region. To quote just some examples: Completely or nearly completely restricted to the Euro-Siberian steppe are species of the genera *Crambe* (Brassicaceae), *Ornithogalum* (Liliaceae), *Salvia* (Lamiaceae), *Seseli* (Apiaceae), *Trinia* (Apiaceae), *Tulipa* (Liliaceae), and *Verbascum* (Scrophulariaceae). Examples for the Mongol-Chinese steppe are *Cymbaria* (Scrophulariaceae), *Filifolium* (Asteraceae), *Hemerocallis* (Liliaceae), *Lespedeza* (Fabaceae), *Panzeria* (Lamiaceae), *Saposhnikovia* (Apiaceae), *Schizonepeta* (Lamiaceae), and *Stellera* (Thymeleaceae). Although the grass genus *Stipa* occurs in both regions, dominant *Stipa* species in the Euro-Siberian steppe are, e.g., *S. lessingiana*, *S. pennata* and *S. orientalis*, while in the Mongol-Chinese steppe, e.g., *S. baicalensis*, *S. krylovii* and *S. glareosa* dominate. Some *Stipa* species occur in both steppe regions as for instance *S. capillata*. There are many species and species groups which do not only bridge the boundary between the two steppe regions but even span the whole Eurasian steppe belt as, for instance, the *Agropyron cristatum* (Poaceae), *Allium strictum* (Alliaceae) and *Scorzonera austriaca* (Asteraceae) species groups, *Anemone silvestris* (Ranunculaceae), *Krascheninnikovia ceratoides* (Chenopodiaceae), *Sisymbrium polymorphum* (Brassicaceae), and *Veronica spicata* (Plantaginaceae). For more examples see, for instance, Walter (1974), Lavrenko et al. (1991), Malyshev et al. (1999), Malyshev (2000) and Peshkova (2001). Distribution maps are provided in Meusel et al. (1965, 1978), Meusel and Jäger (1992) and the relevant floristic literature and floras.

*Climatic factors* – The main differentiating climatic factor is the time of annual rainfall. Maximum precipitation in the Euro-Siberian steppe is in early summer (May to June), whereas in the Mongol-Chinese steppe it is in midsummer (July to August) due to the influence of the eastern Asiatic monsoon. July and August are the main growing season. The Altai Mountains are a western barrier for the eastern

Asiatic summer cyclones and deep pressure systems (monsoon rains). The Dauro-Mongolian region (Central Asia) of the Mongol-Chinese Steppe has an extreme continental climate, which is also reflected in extension of permafrost southwards into Mongolia (Lavrenko, Karamysheva, 1993; Sharkhuu, Sharkhuu, 2012). The forest-steppe zone of northeastern China (Manchuria), however, is influenced by the Pacific monsoon.

*Edaphic factors* – As outlined above, chernozems are the typical zonal soils for the long grass steppe ('wet steppe') in flat to undulating plains. Since the parent material of chernozems are mostly but not exclusively aeolian sediments (loess), the occurrence of chernozems often coincides with loess areas. Kastanozems (chestnut soils) are the typical soils of the short grass steppe ('dry steppe') south of the Eurasian long grass steppe belt. Parent material is a wide range of unconsolidated soils, and a large part of kastanozems has developed in loess (FAO, 2015). The "classic" zonal sequence of the steppe formations from North to South along decreasing humidity and increasing aridity gradients (forest-steppe – long grass steppe on chernozems – short grass steppe on kastanozems – semi-desert steppe – desert steppe) is typical for the European part of the Euro-Siberian 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, prevailing soil types are leptosols in montane areas, kastanozems, burozems and serozems. Chernozem soils are rare and only locally found except for the most eastern part of Mongolia and northeastern China (FAO-Unesco, 1971–1981; Gadghiev et al., 2002). In the Mongol-Chinese steppe, short grass dry steppe and Central Asian bunch-grass dry steppe prevail over large areas. Forest-steppe and black earth steppe are found in considerable area only in eastern Mongolia and in northeastern China (Schmithüsen, 1976; Atlas of the USSR, 1986).

Thus, the Euro-Siberian and the Mongol-Chinese steppes differ in floristic, climatic and in edaphic respects. They probably differ also in their evolutionary and biogeographic history (see below).

#### 4.4 Altai Mountain Country

The Altai Mountain Country (AMC) and adjacent Tuva are the contact zone between the Euro-Siberian and the Mongol-Chinese steppe, and probably were important refuge centres during the Pleistocene (Kamelin, 2005; Pyak et al., 2008). The AMC as defined in the new Flora of Altai (Kamelin, 2005)

includes the Russian, Kazakh, Chinese and Mongolian Altai, the mountains bordering Dzungaria, the mountains of southwestern Tuva, and the main parts of the western Sayan ridges. In the far South, the Baitak Bogdo and the Adzh Bogdo ranges form the boundary of the AMC. Environmental differences between the areas of the AMC are tremendous and thus are biome types. From North to South, the AMC is embedded within the zonal vegetation types (biomes) of taiga (boreal forest), forest-steppe, steppe, semi-desert and desert. Zonal and altitudinal taiga prevail in the northeast and forest-steppe in the Northwest, whereas steppe, semi-desert and desert are characteristic for the eastern and southern parts. The flora of the AMC is very heterogeneous, too. It comprises species of diverse floristic regions of different biogeographic origin (Kamelin, 2005; Pyak et al., 2008).

#### 4.5 Altitudinal zonation

High mountain systems within the Eurasian steppe belt occur in the eastern part of the steppe belt (Altai, Sayan, Hangay, Hentiy-Daurian Mountains). Vegetation belts in the mountains are generally determined by vertical gradients in climatic conditions, but the vegetation type also depends on landform, water availability, soil characteristics, exposition, etc. The term “mountain steppe”, often referred to, is not suitable to classify altitudinal steppe zonation. Mountain steppe means a steppe formation, which is peculiar to almost all altitudinal belts, especially in Altai Mountains. Mountain steppes in the AMC occupy diverse habitats and represent very heterogeneous vegetation types: shrub steppe, short grass dry steppe, central Asian bunchgrass dry steppe, desert-like and desert steppe, sandy steppes and stony (petrophytic) steppes (Kamelin, 2005). These steppe formations can also occur in the plains. However, there are some steppe formations, which are not found in the plains as, for instance, the cold cryophytic steppes.

With regard to the steppe, there is no simple scheme for the altitudinal zonation available. Altitudinal zonation of steppe in the AMC is an excellent example to demonstrate its dependency on various parameters. As outlined above, different parts of the AMC belong to different floristic regions and steppe provinces. Major phytogeographical boundaries cross the Altai, and there are also climatic and edaphic differences in latitudinal as well as longitudinal zonation (see above). Kamelin (1998) proposed a first altitudinal zonation scheme for the entire AMC. Steppe complexes including the cryo-

phytic steppe and semi-deserts are typical for the dry southern and eastern parts of the AMC throughout the whole altitudinal range. Small forest stands (often *Larix*) are confined to northern slopes, groves and along watercourses. In the more wet northern and western parts taiga complexes, pine forests and forest-steppe prevail. There, steppes are confined to the southern slopes.

### 5. Human impact on Eurasian steppe formations and present state

We will mainly concentrate on two periods, on prehistoric times when the first human cultures emerged in the steppes, and on the last ca. 100 to 200 years when drastic changes occurred and in many regions steppe nearly completely disappeared.

#### 5.1 Introductory remarks, use of terms

When dealing with human impacts on steppe formations, one is confronted with terms like ‘primary’ and ‘secondary’ grassland, ‘natural’ and ‘semi-natural’ grasslands, ‘permanent’, ‘anthropogenic’ and ‘man-made’ grasslands. Unfortunately, these terms are not standardized. Authors use the terms differently, sometimes even differently by the same author. ‘Natural grasslands’ are subject to little or no deliberate direct modification by humans in contrast to grasslands, which are subjected to various degrees of intensive management (Gibson, 2009). Since large grazing mammals are an integral part of the steppe ecosystem, be it wild game or domestic livestock, the transition between ‘natural’ and ‘non-natural’ steppe grasslands is fluid. Natural grasslands are sometimes termed ‘primary’ grasslands (Bredenkamp et al., 2002). But the term ‘secondary grasslands’ is not consistently used to describe ‘non-natural’ grasslands, as, e.g., Bredenkamp et al. (2002) do when they use ‘anthropogenic’ or ‘man-made’ grasslands as synonyms for secondary grasslands. Steppe grassland, which has emerged through long time low-intensity human land use, is termed ‘semi-natural’, and grassland mown for hay is a meadow and one used for grazing is a pasture (Gibson, 2009; Dengler et al., 2014). In addition, the term ‘semi-natural’ grassland is restricted to those steppe formations, which have developed from forests as potential vegetation (Gibson, 2009; Dengler et al., 2014). Sometimes, ‘semi-natural’ grassland is used as synonym to ‘secondary’ grassland (Dengler et al., 2014), and sometimes secondary grassland (also termed ‘permanent’ grassland by Gibson, 2009) is a subcategory of the semi-natural

grasslands (Gibson, 2009). The term ‘semi-natural’ grassland as defined by low-intensity human land use and emerging from forests as potential natural vegetation might make sense for Europe, but large parts of the Eurasian steppe as a whole, especially in Central Asia, would not be ‘semi-natural’ despite developing from low-intensity human impact since they did not originate from forests. In the light of these terminological confusions, we will avoid these terms when discussing human impact on steppe formations, or comment on it if used.

Referring to dates, we use BP (years before present), the most commonly used convention in radiocarbon dating. ‘Present’ refers to the year 1950, when the calibration curves were established (in more recent literature, ‘present’ often refers to the year 2000). We also use the traditional date descriptions BC (before Christ) and AD (Anno Domini for after Christ) being aware of the recent recommendation to replace BC by BCE (Before Common Era) and AD by CE (Common Era).

In periodization of human history, we follow the Three-Aged System: Stone Age - Bronze Age - Iron Age. The Stone Age is subdivided into the Pleistocene Palaeolithic and the Holocene Meso- and Neolithic. The Mesolithic/Neolithic period starts at ca. 10,000 BC and ends with the rise of the Bronze Age, ca. 3500 BC. In the so-called ASPRO system, the Neolithic begins with the start of farming and ends when metal tools became widespread in the Copper Age, Bronze Age or Iron Age, depending on the geographical region. It can be roughly dated from 9000 BC to ca. 2000 BC or even younger. The Three-Age System is nowadays commonly used in archaeological literature, and we refer to this chronology as given in Hanks (2010) for the Eurasian steppes.

The Iron Age is traditionally subdivided into the Prehistoric (or Proto-historic) and the Historic Iron Age, delimited from each other by the development of written language. Both sub-periods together constitute the ‘Classic Iron Age’. It lasts from ca. 1300 BC to ca. 500 AD, the prehistoric sub-period from ca. 1300 BC to ca. 300 BC, and the historic sub-period from ca. 300 BC to ca. 500 AD. The end of the Classic Iron Age is the beginning of the Middle Ages. This terminology and time division, which we follow here, is not fully compatible with divisions in usage at regional scales. In Middle Europe, for instance, the term ‘Iron Age’ is more or less confined to the prehistoric Iron Age of the Three-Age System. In northern Middle Europe and Scandinavia, a ‘Pre-Roman Iron Age’ (ca. 700 BC to 1 BC)

is followed by the ‘Roman and Germanic Iron Ages’ (1 AD to ca. 800 AD), and finally by the ‘Viking Age’ (ca. 800 AD to 1100 AD), eventually termed ‘Late Iron Age’. One has to take these different applications of the term ‘Iron Age’ into consideration to avoid misinterpretations of the time scales.

## 5.2 Prehistoric times

Early colonization by man across the vast northern Eurasian plains has been proved already for the upper Palaeolithic in the late Pleistocene, 46,000–10,000 BP, including northeastern and eastern Siberia, the Russian Far East, southern Siberia and the east of European plain (Hanks, 2010 and literature cited therein; Pitulko et al., 2016). In the Mesolithic to Early Neolithic period (ca. 10,000–6000 BC), early Holocene hunter-forager societies have been proved for Europe and for the southern Siberian region (Parzinger, 2006; Hanks, 2010 and literature cited therein). A key development was the domestication of horse in the Neolithic – Eneolithic period (ca. 6000–3500 BC). Molecular studies point to multiple origins of modern horses (Warmuth et al., 2011; Achilli et al., 2012), but one origin of horse domestication was the Eurasian steppe, probably its western central region (Warmuth et al., 2012). Much later, camels were domesticated. During the Bronze Age (3500–1200 BC) the Eurasian steppe region saw large-scale patterns of movements and inter-regional trade. Key developments were the emergence of spoke-wheeled chariot technology, metal mining and metallurgy (Hanks, 2010 and literature cited therein), which did not only fuel inter-regional trade but also military conflicts and wars of conquest (Anthony, 2007). The prehistoric Iron Age (1200–300 BC) was a period of strong social and technological change connected with territorial conflict and control. In the Euro-Siberian steppe, the whole period is characterised by kurgans, namely the Scythian tombs, which provided an image of the Eurasian steppe during the Iron Age (Parzinger, 2006, 2009; Hanks, 2010). Mobile pastoralism (‘nomadic pastoralists’) and mounted warfare (cavalry) increased tremendously, and fundamentally depended on horse and cattle breeding. Recent field research, however, provided also evidence for agriculture in the steppe and forest-steppe zones. Domesticated cereal production and agro-pastoral economic regimes have been proved for Kazakhstan (Miller Rosen et al., 2000), and southern Siberia (Murphy et al., 2013), and agriculture appears to have become well established in the western steppe during the Iron Age. In the Pontic steppe region, the Scythian

farmers apparently grew wheat, barley, millet, beans and onions for their domestic use and exported great amounts of cereal crops to the Greece (Parzinger, 2009). Pollen diagrams from the forest-steppe zone in northwestern Romania corroborate the cultivation of cereals during the Iron Age (Feurdean et al., 2015).

The impact of the prehistoric cultures on the steppe ecosystems is generally regarded as low, except locally around sites of special interest such as settlements, water holes, mines of ores and salt, and agricultural land (see Preface in Werden, van Staaldin, 2012). Nevertheless, it stands for discussion to what degree the climate borders of steppe, especially the forest-steppe region, were extended at that early times already by biotic factors such as human activities and herbivores, be they domestic or wild grazers. Biotic and climatic drivers as competing hypotheses are of particular relevance for the Holocene (Craine, McLauchlan, 2004).

The vegetation history of the Eurasian steppe region in prehistoric times is different from that of Central Europe. In Central Europe, the anthropogenic transformation of the early Holocene woodlands into a cultivated landscape started already ca. 6000–5000 BC by opening of the forests and forest clearing (Pott, 1995; Kalis et al., 2003; Kuneš et al., 2008; Poschod et al., 2009; Ellenberg, Leuschner, 2010; Hejman et al., 2013; Poschod, 2015). We will come back to this issue later when discussing possible Holocene refuge centres in Central Europe. In this context, we will also shortly deal with the ‘Steppenheidetheorie’ of Gradmann (1933).

### 5.3 Middle Ages and modern times

Historically, nomadic herders used nearly all Eurasian steppe regions extensively for sheep, horse, cattle, and camel breeding. During the Middle Ages and modern times steppe was increasingly used as pastureland, but it was also the beginning of ploughing up forest-steppe habitats for agriculture. Human activities transformed steppes and forest-steppes more than any other part of northern Eurasia. “It is fair to say, that with the exception of rather small protected areas, the biogeography of the European steppes and forest-steppes is now cultural rather than natural” (Chibilyov, 2002). The Hungarian Puszta, for instance, is largely an anthropogenic steppe replacing the natural forest-steppe (De Soó, 1929). In Hungary, most of the land suitable for agriculture had been ploughed already by the eleventh century, and the forest cover reached its minimum in the eighteenth century, when steppe

woodlands had largely disappeared (Molnár et al., 2012). “Russian agriculture was born in the forest zone” as well (Levykin et al., 2012). In the seventeenth century, modern crop-based agricultural development started in Russia in the East European forest-steppe and meadow steppes zones and gradually extended to the East and South. In the eighteenth century, ploughing of steppe and intensified grazing began also in Ukraine, and at the end of the nineteenth century, large areas of steppes and hygric herb-rich bunch-grass steppes (tall grass steppe on chernozems) in Russia were turned into arable land for crop and fodder production. At the end of the nineteenth century, cropland reached the desert steppes near the Caspian Sea in European Russia (Smelansky, Tishkov, 2012).

## 5.4 Soviet Era and post-Soviet time

### 5.4.1 Soviet Era

Grand-scale destruction of steppe ecosystems occurred in the Soviet era (1917 to 1990), when the official agrarian policy was dominated by the ‘transformism’ approach in land use. These developments reached their zenith in the ‘virgin lands campaign’ of 1954 to 1963. Big collective state-owned farms were created to expand food production, mainly wheat and barley, and livestock breeding was also intensified. Rivers and wetland were drained on a large scale, and roads and canals were constructed. The ‘virgin lands campaign’ transformed the face of the steppes and led to large-scale changes in society and ecology (Levykin et al., 2012). Nearly all plain black-earth and chestnut soil steppes in the former Soviet Union in the west of the Volga were ploughed up. Some steppes in the east of the Volga survived in larger areas, e.g., in the southern Ural and foothills of the Altai Mountains as well as in the west Siberian and Daurian plains. However, the conversion of the dry herb-poor bunch-grass steppe (short grass steppe on kastanozems) into arable land failed mainly due to climate fluctuations, aridity and widespread salinity. Inappropriate agricultural land use caused severe ecological damages. Vast areas were affected by desertification processes as deflation and soil salinization. Some of this new cropland had to be abandoned already at the end of the 1960s (Smelansky, Tishkov, 2012; see also Rachkovskaya, Bragina, 2012). Notorious example of desertification is the Kalmykian steppe (Zonn, 1995). The sensitive dry steppe ecosystems, traditionally used as pasture lands, were overexploited by excessive animal production, and fragile pastures were converted into cropland, which resulted “in the creation of

Europe's first anthropogenic desert" (Saiko, 2001). Another infamous example is the desiccation of the Aral Sea due to mismanagement of irrigation during the so-called 'cotton independence' policy (Saiko, 2001).

Grassland was also strongly converted in China. About 90 % of the grassland, including steppe ecosystems, is degraded due to long-term inappropriate human activities. With the explosive growth of human population mainly in the second half of the twentieth century, livestock numbers increased excessively leading to severe overgrazing. In addition, great parts of steppe land were ploughed and cultivated but inappropriately managed, e.g., by overharvesting and improper mowing (Cui et al., 2012). The degradation of the Chinese steppe ecosystems led to serious desertification, and China is worldwide one of the countries most affected by it (Dong et al., 2012). The most desertified steppe regions in China are the 'sandlands', shifting inland sand dunes.

The Soviet Union and Chinese governments explicitly aimed at ending nomadism in the steppe, the Mongolian communist government, however, supported pastoral nomads and improved infrastructure for them. Mongolia is the only Eurasian country where today substantial numbers of nomadic pastoralists still exist. However, during the last three decades, the total number of livestock has increased almost twice from 23 to ca. 45 million animals, and the herd structure changed: the number of goats increased 3–4 fold. This burgeoning animal load has disrupted the natural balance by overgrazing and promoted degradation and desertification (Hilbig, 1995; Bazha et al., 2012; Wesche, Treiber, 2012).

#### 5.4.2 Post-Soviet time

The first decade after the collapse of the Soviet Union (from 1990 to 2000) was characterised by a breakdown of industry, infrastructure and social systems in post-Soviet countries. The transition from state-controlled to market-driven economies caused drastic socio-economic changes (Levykin et al., 2012). These changes had a great impact on landscapes and biodiversity in the steppe zone. Arable land over vast areas was abandoned, and a massive decline in livestock reduced grazing pressure on pastures. This led to a recovery and return of steppe vegetation in certain areas (Hölzel et al., 2002; Charles, 2010). However, rates of land-use change varied considerably within Russia and between the post-socialist countries (Prishchepov et al., 2013). Since about 2000, the trend towards land abandon-

ment and decrease of livestock numbers reversed in many parts of the former Soviet Union. Crop production was again given priority by Russian authorities, and, with governmental support, re-ploughing of fallow lands in the steppe zones was intensified and expanded during the last decade (Levykin et al., 2012), which again threatens steppe vegetation and steppe wild life (Kamp et al., 2011; Neronov et al., 2012).

The decline of agricultural production at the end of the Soviet era and beginning of the post-Soviet time led to a significant increase of steppe wildfires. Studies in the trans-Volga-Ural region revealed that improper management practices, which, among other consequences, led to accumulation of leaf litter, are the main reasons (Pavleychik, 2015, 2016). Similar conclusions about causes and dynamics of fire risk are also reached for other steppe regions of the Russian Federation (Pavleychik, 2017).

#### 5.5 Present state, conservation status

Since thousands of years and especially today, the primary climax steppe biome is highly influenced, disturbed and transformed by human activities as, e. g., forest clearing, agriculture, and pastoralism. In many regions, natural steppe vegetation remains only in nature reserves, in gullies and ravines, on the slope of river valleys, on the edges of fields, and along roadsides. Main destructive threats for the steppe biome are conversion of steppe into cropland, overgrazing, mining, oil and gas development, urban encroachment and afforestation. The magnitude of these threats varies between regions. The worst threat in Russia, for instance, is conversion into agricultural land, but in Mongolia, it is overgrazing and expanding mines and oil fields.

When talking about protected areas one has to bear in mind that protected area types are often different between countries, which makes it more difficult to draw comparisons between countries. Furthermore, the IUCN has developed a protected area management categories system. However, the classification systems of single countries are often distinct from that of the IUCN.

Temperate grasslands, savannas and shrublands are the least protected biomes worldwide with only 5 % of their total area being conserved (Brooks et al., 2004). In addition, protected areas are often biased towards places that are unlikely to face land conversion pressures even in the absence of protection, as being situated on steep slopes, at higher elevations, and with greater distances to roads and cities (Joppa, Pfaff, 2009). They are biased also towards locations

that are cheap to protect and distant from important areas of biodiversity (Venter et al., 2014).

Conservation status of the Eurasian steppes follows these trends. In all post-Soviet countries, protected areas (nature areas of preferential protection) in the steppe zone do not concentrate on typical, zonal steppe ecosystems and landscapes but mainly cover intrazonal locations restricted to special habitats as, e.g., saline or rocky or sandy places (Levykin et al., 2012).

In Russia, most of the steppe biome remains unprotected. Only 0.1 % of the steppe biome area is formally conserved, which is the lowest value of protected area coverage among all biomes of Russia (Smelansky, Tishkov, 2012). The situation is similar for Europe with only ca. 0.2 % of temperate grassland being protected (Knapp, 2005; for Ukraine see Korotchenko, Peregrym, 2012; Moysiienko et al., 2014). Protection level of steppe ecosystem types (meadow steppe, dry steppe, semi-desert steppe and desertified steppe, excluding forest-steppe) for Kazakhstan averaged prior to 2009 about 1.5 %. The target for 2010 was to protect 1.9 % of the steppe zone, and 2.2 % by 2013 (United Nations Development Program UNDP/Global Environmental Facility GEF project, contracting authority: Government of Kazakhstan, project scheduled for the period 2009–2014; see also Rachkovskaya, Bragina, 2012). In Mongolia, less than 6 % of the steppe region has protected status and only 2 % of that is adequately managed and enforced (The Nature Conservancy, internet accessed 29.3.2016). Protected areas in China known as Nature Reserves (NR) are divided into several categories, the National Nature Reserves (NNR) being the strictest. NNR protected areas in East China, where most of the steppe and meadow steppe ecosystems are located, are only 4.75 % (Inner Mongolia 2.9 %). Less than 2 % of the total NR area is covered by steppe and meadow steppe, and only 0.76 % of the total NNR area comprises steppe and meadow steppe ecosystems (Cui et al., 2012; Guo, Cui, 2015). By the end of the last century, the Daurian steppe in Mongolia, Russia and China had still ca. 72 % remaining in grassland and is the largest remaining grassland in the Eurasian steppe biome and the second largest worldwide (White et al., 2000). Here, as part of the WWF ‘Global 200’ initiative, a model for transboundary conservation was founded in 1994, the Chinese-Mongolian-Russian ‘Dauria International Protected Area (DIPA)’. However, there is still urgent need for transboundary cooperative strategies for grassland restoration and conservation, especially regarding habitat conserva-

tion for migrating wildlife such as the Mongolian gazelle (Kirilyuk, 2014).

Palearctic steppes including the Eurasian steppe belt have become one of the most endangered terrestrial biomes of the world. A special issue of the journal “Biodiversity and Conservation” (vol. 25, issue 12, 2016) deals with the ecology, biodiversity and conservation of Palearctic steppes (for definition of the Palearctic steppe biome see Wesche et al., 2016). It comprises research papers from different regions throughout the biome, giving an overview of current knowledge and knowledge gaps (see Editorial by Török et al., 2016).

A coherent European ecological network of special areas of conservation was set up in 1992 under the title ‘Natura 2000’ to “maintain and restore, at favourable conservation status, natural habitats and species of wild fauna and flora of Community interests” (Council of the European Communities, Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora). Annex I of the Council Directive 92/43/EEC (the so called “Habitats” Directive) lists the habitat types whose conservation requires designation of special areas of conservation. Habitat types in danger of disappearance and whose natural range mainly falls within the territory of the European Union are termed priority habitat types. Annex I from 1992 has been updated several times to incorporate habitats occurring in new EU Member States and to correct some errors or add newly acquired information. The latest version EUR28 is from 2013 (European Commission, Scientific reference document, Interpretation Manual of European Union Habitats – EUR28, April 2013). Following priority habitat types with regard to steppe biomes are listed in the EUR28 version: xeric sand calcareous grasslands; semi-natural dry grasslands and scrubland facies on calcareous substrates (class Festuco-Brometalia) as far as they include important orchid sites; Sub-pannonic steppic grasslands; Pannonic loess steppic grasslands; Pannonic sand steppes; Ponto-Sarmatic steppes; Pannonic salt steppes and salt marshes. The “Habitats Directive” is a European Union legislative instrument in the field of nature conservation.

### 5.6 Climate change

On top of all these threats and conservation efforts come the effects of climate change, which seem to be particularly obvious already in the northern zone of the Eurasian steppe biome, Mongolia serving as a concrete example.



The impact of climate change is profound in Mongolia. Annual temperature increased by 2.14 °C in the past 70 years and has intensified in the last ten years, thus warming rates clearly outrange the global average (Sanjmyatav, 2012; Menzel et al., 2016). Annual number of cold days decreased, and the number of hot summer days increased. Precipitation in winter increased and has an effect on snow cover. Snow cover is very sensitive to changes in temperature and experienced the most significant seasonal and inter-annual changes in the whole Northern Hemisphere (Kong, Wang, 2017, and literature cited therein). In Mongolia, extreme winters (high snow cover preventing access to forage on winter pastures) were more frequent since the year 2000. In contrast to winter precipitation, precipitation in summer decreased, which leads to more draughts and water resources drying up. About 75 % of pastureland is affected by medium to intense desertification. The frequency of forest and steppe fires increased because of the drought, and the length of the season of fire risk also increased (Sanjmyatav, 2012, and literature cited therein). Climate cycles in the Daurian ecoregion (alteration of dry and wet stages within about 30-year climate cycles) seem to be destroyed by climate warming, which might have great impact on vegetation and wildlife (Kirilyuk et al., 2012).

Vanishing permafrost is also causing serious concern. Permafrost underlies about one fourth of the land area of the Northern Hemisphere and dominates the landscape and ecosystems of the large tundra and boreal forest areas of northern Eurasia and North America, where it can reach thicknesses of more than 1000 m. Formed in Siberia since the Late Pliocene/Early Pleistocene, permafrost has the largest extension in lowland regions, which were not glaciated during the Pleistocene, where permafrost never disappeared completely during warm phases (Schirrmeister, Hubberten, 2014). Permafrost is highly sensitive to a warming climate. The most significant increases in permafrost temperature were found in northern Alaska and in northern European Russia, increasing 2–3 °C between 1971 and 2010 (Kong, Wang, 2017).

Mongolia is located in the southern fringe of the Siberian permafrost zones, and permafrost occupies almost two-thirds of Mongolia, predominantly in the Khentei, Khovsgol, Khangai and Altai Mountains and surrounding areas. Most of the permafrost in Mongolia is at a temperature close to 0 °C, and thus thermally unstable (Sharkhuu et al., 2007). Scenarios of climate change models predict that at the end

of this century (2070–2099) continuous permafrost in Mongolia will be nearly gone and only remain in valleys of the mountains (Azzaya, Khaulenbek, 2008). There is strong concern about an increased degradation of mountain permafrost and a possible impact on river discharge and water availability. Decreased water availability from the mountains would have strong socio-economic implications for the population living in the steppe belt downstream the mountains (Menzel et al., 2016).

In summary, Mongolia is warming and becoming drier from year to year. Desertification and weather extremes will increase, and weather extremes are more severe. Decreasing permafrost will intensify desertification and deforestation in the steppe and taiga zones, respectively.

## Part II: The Eurasian steppe: Origin and evolutionary history

### 6. Origin of grasses and grassland biomes

The history of the steppe biome is per se closely meshed with the origin of grasses and grassland biomes. Phylogeny of grasses (Poaceae), the origin of grassland biomes, and traits, which might have facilitated the global success of grasses, have been summarized and reviewed by Strömberg (2011), Kellogg (2015), and Linder et al. (2018). We focus on aspects, which we think are essential in the context of the evolutionary history of the Eurasian steppe.

#### 6.1 Origin and evolution of grasses

There are ca. 10,000 grass species (Poaceae), which nearly all can be assigned to one of the two clades BEP (subfamilies Bambusoideae – Ehrhartoideae – Pooideae) and PACMAD (subfamilies Panicoideae – Arundinoideae – Chloridoideae – Micrairoideae – Aristidoideae – Danthonioideae). These two clades are sister clades and represent the ‘crown’ or ‘core’ grasses, whereas three lineages are basal (Anomochlooideae, Pharoideae, Puelioideae) (GPWG II, 2012). The BEP clade comprises only grasses with the C<sub>3</sub> photosynthetic pathway whereas in the PACMAD clade C<sub>3</sub> and C<sub>4</sub> photosynthesis grasses occur (Kellogg, 2015). The transition from the C<sub>3</sub> to C<sub>4</sub> photosynthesis pathway evolved 22–24 times independently in the PACMAD clade (with one possible reversion), with most transitions (16–18 times) in the subfamily Panicoideae (GPWG II, 2012). C<sub>4</sub> grasses are mostly confined to tropical and subtropical climates in low latitudes and

altitudes, whereas  $C_3$  species dominate the cooler temperate regions at higher latitudes and elevations. These patterns correlate strongest with minimum temperatures during growing seasons: low minimum temperatures favouring abundance of  $C_3$  grasses and high temperatures the abundance of  $C_4$  grasses (Teeri, Stowe, 1976). Regarding the Eurasian steppe, by far the majority of the grasses are  $C_3$  grasses of the Pooideae. The only widespread  $C_4$  grass in the Eurasian steppe is *Cleistogenes squarrosa* and *Bothriochloa ischaemum*.

Poaceae have been subject of numerous phylogenetic studies, but the time of origin and early diversification of the Poaceae is still under debate. On the one hand, taxon sampling, molecular dating methods, and molecular marker data sets (e.g., plastid vs. nuclear markers) may strongly influence phylogenetic inference and time divergence estimates. On the other hand, estimates of divergence times based on molecular data are strongly affected by fossil calibration points. The most reliable fossils of grasses are macrofossils such as leaves, stems, spikelets, and inflorescences. The oldest unequivocal remains of grasses are macrofossils from the Palaeocene/Eocene boundary (Crepet, Feldman, 1991), and from the Oligocene (Thomasson, 1987) from North America. Probable grass leaf cuticles from the Eocene and Oligocene are reported from Europe (Thomasson, 1987). Grass microfossils such as pollen and phytoliths (plant silica bodies) are reported from older strata but give rise to questions on homoplasy and preservation/identification the older they are (Jacobs et al., 1999). It would appear that the earliest firm record of grass pollen are from the Palaeocene of South America and Africa before ca. 60 and 55 Ma, respectively. The oldest report of grass fossils at all are phytoliths from late Cretaceous coprolites from India (Prasad et al., 2005). They seem to indicate considerable diversification of the grass family already by the upper Cretaceous, 67–65 Ma (Prasad et al., 2005, 2011). However, the identity of these phytoliths as grass fossils is questioned (e.g., Kellogg, 2015).

Macrofossils, pollen, and most phytolith data point to the origin of the grasses in the upper Cretaceous, about 80 Ma (summarized in Kellogg, 2015). Incorporation of the Indian phytoliths as calibration points would place the origin of grasses considerably earlier, in the lower Cretaceous, about 125 Ma (Vicentini et al., 2008; Prasad et al., 2011) or even in the upper Jurassic, about 114–180 Ma (Jones et al., 2014) which is critically discussed by Kellogg (2015). The origin of the core grasses (BEP and

PACMAD clades) from the basal lineages is placed at about 50–60 Ma (late Palaeocene - early Eocene) but again is strongly affected by fossil calibration points. Inclusion of the Indian phytolith evidence pushes this age to about 70 to 85 Ma (upper Cretaceous) (Vicentini et al., 2008; Bouchenak-Khelladi et al., 2010, 2014a, b; Prasad et al., 2011; Christin et al., 2014; Jones et al., 2014).

The upper Cretaceous when the first grasses (Poaceae) seem to have originated and the Palaeocene-Eocene transition as the origin of the core grasses (BEP and PACMAD clades) are periods, when the global climate was generally warm and wet and no ice existed at the poles. The vegetation on Earth was dominated by tropical, warm temperate and cool temperate forests (Wolfe, 1985; Utecher, Mosbrugger, 2007). However, many regions at lower latitudes especially on Gondwana and SW Laurasia experienced arid climates (Scotese, 2000; Zhang et al., 2012). Molecular dating and habitat reconstructions let Bouchenak-Khelladi et al. (2014a) argue, that members of Poales originated in the early Cretaceous (118.4 Mya) in sunny and dry environments, and that in late Cretaceous ancestral members of the Poaceae diverged in shaded and dry habitats and invaded forest understorey, a view which is also held by Linder and Rudall (2005), Edwards and Smith (2010), Jones et al. (2014), and others. Some basal Poaceae (Anomochlooideae, Pharoideae, Puelioideae) are still found in deeply shaded forest understorey. Differing from dry habitats, Strömberg (2011) favours tropical wet forests as ancient Poacean habitats except for India.

The origin of  $C_4$  photosynthesis is dated along the Eocene-Oligocene transition 30–35 Mya (Christin et al., 2008; Vicentini et al., 2008; Strömberg, 2011; Bouchenak-Khelladi et al., 2014b; Cotton et al., 2015), and coincides with a steep declining of atmospheric  $CO_2$  and global cooling following Antarctic glaciation events (Beerling, Royer, 2011). It has often been argued that periods with declining atmospheric  $CO_2$  concentration and increasing global aridification would promote the evolution of  $C_4$  grasses (Sage, 2004 and literature cited therein; Christin et al., 2008; Vicentini et al., 2008; Bouchenak-Khelladi et al., 2009). Subsequent to the earliest origin of  $C_4$  photosynthesis, additional clustered origins occurred during or after the Oligocene (Vicentini et al., 2008; Christin et al., 2014) and would suggest more complex patterns and drivers of  $C_4$  origin and expansion (Edwards et al., 2010). The Indian phytolith-based ages for Poaceae result in a scenario by which  $C_4$  grasses appeared already

in the Eocene when atmospheric CO<sub>2</sub> was elevated (Zachos et al., 2008; Beerling, Royer, 2011). This would need to reconsider potential environmental drivers for the evolution of the C<sub>4</sub> pathway (Prasad et al., 2011).

As outlined, it is believed that grasses originated in a warm tropical or subtropical climate (Edwards, Smith, 2010), and the majority of grasses of the PACMAD clade today are adapted to a warm climate. *Pooideae*, which encompass the majority of Eurasian steppe grasses, and *Danthonioideae*, however, show cold tolerance. It has been argued that the climate cooling at the Eocene-Oligocene boundary could have triggered the evolution of cold tolerance in certain C<sub>3</sub> lineages and would thus be a key innovation, which enabled certain C<sub>3</sub> lineages to spread into cool temperate regions (Edwards, Smith, 2010; Edwards et al., 2010; Sandve, Fjellheim, 2010; Vigeland et al., 2013).

## 6.2 Origin of grassland biomes

Palaeobotanical evidence, phytolith data, vertebrate fossils, isotopic records in fossils and palaeosols, palaeoclimate reconstructions and dated molecular phylogenetic inference are increasingly employed to understand the origin and evolution of grasslands. Phytolith microfossils now play an important part in tracing the origin and spread of grasses, and analysis of phytolith assemblages has become a powerful tool in reconstructing past environments and vegetation types as, e.g., forest vs. grassland (Strömberg, 2004, 2005, 2011).

The origin of grass-dominated ecosystems is comprehensively discussed in the literature (e.g., Jacobs et al., 1999; Bredenkamp et al., 2002; Edwards et al., 2010; Strömberg, 2011). Here, we will outline the essential features and address open questions before concentrating on the Eurasian steppe. The evolution of grasslands can be split into several major phases: (a) origin of C<sub>3</sub> grasses (BEP and PACMAD clades) in the Palaeocene (see above); (b) origin of first C<sub>4</sub> grasses along the Eocene-Oligocene transition (see above); (c) origin of C<sub>3</sub> grass-dominated open habitats in the late Oligocene and Miocene; (d) spread of C<sub>4</sub> grass-dominated ecosystems in subtropical and tropical regions in the late Miocene-early Pliocene. This pattern is valid for all continents but there is variation among continents in the timing of grassland evolution. Whereas grass-dominated ecosystems seem to appear in North America already by the late Oligocene, widespread grass-dominated ecosystems in northern continents did not occur until the early to middle Miocene, in

Australia even later (Jacobs et al., 1999; Strömberg, 2011). The grass-dominated habitats reported from the Eocene from South America (Patagonia) were, according to Strömberg et al. (2013), only minor floral elements in overall forested habitats. In all areas, grass-dominated vegetation was initially predominantly C<sub>3</sub>, but by 7–5 Mya C<sub>4</sub> grasses prevailed everywhere in the lower tropical to subtropical latitudes except Australia (Jacobs et al., 1999; Strömberg, 2011).

### 6.2.1 Time lag between origin and dominance of grasses

It would appear that C<sub>3</sub> and C<sub>4</sub> grasses were present and diversified in many areas millions of years before they became dominant in open-grass habitats. This time lag provokes the question whether the gap between the emergence of C<sub>3</sub> and C<sub>4</sub> grasses and the proof of C<sub>3</sub> and C<sub>4</sub> grass-dominated open habitats is artificial due to poor fossil preservation and/or to the scarceness, smallness and patchy occurrence of open habitats. In other words, open habitats may have occurred much longer before they became ecological dominant, but this cannot be proved directly until yet. However, there is indirect evidence of open and dry habitats continuously from the Palaeogene to the Neogene (see below) justifying the assumption of suitable habitats for open-habitat grasses long before the grasses became dominant.

### 6.2.2 Origin and spread of grass-dominated open habitats

The emergence of grass-dominated open habitats covering large areas worldwide implies the question on the driving forces and can be finally put down to the question of what prevents tree growth. Temperature effects, as the length of the growing season, the annual sum of rainfall and its seasonal distribution, strongly influence tree growth. Beyond certain thresholds along the temperature gradient, aridity and seasonality favour the ‘non-tree’ climax formations savannas and steppe. Tree growth also depends on edaphic factors as nutrient-poor and nutrient-rich soils as well as on local relief characters. It also depends on disturbances as caused by fire and on large mammal herbivores. Vast areas of present day humid C<sub>4</sub> grasslands and savannas have the climate potential to form forests. Without fire, closed forests would double from 27 % to 56 % of vegetated grid cells, mostly at the expense of C<sub>4</sub> grasses but also of C<sub>3</sub> shrubs and grasses in cooler climates (Bond et al., 2005; Bond, 2008). Hypsodonty (high-crowned teeth adapted to feeding on silica-rich or fibrous

plants) of large mammal herbivores (ungulates) in the fossil record is conventionally taken as proof of open grass-dominated habitats. In North America and western Eurasia, hypsodonty evolved or became common several million years after open-habitat grasses dominated whereas in China, Africa and South America such a delay is not indicated by the fossil record (Jacobs et al., 1999; Strömberg, 2011). However, the evolution of hypsodonty does not necessarily coincide with the spread of grasslands since hypsodonty can also evolve in connection with other dietary, for instance abrasive leaf browsing (for discussion see Jacobs et al., 1999; Strömberg et al., 2013).

Relating these factors to palaeoclimates and palaeoenvironments, the following scenario emerges. The end of the Paleogene was characterized by a global cooling (Beerling, Royer, 2011; Figueirido et al., 2012). Rainfall was locally monsoonal (Huber, Goldner, 2012; Quan, Utescher, 2012) and therefore seasonal, indicating climates of open habitats (Utescher, Mosbrugger, 2007; Zhang et al., 2012). At the Paleogene-Neogene transition, aridity increased (Zachos et al., 2001, 2008) and may have reduced tree cover possibly also through increased fire (Bond et al., 2005; Bond, 2008). At the end of the Oligocene, global temperatures raised and first open grass-dominated habitats appeared, and they became dominant biomes during the Miocene and Pliocene (Jacobs et al., 1999; Bredekamp et al., 2002; Strömberg, 2011). The warm climate continued to the middle Miocene climate optimum followed by a cooling trend and increased seasonality culminating in the Pleistocene. It appears that convincing evidence of an increase in area of open and dry habitats from the early Eocene to the present has accumulated (Jacobs et al., 1999; Retallack, 2001; Strömberg, 2011; Bouchenak-Khelladi et al., 2014a, b).

### 6.2.3 Spread of $C_4$ grass-dominated open habitats

Emergence of  $C_3$  grass-dominated habitats seems to precede the spread of  $C_4$  grasslands by up to 20 million years. The spread of  $C_4$  grass-dominated open habitats at the late Miocene/early Pliocene at the expense of  $C_3$  grass-dominated open habitats in tropical and subtropical regions remains one of the less understood phases in the evolution of grass-dominated ecosystems and is extensively discussed in the literature. Since the Eurasian steppe belt is situated outside subtropical latitudes and is dominated by  $C_3$  grasses, we will only shortly deal with the rise of  $C_4$  grasslands.

The appearance of  $C_4$  grassy ecosystems 6–8 Mya was not correlated with shifts between temperate and tropical biomes since grasses are believed to be *a priori* a warm-adapted clade (see above). Dominance of  $C_4$  grasses has been attributed to decreasing atmospheric  $pCO_2$ , reductions in mean annual precipitation, and the development of seasonal climates (Edwards et al., 2010; Edwards, Smith, 2010). Above that, increased fire frequencies probably have been an additional major factor in the spread of  $C_4$  grass-dominated ecosystems (Cerling et al., 1993; Bond et al., 2005; Keeley, Rundel, 2005; Bond, 2008). This is corroborated by fossil charcoal records, which parallel the late Miocene expansion of  $C_4$  grasslands (Keeley, Rundel, 2005; Bond, 2008). Fire does not only limit trees in  $C_4$  grasslands but creates high light environments, which favour  $C_4$  grasses. The expansion of  $C_4$  grasslands is not strictly synchronous between continents and regions and leads one to assume complex and different ecological triggers between regions (Jacobs et al., 1999; Edwards et al., 2010; Strömberg, 2011).

## 7. Climate and landscape history in the Cenozoic Era

The Cenozoic climate history of Eastern Asia is a complicated and contentious issue and remains a matter of continuous debate, particular because of its bearing on the development of the East Asian monsoon system and the initial aridification in the Asian interior. Uplift of the Himalayan-Tibetan Plateau, changes in land-sea distribution and global climate trends have been invoked as driving forces behind Cenozoic palaeoclimate changes. However, there is little consensus about which one is the most important driver.

### 7.1 Global Cenozoic climate

Global climate during the Cenozoic era changed from ice-free poles and warm conditions in the Paleocene to ice-covered poles and cold conditions in the Neogene. This occurred in several steps. Long-term transitions and short-term changes are observed, and the overall cooling trend was interrupted by warming periods. The most pronounced climatic cooling event during the whole Cenozoic era was the Eocene-Oligocene transition (EOT), the transition from a 'greenhouse' to an 'icehouse' climate, followed by the cooling/glaciation event at the Oligocene-Miocene boundary and the middle Miocene cooling (Zachos et al., 2001, 2008; Mudelsee et al., 2014, and literature therein).

Geological and geographical events in the Cenozoic era strongly affected climate and vegetation patterns in extratropical Eurasia. Two marine seaway systems were of extraordinary importance for Cenozoic climate development, the North - South stretching Arctic Sea - Tethys system of seas and straits, and the West - East stretching seas and straits of the Tethys and Paratethys. The uplift of the Himalayan-Tibetan Plateau has been invoked as one of the driving forces behind Cenozoic palaeoclimate changes in East and Central Asia.

### 7.2 Tethys and Paratethys

The Tethys Sea separated the supercontinents Laurasia in the North from Gondwana in the South. It began to form during the earliest part of the Mesozoic Era. With the break-up of Pangaea into Laurasia and Gondwana during the Jurassic, the Tethys gradually opened into a dominant marine seaway of the Mesozoic. Plate tectonic activities and the collision of India with Asia caused the destruction of the Western Tethys in the late Eocene. The Mediterranean and the intracontinental Paratethys basins came into existence. In the Eocene, the Paratethys spread from the Molasse basin north of the Alps eastwards up to the Tarim Basin in western China. Strong changes occurred in the history of the Paratethys. From an open ocean in the Eocene with connections to the Polar Sea via the Turgai Strait, it changed to an enclosed basin in the early Oligocene. The emerging mountain systems of the Alpine fold belt increasingly separated the Paratethys from the Mediterranean. By the middle Miocene the final disconnection of the Paratethys occurred (Rögl, 1998, 1999; Popov et al., 2004; Harzhauser, Piller, 2007) but Tethys - Paratethys connections remained extant (Popov et al., 2006). The central Paratethys (Pannonian basin) was isolated from the Eastern Paratethys at the beginning of late Miocene ca. 11.6 Mya (Ter Borgh et al., 2013) and became modified into a long-lived brackish lake-sea (Lake Pannon). Lake Pannon continuously shrank and disappeared during the Pliocene (Popov et al., 2006). During the late Miocene, the eastern Paratethys turned into an intracontinental brackish basin and was subdivided into two major basins, the Dacian-Euxinian basin system and the Caspian basin. Major deformation in the eastern Paratethys area and its surrounding mountain ranges occurred in the early Pliocene. The two basins existed as long-lived lake-seas until middle to late Pliocene (Akchagylian-Caspian basin) and middle Pleistocene (Karangation-Euxinian basin) (Popov et al., 2006). Remnants of the Para-

tethys are from West to East the Black Sea, Azov Sea, Caspian Sea, Aral Sea and Lake Balkhash.

### 7.3 Arctic Sea – Turgai Basin

The West Siberian Turgai Basin stretched over 3500 km from the Aral Sea in the South to the recent Franz Josef Land and Severnaya Zemlya in the North and connected the open sea basins of the Arctic and Tethys. Opening, closure, widening and narrowing of these straits had a strong influence not only on marine ecosystems but also on land biota. The evolution of this system of epicontinental seas and straits started in the early Palaeocene. The connection of the Tethys with the Arctic Sea via the Turgai Strait enabled warm-water exchanges, and the different water masses (Arctic, Tethys and North Atlantic) affected direction of atmospheric currents and, therefore, heat transport and climatic fluctuations (Akhmetiev, Beniamovski, 2009; Akhmetiev, Zaporozhets, 2014). The West Siberian Sea and the Turgai Strait disappeared in the early Oligocene. When the straits became closed or land bridges were formed, animal and plant communities could migrate to the West and East of Eurasia more easily than before (Akhmetiev, Beniamovski, 2009; Akhmetiev et al., 2012; Akhmetiev, Zaporozhets, 2014).

### 7.4 Uplift of the Tibetan Plateau

The history of the Tibetan Plateau uplift and its effects on climate during Cenozoic time are still a matter of considerable debate (Renner, 2016 and literature therein). Evidence for the Tibetan Plateau uplift comes from a wide range of studies, including earth sciences, palaeoclimate and palaeoenvironmental studies, and climate simulations. In the light of recent studies, it would appear that the uplift is much older than previously assumed. It started after the Indian-Eurasian collision in the early Eocene (55–50 Mya), and the central Tibetan Plateau reached a height of ca. 4000 m already in the mid-Eocene (Wang et al., 2008; Lippert et al., 2014). A proto-Tibetan Plateau probably developed already in Cretaceous – Paleogene time due to crustal thickening (Lippert et al., 2014). During the past 15 Ma, the Tibetan Plateau has grown outward on its north-eastern and eastern sides, and northern Tibet may have risen higher (Molnar et al., 2010). The high mountain ranges to the North of the Tibetan Plateau have developed largely in mid- and late-Miocene time (Tian Shan, Altai-Sayan) or are thought to be at least of Oligocene age (Hangay Mts.) (Caves et al., 2014, 2017). However, elevation estimates for

the Tibetan Plateau region may differ by kilometres depending on the proxy data used and on palaeogeography and climate models employed (van Hinsbergen, Boschman 2019).

### 7.5 Onset of monsoonal circulation

Climate in Eastern Asia is composed of humid (monsoon) climate in the East and South, arid and semi-arid climate in the North and its western parts. Three prominent features characterize the humid/arid climates in East Asia: the East Asian summer monsoon, the South Asian (Indian) monsoon and the winter monsoon. The onset of monsoonal circulation has been placed in the Eocene (Licht et al., 2014; Caves et al., 2015), early Miocene (Guo et al., 2008; Lu, Guo, 2014), and late Miocene (An et al., 2001). Meanwhile, however, a Palaeogene age of monsoonal circulation can be regarded as definite. Recent evidence for strong Eocene monsoons indicated by varying oxygen isotope values in gastropod shells and mammalian teeth and aeolian dust deposition (Licht et al., 2014) is confirmed by climate proxy data from cyclic geochemical alternations in fossil oysters (Bougeois et al., 2018). Palaeobotanical data point to the origin of the Asian winter monsoon to at least late Oligocene (Sun, Wang, 2005), and convincing evidence accumulated to prove that the Asian winter monsoon existed by at least the early Miocene inferred by loess deposition in basins northwest of the Tibetan Plateau (Guo et al., 2002; Lu, Guo, 2014). A study by Srivastava et al. (2012) on a fossil megafloora suggest that the South Asian monsoon (Indian monsoon) was already established by late Oligocene times but probably existed as early as the early Eocene as evidenced by palaeobotanical and palaeozoological data (Shukla et al., 2014). The East Asian summer monsoon also existed by at least the late Oligocene evidenced by palaeobotanical data (Srivastava et al., 2012; Meng et al., 2018).

Origin of the winter monsoon and the East Asian monsoon are of particular importance for unravelling the evolutionary history of the semiarid steppe climate in Central Asia. The East Asian monsoon influences precipitation patterns of the Mongol-Chinese steppe region in bringing summer rain. The winter monsoon-in-itself does not directly affect steppe climates. However, since the winter monsoon circulation is dominated by the Siberian High, which as a semi-permanent high-pressure system in winter time is a prerequisite for the steppe climate, the winter monsoon provides palaeoclimate proxy data for the strength and age of the Siberian High and thus steppe climate.

### 7.6 Aridification of Central Asia

With respect to the origin of the Eurasian steppe, the temporal and spatial development of a steppe climate (seasonal and semiarid climate) is of special importance. Establishment of arid conditions within interior Asia is thought to have occurred already during the Eocene (Dupont-Nivet et al., 2007; Bosboom et al., 2014; Li et al., 2018), Eocene-Oligocene transition (Sun et al., 2010; Sun, Windley, 2015), throughout the Neogene (Caves et al., 2016), early Miocene (Guo et al., 2002, 2008) and late Miocene (Sun et al., 2009; Liu et al., 2016). Researchers arguing for a Paleogene aridification onset, suggest that the Eocene climate of Asian continental interior was semi-arid and strongly seasonal, and retreat of the Paratethys and global cooling at the Eocene-Oligocene transition (EOT) affected Central Asia and caused enhanced aridification (Bosboom et al., 2014; Sun, Windley, 2015). Li et al. (2018), however, argue for global cooling and uplift of the Tibetan Plateau as main factors, and only insignificant role of land-sea redistribution, whereas Sun et al. (2014) claimed global cooling rather than tectonic uplift. It would appear that global cooling and retreat of the Paratethys Sea together with the uplift of the Tibetan Plateau were major factors in the initial aridification of Central Asia.

It has been suggested that the Paleogene climate in East Asia was dominated by a zonal pattern with a latitudinal arid/semiarid band stretching from the Chinese eastern coast (ca. 25–35°N latitude) to Central Asia (ca. 30–45°N latitude), and it has been argued that this so-called ‘middle arid zone’ was controlled to a large extent by desert and steppe climates (BWh and BSh climates in the Köppen-Geiger climate classification system) (Zhang et al., 2012 and literature cited therein). However, according to Quan et al. (2012, 2014), the middle part of East Asia was apparently not covered by desert and/or steppe vegetation during most of the Paleogene.

A renewed aridification step occurred in Central Asia at the end of the Oligocene/early Miocene. Miocene uplift of the Pamir, Tian Shan and Altai blocked the westerlies and led to enhanced aridification and recycling of precipitation patterns (Caves et al., 2016; Bougeois et al., 2018, and literature cited therein). Elevation of the Tian Shan and Altai during the Miocene created a seasonality boundary with predominantly spring and fall precipitation to the west (Kazakhstan) and primarily summertime precipitation to the east (NW China and Mongolia) (Caves et al., 2017).

The aeolian red clay and loess deposits from the Chinese Loess Plateau in northern Central China are derived from Mongolia and were transported by winter monsoon in the late Oligocene/early Miocene to the Loess Plateau (Lu, Guo, 2014). The aeolian deposits from the Junggar Basin in north-western China, however, are derived from Kazakhstan and were transported by westerly winds (Sun et al., 2010). They indicate that aridity in Kazakhstan started during the Paleogene (late Oligocene/early Miocene: Sun et al., 2010; early Oligocene after retreat of the Paratethys: Akhmetiev, Zaporozhets, 2014; Eocene: Velichko, 1999; Utescher, Mosbrugger, 2007).

## 7.7 Paleogene vegetation in extratropical Eurasia (Palaeocene to Oligocene)

### 7.7.1 General features

Vegetation belts in the Paleogene were mainly determined by the global climatic zonation. In the Northern Hemisphere, two main climate/vegetation belts can be distinguished, the Boreal zone (Boreal Flora) and the Tethys zone (Tethys Flora). The Boreal belt extended from the southward adjoining Tethys belt to the Polar region, the Tethys belt from its northern border with the Boreal belt to the northern rim of the Tethys in the South. Climate in the Boreal zone was warm and humid, and a subtropical to paratropical climate prevailed in the Tethys zone. However, the two seaway systems outlined above (Tethys - Paratethys and Arctic Ocean - Turgai Basin) strongly affected these zonal patterns. This situation caused distinct latitudinal temperature gradients in the western and eastern part of the Eurasian continent and led to a climate asymmetry of Eurasia during the Paleogene. With the vanishing Tethys during the second half of the Eocene, the Tethys Flora belt was reduced and finally disappeared.

In summarizing the major vegetation types and floras of the Paleogene in Eurasia, we rely mainly on Wolfe (1985), Mai (1995), Velichko (1999) and relevant chapters in Velichko and Nechaev (1999), Akhmetiev and Beniamovski (2009), Akhmetiev (2010), Akhmetiev and Zaporozhets (2014), Utescher and Mosbrugger (2007), and literature cited therein.

In the early Palaeocene in Eurasia, the Boreal - Tethys zonal border runs approximately from England - Balticum - Middle Ural - Altai - Mongolia - Primorye to Japan. Thus, a significant part was occupied by the Boreal zone characterized by a mesophyllous moderately thermophilic coniferous-broadleaved deciduous forest flora ('Tsayagan Flora'), particularly in the northern and eastern parts

of the continent. In the Tethys zone, paratropical rainforests (mixture of temperate and tropical forest elements) prevailed in western and southern parts ('Gelinden Flora'). During the maximal warming in the late Palaeocene to early Eocene, the paratropical Tethys Flora extended to high latitudes and reached its maximal extension. It is characterized by a most thermophilous vegetation of polydominant broad-leaved forests. The second half of the Eocene is characterized by a long-term cooling trend. The paratropical rainforests of the Gelinden Flora were replaced and impoverished by subtropical evergreen laurophyllous vegetation and rainforests ('Poltavian (= Volhynian) Flora').

Seasonal subtropical monsoon-type floras developed in eastern Eurasia and extended northwards. These humid subtropical forests pushed back the Boreal forests. The late Eocene is generally characterized by relative low temperatures and aridization tendencies. In southerly regions of Kazakhstan and Central Asia, a sclerophyllous small-leaved shrub vegetation developed and expanded with a flora close to the 'Ancient Mediterranean Flora' sensu Takhtajan. At the end of the Eocene/beginning of Oligocene, the Antarctic glaciation induced the transition from the 'warm' to the 'cold' biosphere (see above). The Oligocene is marked by the notable expansion of the Boreal zone and the formation of temperate deciduous mesophyllous coniferous-broadleaved forests (Turgai Flora). The Turgai Flora occupied great parts of extratropical Eurasia and replaced the subtropical Tethys Flora in the middle and high latitudes of Eurasia. Evergreen plants disappeared. In the plains, formerly occupied by sea basins of the Paratethys, polydominant coniferous - broad-leaved forests became the zonal vegetation types, which were replaced at the Oligocene/Miocene boundary by xerophyllous vegetation. This Old Mediterranean zone was the core of the ancient Mediterranean Miocene flora.

Despite the general cooling trend, the Paleogene was nevertheless a warm period with sea surface temperatures and terrestrial temperatures significantly higher than modern ones, at least in the early Paleogene (Bosboom et al., 2011; Hansen et al., 2013; Naafs et al., 2018 for review and summary). For northern Eurasia, terrestrial temperatures below 0 °C are reported not before the end of the Oligocene (Velichko, 1999). Thus, a modern steppe climate equivalent with hot summers and cold winters (temperatures well below 0 °C) cannot be expected but arid and semiarid climates and steppe/savannah landscapes under a then higher temperature regime might well have developed.

Subtropical subarid and arid regions were widespread in southern Europe, Southwest Asia and Central Asia (see chapter 7.6 above). In Kazakhstan and Central Asia there are signs of aridity in the first half of the Paleogene (*Ephedra*, *Artemisia*, *Salicornia* pollen). The belt of aridity moved to the South and became semiarid in the second half of the Eocene (Velichko, 1999). A small-leaved Lauraceae and *Rhus* shrub vegetation expanded and evaporites formed (Velichko, 1999). Utescher and Mosbrugger (2007), however, did not find indications for Eocene xerophytic vegetation types in the seasonally drier regions of southeastern Europe, western Asia and southern China. On the other hand, a steppe environment with xerophytic shrublands as indicated by *Ephedra* pollen constituted a large part of the Xining Basin in the northeastern Tibetan Plateau region. This arid landscape initially lacked typical Neogene and present Asian steppe elements such as *Artemisia*, Chenopodiaceae and Poaceae but these emerged and increased toward the Eocene-Oligocene Transition (Dupont-Nivet et al., 2008). Aridification of the Xining Basin in the late Eocene is also indicated by well-dated sediment records (Abels et al., 2011).

Across the EOT, large mammalian faunal turnovers and extinctions are documented for Europe ('Grande Coupure', e. g., Hooker et al., 2004) and Mongolia ('Mongolian Remodelling', Meng, McKenna, 1998). Open steppe formations at the EOT are reported from southwest Mongolia (Sun, Windley, 2015). Simultaneous changes in fauna, flora, and climate across the EOT in the Junggar Basin, northwestern China, indicate a change from a mixed coniferous - broad-leaved forest in a warm-humid climate to a forest-steppe landscape in a dry-temperate climate (Sun et al., 2014). The pollen flora of this ecosystem includes typical contemporaneous steppe elements (*Artemisia*, *Ephedra*, Poaceae, Cyperaceae, Chenopodiaceae, Asteraceae, Brassicaceae and others).

The Oligocene was characterized by recurring glacial episodes and a warming trend at the end of the Oligocene (Zachos et al., 2001; Pälike et al., 2006; Mudelsee et al., 2014). Stepwise aridification of Central Asia after the EOT climate cooling is indicated by major turnovers in Oligocene mammal faunal communities (Harzhauser et al., 2016). According to these authors, a semiarid steppe developed at the EOT in Mongolia, and during the early Oligocene, Serengeti-like mammal communities are recorded. An Oligocene woody savannah is also hypothesized for northern China (Gomes Rodrigues et al., 2012).

### 7.7.2 Synopsis of Paleogene climate and vegetation history in extratropical Eurasia

A synopsis of the extratropical Eurasian climate and landscape changes and vegetation history during the Paleogene is presented in Table 1, based mainly on Mai (1995), Velichko (1999), Akhmetiev and Beniamovski (2009), Akhmetiev (2010), Gomes Rodrigues et al. (2012), Akhmetiev and Zaporozhets (2014), Sun et al. (2014), Sun and Windley (2015), Harzhauser et al. (2016), and Popova et al. (2017).

## 7.8 Neogene vegetation in extratropical Eurasia (Miocene to Pliocene)

### 7.8.1 Neogene climate/landscape history

The Neogene (ca. 23–2.6 Mya) is an especially important time period for the formation of the Eurasian steppe belt. During this time, major reorganizations of climate, continents, mountain ranges and oceans occurred in northern Eurasia. These events resulted in the redistribution of precipitation on a continental scale, with some areas drying and others becoming more humid, and affected the distribution of vegetation and mammals. The Miocene was the phase ('precursor') that predetermined the beginning of the present-day zonal structure of the landscape. Especially the late Miocene (ca. 11–5 Mya) was a time of large changes, and a continent-wide restructuring of the distribution of environments. At the end of the Miocene a new zonal structure component appeared – a zone of steppe (Velichko, 1999).

Fossil plants provide one of the best proxy data for palaeoenvironmental reconstructions. Palynological evidence as well as plant macrofossils for forest-steppe and steppe biomes in Neogene Eurasia are numerous, especially documented in the Russian literature. Several methods have been developed to reconstruct palaeovegetation and palaeoenvironments from palaeobotanical proxies and models (Francois et al., 2017). Mammals as consumers of vegetation have also been used to describe and reconstruct palaeoenvironments for at least a century. As a rule, mammal proxy data (for instance hypsodonty values of fossil mammals) seem to agree with paleovegetation data, showing similar large-scale patterns and estimated precipitation values (Eronen, 2006; Eronen et al., 2010; Fortelius et al., 2014).

In the early Miocene most areas of the Eurasian continent were humid and forested, only Central Asia had some areas of drier environment (see chapter 7.6). A general drying trend started in Eurasia around the middle Miocene (ca. 15–11 Mya). Landscape



Table 1

## Synopsis of Paleogene climate and vegetation in extratropical Eurasia

Series/ Subseries	Western Eurasia (west of Turgai Basin)	Eastern Eurasia (east of Turgai Basin)
<b>Oligocene</b> (33.9–23 Ma)	Decreasing temperature; warm-temperate forests with subtropical elements widespread, evergreen plants disappeared at the end of the Oligocene; ‘Turgai Flora’ in some regions;  Pronounced global cooling at EOT and faunal turnover (‘Grande Coupure’)	Decreasing temperature, with frost in Kazakhstan and Central Asia; deciduous mesophyllous coniferous-broadleaved forest widespread (‘Turgai Flora’), evergreen plants disappeared; stepwise aridification, steppe/savannah landscapes in Central Asia;  Pronounced global cooling at EOT and faunal turnover (‘Mongolian Remodelling’)
<b>Late Eocene</b> (38–33.9 Ma)	Subtropical evergreen laurophyllous and rainforest vegetation prevailed	Subtropical monsoon-type forests widespread; ‘Ancient Mediterranean Flora’ in Kazakhstan and Central Asia; steppe landscapes in Central Asia
<b>Middle Eocene</b> (47.8–38 Ma)	Cooling trend, Tethys Flora disappeared, replaced by subtropical evergreen vegetation (‘Poltavian Flora’)	
<b>Early Eocene</b> (56–47.8 Ma)	Maximal extension of Tethys Flora; Cenozoic climatic optimum	
<b>Paleocene</b> (66–56 Ma)	Tethys Flora prevailed in western Eurasia - Boreal Flora prevailed in eastern Eurasia  Climate asymmetry between western and eastern Eurasia  Northern ‘Boreal Flora’: coniferous-broadleaved deciduous forests (‘Tsagayan Flora’); humid warm-temperate climate; Northern ‘Tethys Flora’: paratropical rainforests (‘Gelinden Flora’); humid subtropical-like climate;	

Notes: Standard chronostratigraphy, see Table 2. For References see Text. Table is not scaled to geological time.

opening in many areas of Eurasia appears to be linked with Late Neogene cooling and went along with an increasing seasonality of precipitation and continentality of the palaeoclimate. Forests were replaced by woodlands and grasslands, particularly at mid-latitudes (van Dam, 2006; Utescher et al., 2011, and literature cited therein). This is in line with the global Cenozoic climate history, which shows a clear trend towards a globally drier state, as indicated by the worldwide development and expansion of grassland and desert ecosystems in the Neogene (Retallack, 2001). The ultimate causes of this global aridification are not yet fully understood, although it is commonly believed that there is a general relation with the global Cenozoic cooling.

During the late Miocene, arid conditions, seasonal climates and open environments spread at a continental scale, and mammal communities adapted to open country developed. At the end of the Miocene, typical steppe animals are recorded from

eastern and southeastern Europe (Mai, 1995). They belong to the so-called ‘Pikermian chronobiome’ (Hipparion or Pikermi fauna), named after the small village Pikermi near Athens, Greece. The Pikermi fauna assemblage is characterized by a great diversity of horses, rhinoceroses, antelopes, giraffes, relatives of elephants, hyenas, cats and many other mammals, and by a poor representation of deer. The Pikermi fauna of various regions differed in genus and species composition. In Eurasia, the core area of the Pikermian chronofauna was south of the Paratethys from the Balkans to Afghanistan, but it ranged much further to East Asia and northeastern Africa (Eronen et al., 2009). At its maximal distribution centred on mammal zone MN12 (8.0–6.7 Mya, see Table 2), it was widely distributed also in temperate latitudes throughout Europe and Central Asia. During the early Pliocene (MN14 and MN15, 5.3–3.2 Mya, Table 2), the Pikermian fauna vanished from Eurasia (Eronen et al., 2009).

The Pikermian chronobiome is often taken as a proxy for a steppe/savannah landscape. Several authors have reconstructed the ‘Pikermian palaeobiome’ as a seasonal woodland mosaic including areas with extensive tree cover, open grassy and herbaceous habitats, and shrubland (Eronen et al., 2009 and literature cited therein). An “Old World savannah palaeobiome” has been

suggested by Kaya et al. (2018), which developed in central and western Asia and expanded with increasing aridity to its maximal peak 9–6 Mya. It is also argued that the Pikermian chronofauna may have lived in different biomes, including temperate forests, forest-steppe, steppes/savannahs, and shrubland (Denk et al., 2018; see also Kovar-Eder et al., 2006; Eronen et al., 2010).

Table 2

Neogene Standard chronostratigraphy, correlation with Eurasian regional stages and Neogene mammal zones

Time Scale	Standard Chronostratigraphy				REGIONAL STAGES				European Land Mammals									
	Series	Sub-series	Stage	Ma	Central Paratethys	East European Plain	West Siberian Plain	China	MN Zones	Ma	Mega Zones							
Quaternary PLEISTOCENE PLIOCENE NEOGENE MIOCENE OLIGOCENE	PLEISTOCENE	U	CALABRIAN	0.78	ROMANIAN	KUYALNICIAN	KULUNDINIAN	NIHEWANIAN	18	1.8	VILANYIAN							
			GELASIAN	1.80					17			2.6						
	PIACENCIAN	2.58	DACIAN	KIMMERIAN				NOVOSTANICHNIAN	16	3.2								
	ZANGLEAN	3.6			15	3.9												
	UPPER	M	MESSINIAN	5.33	PONTIAN		PONTIAN	PAVLODARIAN	GAOZHUANGIAN	14	5.0	TUROLIEN						
			TORTONIAN	7.25	PANNONIAN	MAEOTIAN	BAODEAN		13	6.7								
	MIDDLE	L	SERRAVALLIAN	11.63				SARMATIAN	SARMATIAN		TAVOLZHANIAN	BAHEAN	12	8.0	VALLESIAN			
					LANGNIAN	13.82	BADENIAN			KONKIAN KARAGANIAN TSHOKRAKIAN			BESTSHEULIAN			TUNGGURIAN	11	8.7
																	10	
	LOWER	L	BURDIGALIAN	15.97	EGGENBURIAN	EGGERIAN	KARADZHALGANIAN	ABROSIMOVIAN	XIEJIAN	9	11.1	ASTARACIAN						
										OTTNANGIAN			KARPATIAN	KOTSAKHURIAN	SHANWANGIAN	8	13.5	
																7		15.0
										EGGENBURIAN			KARPATIAN	KOTSAKHURIAN	SHANWANGIAN	6	17.0	
																5		18.0
	AQUITANIAN	20.4	EGGENBURIAN	SAKARAULIAN	ABROSIMOVIAN	XIEJIAN	3	20.5	ORLEANIAN									
	20.5	EGGERIAN	KARADZHALGANIAN	ABROSIMOVIAN	XIEJIAN	2	22.5											
	23	EGGERIAN	KARADZHALGANIAN	ABROSIMOVIAN	XIEJIAN	1	23.8	AGEANIAN										
	23	EGGERIAN	KARADZHALGANIAN	ABROSIMOVIAN	XIEJIAN	1	23.8	TABENBULUKIAN	1	23.8	AGEANIAN							

References: Standard Chronostratigraphy: International Chronostratigraphic Chart. <http://www.stratigraphy.org/index.php/ics-chart-timescale>;  
Central Paratethys and Eastern Paratethys adopted from Rögl (1998) and Steininger, Wessely (2007); West Siberian Plate: adapted from Akhmetiev (2005) and Popova et al. (2012); China: Deng, Hou (2014), see also Wang et al. (2013).

**7.8.2 Synopsis of Neogene climate and vegetation history of the Mongol-Chinese steppe region**

Standard chronostratigraphy and correlation with Eurasian regional stages are presented in Table 2. A synopsis of the climate and landscape changes and vegetation histories during the Neogene is presented in Table 3, and is based mainly for northern China and adjacent Mongolia on Jia et al. (2003), Fortelius et al. (2006), Jiang and Ding (2009), Liu et al. (2009, 2011), Utescher et al. (2011), and Jacques

et al. (2013), and for the Asian interior and Baikal region on Erbajeva and Alexeeva (2013).

**7.8.3 Synopsis of Neogene climate and vegetation history of the Euro-Siberian steppe region**

Standard chronostratigraphy and correlation with Eurasian regional stages are presented in Table 2. A synopsis of the climate and landscape changes and vegetation histories during the Neogene is presented in Table 4 and is based mainly on the following literature.

Table 3

## Synopsis of Neogene climate and vegetation in the Mongol-Chinese steppe region

Series/ Subseries <sup>1)</sup>	Northern and western China (and adjacent Mongolia) <sup>2)</sup>	Baikalian Region <sup>3)</sup>
<b>Pliocene</b> (5.3–2.6 Ma)	Western China is arid, aridification of north China, strengthening of the winter monsoon, Pliocene cooling.  Replacement of forests by forest-steppe and steppe, increase in deciduous and herb components in north and northeast China	Cooling and aridity increased but climate was still mild  Forests were gradually replaced by forest-steppe and steppes; most thermophilic elements disappeared
<b>Upper Miocene</b> (11.6–5.3 Ma)	Increasing aridity in western and central China, aridisation in north China; at the end a cool and humid episode  Forests and increasing steppe vegetation, reversed development during cooler episode	Climate warm and humid but trend towards cooling and aridification  Broad-leaved and mixed coniferous forests, open landscapes extended
<b>Middle Miocene</b> (16–11.6 Ma)	North China humid and warm, extension of drier areas from western China to the east.  Mixed mesophytic forests; at the end of Middle Miocene, steppe vegetation dominated in northwest China	Climate similar to Lower Miocene  Vegetation similar to Lower Miocene
<b>Lower Miocene</b> (23–16 Ma)	Western China humid, later increasing aridity in western China  At beginning evergreen and deciduous forests, later more open vegetation, increase in herb component	Warm and moist climate  Broad-leaved/coniferous forests widespread, but also forest-steppe and restricted steppe landscapes

Notes: <sup>1)</sup> Standard chronostratigraphy, see Table 2. For references <sup>2), 3)</sup> see the text. Table is not scaled to geological time.

References for eastern and southeastern Europe: Mai (1995), Velichko (1999), Velichko et al. (1999), Popescu (2006), Syabryaj et al. (2007), Kovar-Eder et al. (2008), Bruch et al. (2011), Ivanov et al. (2011), and Utescher et al. (2011). References for the West Siberian and Kazakh Plains: Akhmetiev et al. (1999), Arkhipov et al. (1999), Velichko (1999), Bruch and Zhilin (2007), and Popova et al. (2012, 2013, 2017).

## 8. Climate and landscape history in the Pleistocene

### 8.1 Pleistocene classification systems and climate history

The Quaternary (Pleistocene and Holocene) is characterized by the development of widespread glaciations in temperate mid-northern latitudes and by associated physical and biotic readjustments. In the context of progressive Cenozoic cooling, the onset of significant Northern Hemispheric glacia-

tions started 2.8–2.4 Mya. Based on this evidence, the base of the Pleistocene and thus the beginning of the Quaternary period/end of the Neogene has been recently shifted by the International Commission on Stratigraphy ICS from the base of the Calabrian stage (1.8 Mya) to the base of the Gelasian stage (2.58 Mya; Gibbard, Head, 2009). This issue is of considerable relevance for our discussions since Quaternary system classifications are different depending on when they were compiled. In addition, traditional Russian terminology of Pleistocene chronostratigraphic units differs from the standard ICS terminology. Table 5 presents correlation between the ICS chronostratigraphical units and those used in Western Europe, East European Plain and Siberian Plain as well as Marine Isotope Stages (MIS). Isotope studies from the bottom sediments of the World's oceans have indicated that as many as 52 cold and interspersed warm climate periods occurred during the last 2.6 million years. In contrast to the deep sea, continental evidence is

so incomplete and regional variable that terrestrial ocean record for a global chronological foundation glacial-interglacial stratigraphies must refer to the (Cohen, Gibbard, 2011).

Table 4

## Synopsis of Neogene climate and vegetation in the Euro-Siberian steppe region

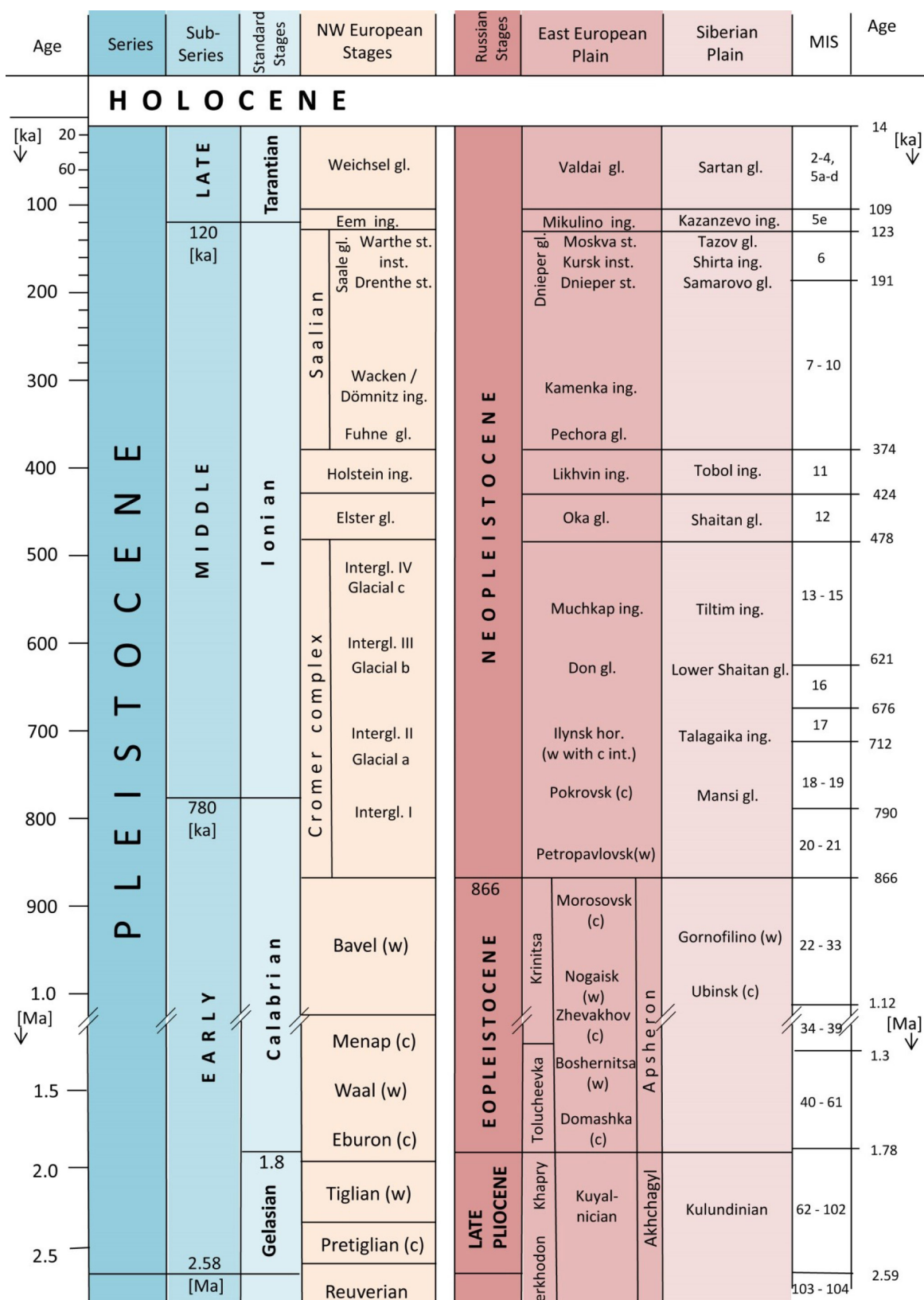
Series/ Subseries <sup>1)</sup>	Eastern and Southeastern Europe <sup>2)</sup>	West Siberian Plain <sup>3)</sup>	Kazakhstan Plains <sup>4)</sup>
<b>Pliocene</b> (5.3–2.6 Ma)	Frequency of cooling phases increased; aridity in cool epochs; continentality and aridity increased sharply from west to east;  Mixed coniferous forests in warm, steppe in cool epochs	Climate similar to modern one, only slightly different;  Spreading of dry steppes and semi-deserts, close to modern analogous	Dry and wet climate phases, basic cooling in 2 <sup>nd</sup> half of the Pliocene  Vegetation similar to southern parts of West Siberian and East European plain
<b>Upper Miocene</b> (11.6–5.3 Ma)	Slight cooling and drying; humid/drier and warmer/cooler cycles; increasing seasonality, continental climate in east Europe;  Forest in the north, forest-steppe in the south; true steppe only along Black and Caspian Sea	Boreal warm-temperate climate, change to drier conditions; semi-arid to arid climates;  Forests were replaced by forest-steppe in the north, further south dry steppes and semi-deserts on saline soils	Warm and dry climate, southern regions more arid than northern  Dry steppe and semi-desert landscapes
<b>Middle Miocene</b> (16–11.6 Ma)	Climate optimum, subtropical to warm-temperate;  Mixed coniferous and/or broad-leaved forests	Climatic optimum in whole Siberia; longitudinal temperature gradient from western Siberia to warmer conditions in the west;  Opening of landscape, spread of post-Turgai forested steppe	Climate more continental and higher seasonality; intensified aridization  Forest-steppe but herb- and grass-rich coenoses prevailed
<b>Lower Miocene</b> (23–16 Ma)	Warm and humid;  Mixed coniferous and/or broad-leaved forests	Warm-temperate;  Mixed coniferous and/or broad-leaved forests	Warm-temperate, trend to seasonality and continentality, beginning aridization;  Forests of Turgai type, forest-steppe and ‘prototypes of steppe’ (herbaceous coenoses) appeared

Notes: <sup>1)</sup> Standard chronostratigraphy, see Table 2. For references <sup>2), 3), 4)</sup> see text. Table is not scaled to geological time.

In the Early Pleistocene, global temperatures gradually cooled until roughly 1.2 Mya and cooling then stalled until the present (Snyder, 2016). The time between ca. 1.2 and 0.5 Mya, known as ‘Mid-Pleistocene transition’ (Head et al., 2008b), was a transition period in which low-amplitude ca. 41-ka climate cycles of the earlier Pleistocene were

replaced progressively by high-amplitude quasi 100-ka cycles. The latter variability begins at ca. 1.2 Mya, strengthens at ca. 1.0–0.9 Mya, and intensifies about 700–650 kya. Climatic cycles after about 700 kya were conspicuously asymmetrical (‘saw-toothed’ pattern) indicating slow ice build-up and subsequent rapid melting (Head et al., 2008b). This

**Table 5**  
**Pleistocene standard chronostratigraphy and correlation with Eurasian regional stages.**  
**Marine Isotope Stages are indicated**



Abbreviations: MIS – Marine Isotope Stages; c – cold, w – warm; hor. – Horizon; Intergl., ingl. – interglacial; gl. – glacial; inst. – interstadial, st. – stadial; int. – intervals.  
 References: Cohen, Gibbard (2011). Russian regional stages and their correlation with the standard chronostratigraphy are based on Cohen, Gibbard (2011), and on Velichko et al. (2005).

Early-Middle Pleistocene transition, through the increased severity and duration of cold stages, had a profound effect on the biota and the physical landscape, especially in the northern hemisphere.

### 8.2 Pleistocene landscape history

At the end of the Pliocene, various types of forest vegetation were characteristic for northern Eurasia, mixed forests of conifers and deciduous broadleaf trees in Europe, broad-leaved forests of several conifer taxa in Siberia. Forest steppe was widespread in southeastern Europe and western Siberia, whereas treeless steppe seems to have been confined to the dry regions of Middle and Central Asia (Frenzel, 1968a; Velichko, 1999). At the beginning of the Pleistocene (MIS 103, see Table 5) the climate began to cool down significantly initiating the first glacial period of the Pleistocene. Forests disappeared

in most regions of northern Europe and western Siberia and were replaced by various steppe formations. Only in eastern Siberia coniferous forests survived. In northern Eurasia, glacial periods were characterized by maximum distribution of various steppe communities, and interglacial periods were characterized by forests, which covered the Eurasian continent from the Atlantic coast in the West to the coast of the Okhotsk and Japanese seas in the East (Frenzel, 1968a, b; Velichko, 1999). “The recent vegetation of northern Eurasia resulted from a relentless contest between steppe and forest” (Frenzel, 1968b). Major events during the Pleistocene in Eurasia are presented in Table 6, based mainly on Velichko (1999), Head et al. (2008a, b), Dolukhanov et al. (2009), Ehlers and Gibbard (2011), and on literature cited therein.

**Table 6**

### Major events during the Pleistocene in northern Eurasia

<b>Geological time</b> (corresponding MIS stages)	<b>Climate/landscape and biotic events</b>
<b>130 to 10 ka</b> <b>Late Pleistocene</b> (MIS 5 to MIS 2)	Severity of continental climate reached a maximum, maximal spread of cryolithic zone, maximum loess deposition; glacial systems were reduced from west to east; open-arid landscapes dominated like tundra-steppe, semi-deserts, deserts; landscape zones shifted to south by 10° latitude; mammoth fauna complex fully developed; Khazarian and Khvalynian transgressions of Caspian Sea
<b>850 ka to ca.130 ka</b> <b>Middle Pleistocene</b> (MIS 21 to MIS 6)	Waves of deep cooling and warming; intensified development of permafrost, loess and glaciers/ice sheets; major continental glaciations; from ca. 625 ka onwards (MIS 16) high amplitude climate systems, highly asymmetrical variability; radical transformation of the zonal landscape structure; around 850 to 700 ka spread of large mammals across northern Eurasia, steppe mammoth first appeared; Baku transgression of Caspian Sea
<b>1.8 Ma to ca. 850 ka</b> <b>Upper Early Pleistocene</b> (MIS 61 to MIS 22)	Increasing long-term global ice volume, spread of permafrost, beginning dominance of periglacial components; about 1 Ma onset of quasi 100-kyr cycles and development of continental ice sheets; ‘prototypes’ of periglacial steppes during cold phases; Apsheron transgression of Caspian Sea
<b>2.6 to 1.8 Ma</b> <b>Lower Early Pleistocene</b> (MIS 104 to MIS 62)	Overall cooling and climate seasonality, opening of landscapes; onset of severe climate deterioration in NW Europe; strong aridification, expansion of deserts, major loess-palaeosol deposition in Central Asia; herbivore turnover between 2.6 and 2.2 Ma, appearance of modern ruminants; Akhchagyl transgression of Caspian Sea
<b>2.7 Ma</b> <b>end of Pliocene</b>	Synchronous glaciation of Greenland, Scandinavia and North America; weakening of summer monsoon in Central Asia; change from subtropical to boreal vegetation in central Europe; Akhchagyl transgression of Caspian Sea

Notes: Geological time, chronostratigraphical units and MIS stages in accordance with Pleistocene standard chronostratigraphy, see Table 5. Abbreviations: Ma – million years ago; ka – thousand years ago; LGM – Last Glacial Maximum; MIS – Marine Isotope Stages.

Main literature: Velichko, 1999; Head et al., 2008a, b; and literature cited therein. Table is not scaled to geological time.

The climatic macrocycles in eastern Europe and Siberia were associated with latitudinal shifts of the steppe belt (Devyatkin, 1993; Arkhipov, Volkova, 1994; Akhmetiev et al., 1999; Arkhipov et al., 1999; Velichko et al., 1999; Tarasov et al., 2000b). The steppe belt also faced significant longitudinal splits during the ice ages. These were caused by transgressions of the Caspian Sea north to the southern Ural Mountains and the Volga-Kama basin (Dolukhanov et al., 2009; Tudryn et al., 2013; Yanina et al., 2018, and literature cited therein), see Table 6. Ice damming of the Ob – Irtysh – Tobol river system by northern glaciers advancing far to the South followed by backwaters reaching the foothills of the Kazakhstan Highlands and of the Altai Mountains was another factor (Arkhipov, Volkova, 1994; Arkhipov et al., 1995, 1999; Tudryn et al., 2013).

The climatic macrocycles during the Pleistocene had far-reaching consequences for earth's geomorphology and distribution of vegetation zones. This is particularly obvious for the last ice age (MIS 5e – 2). Time since the last glacial maximum and the beginning of the following global warming is short so that the glacial geomorphological surface structures in many parts of the world are still clearly visible and present-day vegetation would mirror to a certain extent interglacial vegetation belts, if humankind would not have severely disturbed and changed the natural vegetation and their habitats. The Pleistocene, especially Late Pleistocene, has a key position in understanding preceding and present-day geographical distribution, structure and floristic composition of the Eurasian steppe belt. We, therefore, deal with the Late Pleistocene-Holocene paleoclimates and palaeoenvironments of the Northern Hemisphere in more detail.

### 8.3 Late Pleistocene classification systems and climate/landscape history

During the last glacial maximum (LGM), ca. 21–20 kyr cal BP, western and central Siberian lowlands remained ice-free (Astakhov, 2013). In northern and northeastern Siberia, glaciation was largely restricted to the mountains (Putorana and Verkhojansk Mts.). In Europe, the southern part of the Scandinavian ice shield stretched over Denmark, Germany north of the river Elbe, northern parts of Poland and Belarus, and covered the northwestern Russian Plain from Belarus to the Arkhangelsk Region (Svendsen et al., 2004; Ehlers et al., 2013a). No ice-dammed lakes during the LGM were observed along the northern glacier rim of the Russian Lowland, contrary to the situation at earlier glaciations (Astakhov, 2006, 2013; Ehlers et al., 2013a, b).

Greater mountain glacial complexes occurred in the Alps (Ehlers et al., 2013a) and in the Central Asian high mountains (Owen, 2013) including the Altai and neighbouring mountain systems (Lehmkuhl et al., 2011). Limited and local mountain glaciers are known from the Pyrenees, Carpathians and Caucasus.

Permafrost and loess deposition reached a maximum during Late Pleistocene. The Eurasian loess belt stretches from western Europe across the East European Plain, central and south Siberia to the central Chinese loess-plateau. The Siberian high-resolution loess-palaeosol sequences represent a significant data source of Quaternary climatic history in northern Asia. Palaeoenvironmental multiproxy data (sedimentary, pedogenic and biotic) from the series of palaeosols separated by loess beds provide evidence for strongly fluctuating climates and landscape development during the Late Pleistocene, and for changes in the vegetation zones during interglacial/interstadial and stadial stages (Chlachula, 2003; Rutter et al., 2003).

Correlation of Late Pleistocene chronostratigraphical terminology for eastern Europe and Russia is presented in Table 7. Major events during the Late Pleistocene in northern Eurasia are summarized in Table 8. The listed essentials are based mainly on Golubeva (1979), Frenzel (1992), Grichuk (1992), Akhmetiev et al. (1999), Arkhipov et al. (1999), Fradkina et al. (1999a, b), Korotky et al. (1999), Velichko et al. (1999), Chlachula (2001a, b, 2010), Shichi et al. (2007), Tarasov et al. (2009), Felauer et al. (2012), and Yanina et al. (2018).

During the last interglacial (MIS 5e), steppes were only found in southeastern Europe, near the Black and Caspian seas. In western Siberia, Kazakhstan and Central Asia (Mongolia) the southern boundary of this vegetation lay far to the South of its present position (Fig. 1). In northern Eurasia, main types of vegetation during the maximum cooling of the last glacial (MIS 2) were a mixture of cryophytic steppe and tundra communities, often summarized as “periglacial tundra”, “tundra steppes” and “periglacial steppe”. The more thermophilic loess-steppe and herb-steppe spread over interior regions of the Middle East and Central Asia. In northern Mongolia, grass-herb and sagebrush steppe formations dominated, while larch, birch and pine grew on the mountain slopes. Boreal forests were limited to mountainous areas in Europe and Asia, whereas broadleaved forests of nemoral type were restricted to southern Europe, Asia Minor, southern Urals and parts of the Altai. Also in China, Korea, Manchuria and central Japan (Fig. 2).

Table 7

## Late Pleistocene chronostratigraphic correlation for eastern Europe and Russia

Late Pleistocene (MIS)	East European Plain	Siberia	Russian Far East
ca. 25 – 10 ka (MIS 2, glaciation)	Late Valdai	Sartan	Partisanian
ca. 60 – 25 ka (MIS 3, interstadial)	Mid-Valdai (Dunalvo or Briansk interval)	Karginsky	Chernoruchinsky
ca. 75 – 60 ka (MIS 4, glaciation)	Early Valdai	Zyranka (Yermakovo in W Siberia, Muruktinsky in E Siberia)	Lazovian
ca. 115 – 75 ka (MIS 5a-d, interglacial)	Final stages of Interglacial (Mikulino)	Final stages of Interglacial (Kazantsevo)	Final stages of Interglacial (Nakhodkinsky)
ca. 130 – 115 ka (MIS 5e, interglacial)	Mikulino (Interglacial Optimum)	Kazantsevo (Interglacial Optimum)	Nakhodkinsky (Interglacial Optimum)

Notes: Abbreviations: MIS – Marine Isotope stages. For references see text.

## 8.4 Late Pleistocene vegetation

### 8.4.1 Use of terms

Nomenclature/terminology to describe vegetation and environments during the last ice age is extremely confusing. Terms like “tundra-steppe”, “steppe-tundra”, “periglacial vegetation”, “periglacial cold steppe”, “ice age steppe”, “arctic steppe”, “loess steppe”, “mammoth steppe”, and others, have to be discussed and clarified.

The terminological confusion has several roots. Some terms are synonymous as, for instance, tundra-steppe (preferred in Russian literature) and steppe-tundra (preferred in English literature). The main problem, however, is that the terms were never unequivocally defined. Yurtsev (last in 2001), for instance, used the term tundra-steppe for main vegetation types (ecosystems) and for landscapes (see below). In the “Atlas of Palaeoclimates and Environments of the Northern Hemisphere” Frenzel et al. (1992) attempted to avoid confusion of concepts and used different names for describing/characterization of vegetation, ecosystems (main vegetation), and landscape types of the LGM. However, still there is overlapping terminology as can be seen from Table 9. The term tundra-steppe is applied by Frenzel (1992) to characterize vegetation and by Velichko and Isayeva (1992) to name a landscape type, the term periglacial steppe – to name a main vegetation type (ecosystem) (Grichuk, 1992) as well as a landscape type (Velichko, Isayeva, 1992).

Guthrie (1982) introduced the term “Mammoth steppe” to a wider readership, and this new neologism is often used in recent literature. It indicates a

Late Pleistocene “low sward of herbaceous plants, with grasses, sedges, forbs and sages predominating” (Guthrie, 2001). This kind of vegetation was the grazing area of a megafauna dominated by the key grazers bison (*Bison spec.*), horse (*Equus spec.*) and woolly mammoth (*Mammuthus primigenius*) (Guthrie, 2001). This Mammoth fauna complex was widespread over vast areas of Eurasia and extended into North America during the last glacial (MIS 5d–MIS 2) (see Table 8). For the Eurasian branch (the Palaeartic) of the Mammoth fauna complex, two species became eponymous, *M. primigenius*, the woolly mammoth, and *Coelodonta antiquitatis*, the woolly rhinoceros. The distribution of the Mammoth-Coelodonta faunal complex in Eurasia (Baryshnikov, Markova, 1992; Kahlke, 2014) coincides with the extent of the permafrost landscapes during the LGM (Periglacial Tundra steppes and Periglacial steppes, Table 9). It is an open question whether the introduction of the new/additional term “Mammoth steppe” was/is necessary or not. One may ask whether the “Mammoth tundra-steppe assemblage” concept used preferably in Russian literature (Baryshnikov, Markova, 1992, and literature cited therein; Table 8) would not mean the same, and Walker et al. (2001) used “Mammoth steppe” and “steppe tundra” synonymously. In a narrow sense, however, mammoth steppe often means a Late Pleistocene palaeoenvironment of Arctic steppe-like vegetation with dominance of graminoids (see below).

The terminological confusion characterizes the prevalent situation and attempts to change it appear to be lost time. In this review, we prefer the term-



nology ‘periglacial tundra’ and ‘periglacial steppe’ as outlined in Table 9.

### 8.4.2 Tundra-steppe concept

Scientists now agree that climate over much of northern Eurasia during the Pleistocene glacial maxima was not the same as today’s arctic climate.

It was extremely continental and arid with winters colder and summers warmer than at present. This climate has no modern equivalents. Northern Eurasia was covered by a grassy vegetation characterized by both, tundra and steppe elements, whereas today a mesophytic tundra is the main vegetation of the subarctic-arctic climate zone. It is a moot point

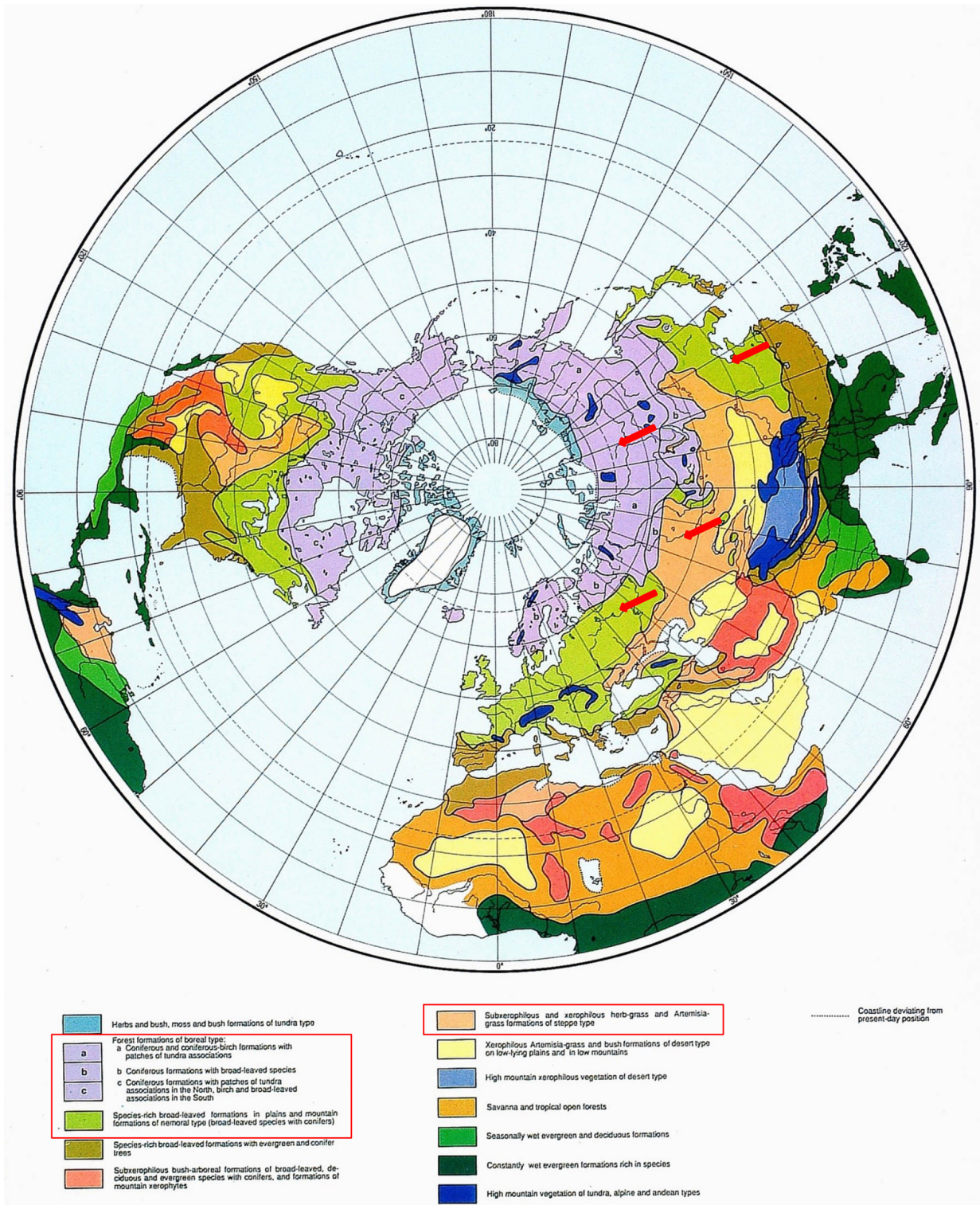


Fig. 1. Last Interglacial Vegetation of the Northern Hemisphere. Modified from: V. P. Grichuk (1992) in “Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere”.

whether the LGM vegetation types have any sort of present-day analogue as argued, for instance, by Walker et al. (2001) and Chytrý et al. (2018).

Evidence for a cold and arid steppe like vegetation was already provided at the end of the 19<sup>th</sup> and early 20<sup>th</sup> centuries when scientists studied loess deposition, vertebrate faunas and pollen spectra

from LGM deposits. Nehring (1890) discovered fossils of steppe mammals in glacial loess deposits in middle Europe. He also provided first evidence for a fauna nowadays characteristic for the northern Eurasian tundra, which preceded this steppe fauna. Later, Büdel (1949b, 1951) indicated a general two-stage climate succession during glacial cycles:



**Fig. 2. Main Types of Vegetation (Ecosystems) during maximum cooling of the Last Glaciation, Modified from: V. P. Grichuk (1992) in “Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere”.**

a period of relatively cold but particularly moist conditions allowing the formation of the inland ice sheets, followed by a period of very cold and very dry conditions. In other words: a shift from an early glacial suboceanic/oceanic climate with tundra-like vegetation to a late glacial extremely continental climate with steppe-like vegetation. Strong winds and substantial loess deposition characterize this latter period.

An important line is the 10 °C-July-isotherm since the polar tree and forest line run approximately parallel to this line, and it marks the commonly accepted southern boundary of the tundra. Büdel (1949a) reconstructed a 10.5 °C-July-isotherm for the last glacial and argued that the course of this line marks the most northern tree line during the LGM.

The 10.5 °C-July-isotherm runs from southern France across central Europe and the east European lowland to the middle Ural Mts. It crossed the great European loess wedge, which stretches from eastern Europe to Brittany. Büdel called the loess region north of the polar tree line “Löss-tundra” (loess tundra) and south of it “Löss-steppe” (loess steppe). Despite the sparse tree growth within the loess steppe and its rich grass and herb vegetation cover compared to the loess tundra, vegetation character of the loess tundra, and loess steppe was very similar and the climate-morphological aspects of the landscapes were identical. The loess tundra was as much steppe as tundra (Büdel, 1949a, b), a view, which comes close to the tundra-steppe concept outlined below.

**Table 8**

**Major events during the Late Pleistocene**

<p><b>Late Pleistocene</b> (MIS; stages from west to east)</p>	<p><b>Climate/landscape and biotic environments</b></p>
<p><b>Last Glaciation</b> (MIS 2; Late Valdai, Sartan, Partisanian)</p>	<p>Severity of cryo-arid conditions reached a maximum; during 14–13 ka degradation of glacial systems, permafrost moved to the northeast. Phenomenon of hyperzonality (super zones).  <b>Periglacial tundra:</b> stretching from western Europe north of the Alps over northern East European Plain, Urals, northern Siberia, Beringia to northern Far East. <b>Periglacial steppe:</b> over most of Eastern Europe, west Siberian lowlands, northern Kazakhstan to central Yakutia. <b>Boreal forests:</b> limited to Urals, some mountains in central and eastern Siberia, Mongolia, Manchuria. <b>Nemoral forests:</b> in mountains of Central Asia, southern Urals, Altai, central and eastern China. <b>Steppe and desert:</b> Central Asia and northern China (see Fig. 2).</p>
<p><b>Last interstadial</b> (MIS 3; Mid-Valdai, Karginisky, Chernoruchinsky)</p>	<p>Coolings and warmings. Considerable degradation of ice sheets, early phases close to interglacial conditions.                      First phase of Khvalynian Caspian Sea transgression.  <b>East European Plain:</b> taiga forests during warmings and periglacial forest-steppe and forest-tundra during coolings. <b>West Siberia:</b> boreal cold-temperate, northern taiga forests. <b>Northeastern Asia:</b> expansion of trees and shrubs to the north. <b>Central Asia:</b> moist and cool climate prevailed, humid and dry steppes.</p>
<p><b>Penultimate Glaciation</b> (MIS 4; Early Valdai, Zyranka, Lazovian)</p>	<p>Cold-humid climate. Scandinavian ice sheet smaller than during LGM, in east Siberia ice sheet larger than during LGM.  <b>East European Plain:</b> northern taiga, meadow steppe, permafrost in the north and middle part. <b>West Siberia:</b> middle and north taiga, forest tundra. <b>Northeastern Asia:</b> meadow steppe. <b>Central Asia:</b> predominantly steppe and desert-steppe.</p>
<p><b>Last Interglacial Optimum</b> (MIS 5e; Mikulino, Kazantsevo, Nakhodkinsky)</p>	<p>Winter and summer temperatures above today’s, permafrost in the plains only along northern ocean coast.                      Late Khazarian Caspian Sea transgression.  <b>East European Plain:</b> main part with nemoral forests, to the north boreal coniferous forests, absence of tundra; steppes only near Black and Caspian Seas. <b>Siberia:</b> boreal forests most important, in W Siberia no tundra, further east tundra vegetation along northern coast; in southern W Siberia forest-steppe. <b>Kazakhstan and Mongolia:</b> forest-steppe and steppes, extending far south to latitude 40°, forests in the mountains. <b>Southern Far East:</b> predominance of polydominant nemoral forests with Manchurian flora elements (see Fig. 1).</p>

For references see text.

Table 9

**Terminology of palaeoenvironments of the Eurasian permafrost zone during  
Last Glacial Maximum (LGM)**

<b>From northern ice/coastlines to southern limit of permafrost (ca. 40° to 50°N latitude)</b>	<b>Vegetation (Frenzel, 1992)</b>	<b>Main types of vegetation (ecosystems) (Grichuk, 1992)</b>	<b>Landscape types (Velichko, Isayeva, 1992)</b>	<b>Main mammal assemblages (Baryshnikov, Markova, 1992)</b>
<b>Northern part</b> south to ca. 60°N latitude	- Tundra-like in W and Central Europe - Mixture of steppe and tundra in E Europe and W Siberia - Tundra-steppe in NE Siberia	Periglacial tundra (in eastern Asia to ca. 50°N)	Tundra steppes	Mammoth tundra-steppe assemblage, arctic sub-assemblage
<b>Southern part</b> from ca. 60°N to ca. 50°N latitude, in Mongolia to ca. 40°	- Steppe from E Europe to W Siberia and Kazakhstan - Loess-steppe from Kazakhstan to Russian Far East - Herb-steppe in Mongolia and NE China	Periglacial steppe; steppe and desert in Mongolia	Periglacial steppes; deserts and high mountain steppes in Mongolia; open forests in Amur basin and Manchuria	Mammoth tundra-steppe assemblage, boreal sub-assemblage; south to it from west to east: Pontian-Kazakhstan steppe, Mongolian desert-steppe and Japan-Chinese forest-steppe assemblages

In the following decades, Russian botanists and palaeobotanists provided evidence for ‘periglacial’ vegetation during the LGM, which resembled tundra, bog, woodland, and steppe. This ‘periglacial’ area comprises not only landscapes in glacial proximity but also vast areas many hundreds of kilometres away from glacial proximity; areas, which still exhibit landscape features similar to those of the landscapes in glacial proximity. This growing knowledge of the late Pleistocene vegetation of northern Eurasia finally resulted in the “Tundra-Steppe” concept (in English literature mostly “Steppe Tundra”). For a short history of the tundra-steppe concept, see Hibbert (1982). Tundra-steppe means either a certain type of plant communities with codominance of both, steppe and tundra species, or a type of (palaeo) landscape, codominated by both steppe and tundra. As such, the tundra-steppe is a ‘hybrid’ ecotonal community between steppe and tundra (Yurtsev, 1974, 1981, 2001). Throughout the Pleistocene the mesic tundra stages alternated many times with the tundra-steppe. A specific feature of the cold hypo-arid epochs of the Pleistocene was the expansion of cryophytic steppes on the northern plains, dominated by steppe xerophytes and arctic-alpine cryoxerophytes, as the zonal types of communities and ecosystems on the

driest habitats, whereas mesic and hygric tundras occupied subordinated positions beyond watersheds (Yurtsev, 2001).

The plant cover of the Pleistocene tundra-steppe landscapes was not homogeneous throughout its distribution area. It exhibited the same kind of regional differentiation seen in the modern steppe regions of the interior regions of Eurasia and North America (Yurtsev, 2001). This is clearly mirrored, for instance, in the characterization of the vegetation by Frenzel (1992) and main types of vegetation (ecosystems) in Eurasia by Grichuk (1992; and Fig. 2). Main formations of the periglacial tundra vegetation and tundra-steppe landscapes (Table 9) in western Siberia included subarctic meadows, low bush tundra and open birch woodlands in the plains, and montane bush tundra in the highlands. In eastern Europe, the tundra and cryophytic steppe communities predominated in combination with open woodlands of larch and birch. In northeastern Siberia, polar deserts and montane tundra with xerophytic steppe associations were widespread. In the periglacial steppe vegetation (Table 9), meadow steppes with larch, pine and birch forests predominated.

The modern flora of the Arctic and Subarctic contains a variety of ‘tundra-steppe’ elements and

may allow reconstructing the Pleistocene tundra-steppe landscapes (Yurtsev, 1974, 1981). The steppe associations of northeastern Asia (meadow steppe, steppe proper, and petrophytic steppe) comprise many relic species (Yurtsev, 1978). The relict steppe vegetation in Yakutia occurs at south-exposed, well-drained, dry and warm extrazonal sites within the taiga zone (Yurtsev, 1982, 2001). The main ecological factor determining the distribution of steppe and its niche in the tundra and taiga landscapes is soil aridity (Yurtsev, 2001). The maximum diversity of northern relic steppes and steppe plants within the Arctic has been recorded in the Beringian sector (Yurtsev, 1981, 1986).

Guthrie (2001) argues that the diverse Late Pleistocene grazing megafauna could have been supported only by arid, grass- and forb-dominated ecosystems (his “Mammoth steppe”). Based on palaeodiet studies and on the combined presence of grazing specialists but absence of browsing specialists in the fossil assemblages, he further concluded that the Mammoth fauna used grasses as their dietary sample. Hence, he argued for dominance of grassland type of environment during full Glacial, an overemphasized view that was never held by Russian and other scientists (see Table 9; Yurtsev, 2001). Plant macrofossils from a permafrost sequence in the Lena delta prove that during the last cold-stage arctic species coexisted with aquatic, littoral, meadow and steppe taxa, and the reconstructed vegetation composition is similar to modern vegetation mosaics in northeast Siberian relict steppe areas (Kienast et al., 2005). Productive meadow and steppe communities played an important role in the Siberian arctic vegetation during the late Pleistocene and could have served as food resources for large populations of herbivores as already argued before by many scientists (e. g., Yurtsev, 2001). This might solve the long debated “productivity paradox”, the discrepancy between the cold and dry palaeoclimate and its supposed sparse vegetation and the highly diverse herbivorous fossil megafauna. Recently, Willerslev et al. (2014) presented a large-scale ancient DNA metabarcoding study of circumpolar plant diversity, representing the last 50 kyr of Arctic vegetation history. They provide evidence that during the LGM in the unglaciated Arctic and adjacent regions a steppe-tundra consisted dominated by forbs. Their analyses also indicated that, in contrast to Guthrie’s (2001) findings, the megafaunal diet comprised both, graminoids and forbs. Thus, recent plant macrofossil and ancient DNA studies question the predominance of a graminoid-dominated “Mammoth steppe”.

## 9. Climate and landscape history in the Holocene

### 9.1 Holocene classification systems

The Holocene Series/Epoch is the latest interval of geologic time (post-Glacial time) and the most recent stratigraphic unit. The Pleistocene - Holocene boundary and thus the beginning of the Holocene Epoch has been selected at several different times in the past. Only recently, it has been formally defined and dated approximately 11,700 +/- 100 cal. years BP (before AD 2000) and accepted by the ICS (International Commission on Stratigraphy) (Walker et al., 2009). Climatically, this boundary coincides with the end of the Younger Dryas cold sub-stage of the last glacial period.

Many attempts to subdivide the Holocene have been undertaken but are inconclusive at a global or at least at a hemispherical scale. Well-known is the Blytt-Sernander classification. Based on climatic fluctuations, the Holocene is subdivided into the five chronozones (Fig. 3): Preboreal (cool/dry) - Boreal (warm/dry) - Atlantic (warm/wet) - Subboreal (warm/dry) - Subatlantic (cool/wet). The scheme was originally defined for northern Europe (Mangerud et al., 1974) but is widely applied to whole Eurasia. Regional pollen stratigraphies are often correlated with the Blytt-Sernander framework, and it has been closely checked by radiocarbon dating, establishing a very useful standard.

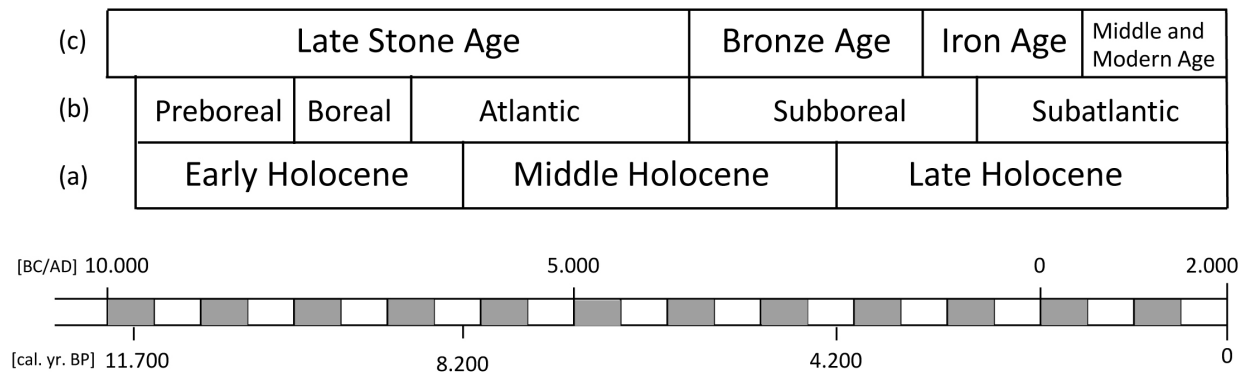
Walker et al. (2012) proposed a formal subdivision of the Holocene into ‘Early’, ‘Middle’ and ‘Late’ Holocene taking up the widespread but variable use of these terms in the relevant literature. These proposals have been accepted by the International Union of Geological Sciences in 2018. The boundary between Early and Middle Holocene is set around 8200 years BP, and the Middle - Late Holocene boundary – around 4200 BP (see Fig. 3). The rationale for choosing these date lines are as follows. The “8.2 ka event” reflects abrupt cooling of near global significance marked by shifts in  $^{18}\text{O}/^{16}\text{O}$  and D/H and numerous proxy climate records. The 8.2 ka event, which may have even caused local resurgence of ice cover, was just a short-lived cold, dry interval with no long-term climatic consequences. Climate after the 8.2 ka event was the same as before (Roberts, 2014). The “4.2 ka event” marks a widespread predominantly mid- and low-latitude aridification reflected in many climatic proxy records worldwide but it is not clear if it was synchronous in different parts of the world. For details and discussions see Walker et al. (2012).

The beginning of the Holocene corresponds with the beginning of the Mesolithic age in most of Europe. During the Holocene climatic optimum (Atlantic zone, see Fig. 3), Neolithic humans spread across Eurasia into northernmost regions.

### 9.2 Holocene climate history

At the beginning of the Holocene, temperature increased considerably and reached a maximum when mean annual temperature was above that of today marking the start of a warm interval. Many climatic proxy data reflect this warming trend, which was interrupted by short warm/cold cycles. This interval is called the Holocene Climate Optimum or Hypsithermal (also Altitheimal and Xerothermic) and lasted from about 9,000 to 5,000 cal years BP (Atlantic zone in the middle Holocene, Fig. 3).

However, statements about duration and time of the Holocene Climate Optimum vary greatly depending on the geographical region, on the availability of proxy data and on methods of data evaluation. Warming was probably not uniform across the planet. Nearly everywhere on the Northern Hemisphere, mean annual temperature was about 0.5–1.0 °C above present, but depended on geographical latitude. Positive deviations from present values were higher in polar and subpolar regions but there was cooling in tropical and subtropical regions. Middle Holocene deviations of temperatures and precipitation from present-day values are shown in maps in Frenzel et al. (1992). After this warm period a gradual temperature decline followed until about two millennia ago.



**Fig. 3.** Holocene temporal range, subdivisions, chronozones and periodization of human history. Abbreviations: cal. yr. BP Calibrated years before present. “Present” refers to the year 2000. BC/AD Date description before Christ / after Christ (= Anno Domini): (a) Formal subdivision of the Holocene according to Walker et al. (2012). (b) Chronozones based on climatic fluctuations, following Mangerud et al. (1974). Radiocarbon years are converted to calendar ages. (c) Periodization of human history according to the Three-Aged-System. The Late Stone Age includes the Mesolithic and the Neolithic.

### 9.3 Megafaunal extinction at the Pleistocene–Holocene transition

During the late Pleistocene and early Holocene, about 75 % of the larger mammals became extinct including mammoths and mastodons. Hypotheses for the late Pleistocene/early Holocene megafauna’s extinction involve climate and habitat changes, but many authors also assign humans a role for the megafaunal extinction (Lister, Stuart, 2008; Campos et al., 2010; McDonald et al., 2012; Prescott et al., 2012).

#### 9.3.1 Causes for the megafaunal extinction at the Pleistocene–Holocene transition

The debate over the causes of the worldwide late Quaternary extinction of the large herbivores (mostly defined as taxa  $\geq 45$  kg in body weight)

and especially of the megaherbivores ( $\geq 1000$  kg in body weight) has continued for over 200 years. Climate change and spread of modern humans and related effects such as hunting (‘overkill’ hypothesis; Martin, 1984; Owen-Smith, 1987) and/or habitat modification and fragmentation are seen as primary drivers, but it remains controversial whether human colonisation or climatic change were more important drivers with hardly any extinction being unambiguously attributable to either. A diversity of extinction patterns has been observed on different continents. Barnosky et al. (2004) assumed that humans contributed to the extinction on some continents but were not solely responsible for the extinction everywhere. For the Northern Hemisphere, for instance, they suggest the intersection of human impacts with pronounced

climatic change drove the timing and geography of the extinction. This is in line with the scenario put forward by Zimov et al. (2012) who argue that Holocene warming became fatal for the mammoth ecosystem not because of climate change per se, but because with warming humans penetrated to the North. They caused a decline of herbivores, thereby decreasing pastures with the eventual extinction of the megafauna. Sandom et al. (2014b) provided strong support for modern humans as the primary driver of the worldwide megafaunal losses with a weak Eurasia-specific link to climate change. Analyses of Bartlett et al. (2016) also identify human colonisation as the most important driving factor on a global scale but assume that climate factors were also important. The low extinction rate found in the fossil record of mainland Asia, however, could not be explained. A potential strong role of rapid climate changes associated with interstadial warming events is emphasized by Cooper et al. (2015) for the Northern Hemisphere, and Rabanus-Wallace et al. (2017) suggest that moisture-driven environmental changes played an important part in the late Quaternary megafaunal extinctions in Europe, Siberia and the Americas.

It thus appears that the causes of the worldwide megafaunal herbivore extinction at the Pleistocene-Holocene transition are still not fully understood. Although great progress has been made, interplay of human influence and climate change, role of environmental change, diversity in timing, regional climate and geography remain complicated problems, and the late Quaternary extinction of the large herbivores continues to be disputed.

### 9.3.2 Consequences of megafaunal extinctions

The ecosystem consequences of the herbivore megafauna loss are not well understood. The ‘wood-pasture’ hypothesis suggests that – before agriculture – large grazing herbivores support a dynamic mosaic of forests and open grassland within the temperate forest biome at the landscape scale. Large herbivores thought to be important ‘ecosystem engineers’ in temperate forest biomes. The contrasting position suggests closed forests with relatively small open areas caused locally by large herbivores. There seems to be increasing evidence for the ecosystem effects of the late Pleistocene and early Holocene megafaunal losses around the world. Decline of large herbivores induces major alterations in landscape structure and ecosystem function (Sandom et al., 2014a, b; Bakker et al., 2016; Malhi et al., 2016, and literature cited therein).

## 9.4 Reconstructions of Holocene environments

Reconstructions of past climates and vegetation types heavily depend on the quality and quantity of proxy data, which include biological, geophysical and geochemical as well as geological and geomorphological data. The reconstructions also depend on dated records and on the methods employed for data evaluation. Great progress has been achieved in these fields in the last decades. Pollen analyses have significantly contributed to the knowledge about late Quaternary vegetation, and the “biomization” approach introduced by Prentice et al. (1996) has become a powerful tool for vegetation reconstruction from late Quaternary pollen data of Eurasia. This is especially true for the Holocene. The Biomization Method (= biome reconstruction) is based on an assignment of pollen taxa to plant functional types (PFTs) on the basis of the known biology of the plants. The PFTs are then assigned to major vegetation types (biomes) on the basis of their closest modern pollen analogues (“best-modern-analogue”, BMA). The BMA is orientated towards modern surface-pollen data sets taking into account present-day ecology, bioclimatic tolerance and geographical distribution of pollen-producing plants. The method then attributes the average climate associated with these “modern analogues” to the fossil pollen (Bartlein et al., 2011). Results obtained both with traditional (qualitative) approaches and the quantitative method of biomization mostly show good compatibility. However, biomization allows for improved quantification of past climate parameters and increasing resolution of vegetation analyses in space and time.

Main sources for Holocene vegetation reconstructions are at present pollen diagrams, plant macrofossils and dated paleontological and archaeological remains. Over the past several decades the number of published late-Quaternary pollen records from northern Asia increased rapidly and enables continental-scale vegetation and climate reconstructions (Tarasov et al., 2007; Binney et al., 2017). It would appear that the Holocene is the best studied of all chronostratigraphical series.

## 9.5 Holocene climate and vegetation of the Eurasian steppe belt

### 9.5.1 General features

In northern Eurasia, Holocene temperature fluctuations decreased in a range eastwards, primarily because of a west to east weakening influence of the westerly air masses and strengthening of continental climate. Climatically triggered vegetation zone

shifts between the tundra, forest-tundra and forest decreased also from West to East, whereas the boundary between forest and steppe remained rather constant over whole northern Eurasia. Only during the Holocene climatic optimum that boundary moved slightly to the North due to an increase of the forest-steppe zone. In general, climate fluctuations were more pronounced in eastern Europe than in Siberia, but mid-Holocene warming characterizes all northern Eurasia although with regional differences (Velichko et al., 1997, 2002; Velichko, 1999).

There have been major shifts in the distribution of animals and plants during the Holocene. Many Pleistocene environments, in which plants and animals coexisted in the cooler climates of the late Pleistocene, were destroyed or fragmented. Relict areas are separated today by hundreds or thousands of kilometres or have been isolated in higher altitudinal 'islands'.

At the end of the Pleistocene, a tremendous increase in rainfall occurred in the mid-latitudes and in the tropics. They caused a vast proliferation of pluvial lakes. In the high- to mid-latitudes, tundra passed to birch forests in the early Holocene. Great moisture in the Polar Regions has caused the disappearance of the tundra-steppe. During the warm period of the middle Holocene, a progressive change to pine forests and then oak, beech or mixed forests can be observed in Eurasia. In the mid-latitude continental interior, hot summers prevailed but winters became colder and drier, and steppe expanded. Many lake levels showed a drop.

The full-glacial landscape of northern Eurasia was largely treeless (Tarasov et al., 2000b; Bigelow et al., 2003; Binney et al., 2017), dominated by herb-rich biomes. Grasses, sedges and forbs are dominant until 15 kyr cal BP (Binney et al., 2017). Between 15 and 8 kyr, herb-dominated biomes are reduced and forest biomes spread across northern Eurasia. However, trees apparently were not completely absent during the LGM. Pollen and macrofossil data demonstrate the existence of woody taxa including *Picea*, *Larix*, *Pinus*, *Alnus* and *Betula* in the periglacial zone across the whole Eurasian region, and it is likely that refugial populations persisted under the cool and dry conditions of the full-glacial (Frenzel, 1968, 1979, 1992; Grichuk, 1992; Velichko, Isayeva, 1992; Tarasov et al., 2007; Binney et al., 2009, 2017).

With a shift to warmer and moister Holocene climates, treeless vegetation was replaced by boreal or temperate forests over much of the region and wetland extent increased (Andreev, Tarasov, 2013; Bin-

ney et al., 2017). The Pleistocene tundra-steppe hyperzone dispersed, and the Altai Mountains became an important climate boundary for the environmental Holocene history of the mid-latitude belt in Asia. In the second half of the Holocene, wetter climate conditions prevailed west and north of the Altai Mountains due to the influence of Atlantic deep pressure systems. In contrast, the eastern slopes of the Altai Mountains and Central Asia became arid during the Middle Holocene due to a weakening of the Pacific monsoon. Thus, Holocene vegetation and climate histories in the steppe regions west of the Altai Mountains are different from those in the regions east of the Altai Mountains (Chen et al., 2008; Rudaya et al., 2009, 2012).

### 9.5.2 Holocene vegetation and climate histories of the Mongol-Chinese steppe region

The Early and Middle Holocene in northern Mongolia is characterised by increasing temperature and humidity as shown by many proxy data (e. g., lake levels, pollen assemblages, eolian sediment records) interrupted by some cold/dry reversals. Steppe vegetation was replaced by forest steppe and boreal woodland expanded (Gunin et al., 1999; Tarasov et al., 2000a; An et al., 2008; Rudaya et al., 2009; and literature cited therein). A decrease in precipitation and changes of vegetation towards steppe occurred at the end of the middle Holocene (Atlantic/Subboreal). Onset and termination of the dry interval differed from place to place (Yang et al., 2004; An et al., 2008). Humidity increased again during the late Holocene in concert with dropping temperatures in Mongolia.

Only few studies deal with southern Mongolia. During the early and middle Holocene, dark taiga forests apparently existed in the desert mountains of the Gobi Altai. Between 4000 to 3500 yr BP the taiga forests disappeared due to aridization in southern Mongolia and were replaced by steppe vegetation (Jäger, 2005; Mische et al., 2007). This is in line with more recent findings. Multi-proxy studies of lake sediments in the Gobi Desert (Bayan Tohomin Nur, Orog Nur) revealed a warm and humid period from the beginning of the Holocene at around 11 cal ka BP until about 3.5 cal ka BP interrupted by some short-term cold/dry reversals. The late Pleistocene *Artemisia* steppe was altered to a Chenopodiaceae desert steppe in the Holocene (Felauer et al., 2012; Yu, 2016). Since about 3.5 cal ka BP aridity increased, Chenopodiaceae desert steppes expanded and the lake basins began to dry out. This southern Mongolian palaeoclimate scenario is more or less



consistent with the palaeoclimatic data from northern Mongolia and surrounding regions of China.

In the last decades, many studies have been conducted in China to reconstruct past vegetation at a broad regional scale using multiple fossil pollen records and applying the biomization procedure (Li et al., 2014; Li, 2016, and literature cited therein). A huge area of northern China is dryland, comprising about one third of the Chinese landmass, and includes both arid and semi-arid regions. Vegetation types in these drylands are diverse and include desert, desert steppe, steppe and scrub-woodland. The boundary between arid and semi-arid regions runs along the Helan Mountains, approximately along 106°E longitude. Regions east of the Helan Mountains are influenced by the East Asian and Pacific summer monsoons and are semi-arid whereas the regions west of the Helan Mountains are arid, climatically mainly controlled by the dry and cold winter monsoon. In China's deserts, extensive lakes occurred during the late Pleistocene, and during the LGM steppe and desert vegetation extended to the modern coast of eastern China (Yang et al., 2011). In the first half of the Holocene, strengthened East Asian summer monsoons led to an increase in moisture in the entire dryland belt of northern China, and the mid-Holocene was warmer than today (Yang et al., 2011; Li et al., 2014). The deserts in northern China were greatly reduced and retreated northwestward. Biome reconstructions for the mid-Holocene revealed steppe as dominating vegetation type in the semi-arid regions east of the Helan Mountains and sites with forest and forest-steppe in the southern part of the east sandy land. West of the Helan Mountains, most of the regions were dominated by desert vegetation as today, but steppe vegetation is also recorded outside the deserts (Li et al., 2014).

A strengthening of the East Asian monsoon at 12 kyr BP associated with an increase in precipitation between 11 and 8 ka BP and a stepwise weakening of the monsoon circulation and climate aridization towards the modern level is mostly thought to be responsible for the Holocene climate change in Central Asia (Chen et al., 2008; Rudaya et al., 2009; Yang et al., 2011, and literature cited therein).

### 9.5.3 Synopsis of the Holocene climate and vegetation history of the Mongol-Chinese steppe region

A synopsis of climate and landscape changes and landscape changes and vegetation histories of the Mongol-Chinese steppe region during the Holocene is presented in Table 10, based mainly on fol-

lowing literature: Gunin et al. (1999), Tarasov et al. (2000a), Miehe et al. (2007), An et al. (2008), Chen et al. (2008), Rudaya et al. (2009), Yang et al. (2011), Felauer et al. (2012), Li et al. (2014), Li (2016), and Yu (2016).

### 9.5.4 Holocene vegetation and climate histories of the Euro-Siberian steppe region

#### 9.5.4.1 West Siberian Plain and Kazakhstan

At the beginning of the Holocene, steppe landscapes predominated in the present-day forest-steppe region of the West Siberian Plain (Arkhipov et al., 1999). With increasing warming (Boreal) forests extended during humid phases and steppe associations during dry phases. During the Atlantic period, forests expanded further, and forest-steppe emerged (Zhilich et al., 2017). Over the Holocene Optimum period, when mean annual temperatures were about 1 °C higher than present, forests contained also broad-leaved taxa like *Tilia*, *Quercus*, and *Ulmus*. Especially *Tilia* spread widely in the area of the modern West Siberian forest-steppe (Arkhipov et al., 1999). In the second half of the Holocene (Subboreal and Subatlantic) temperatures decreased and fluctuated around modern ones. Tree vegetation became impoverished and *Betula-Pinus silvestris* open forests spread (Arkhipov et al., 1999). From the early Atlantic to the early Subatlantic, forest-steppe and northern Kazakh steppe biomes moved several times beyond the present-day border up to 200 km to the North coincident with climate aridization (Zakh et al., 2010). The onset of the late Holocene is characterised by the dominance of steppe with birch and pine forests. This is consistent with the general pattern of mid-late Holocene vegetation and climate dynamics of the Kazakh Upland and western Altai (Rudaya et al., 2012).

Repeated climatic changes occurred in the steppe zone of Kazakhstan. A general warming trend from the beginning of the Holocene to the end of the Atlantic period is obvious. After that, temperatures fluctuated about 2–3 °C near the present values (Akhmetiev et al., 1999). Poaceae and *Artemisia* dry steppes dominated in the Kazakh steppe region at the beginning of the Holocene (Tarasov et al., 1997). In the early Atlantic period, birch forests expanded. From the late Atlantic on, *Pinus silvestris* penetrated from the southern Ural and west Siberia to northern and central Kazakhstan and spread throughout the steppe zone of Kazakhstan (Andreev, Tarasov, 2013). From that time on, vegetation cover received its present-day aspect (Tarasov et al., 1997; Akhmetiev et al., 1999; Andreev, Tarasov, 2013).

Table 10

## Holocene climate and vegetation histories in the Mongol-Chinese steppe region

Series/ Subseries Blytt-Sernander classification	Northern Mongolia	Southern Mongolia	Northern China
<b>Late Holocene</b> (4.2 ka – to present)	Modern natural vegetation: Alpine vegetation, forest-steppe, mountain steppe, taiga, steppe and desert-steppe	Modern natural vegetation: desert-steppe, desert	Modern natural vegetation: desert-steppe and desert in the NW; steppe and temperate forests in NE
Second half of Subboreal – Subatlantic	Dropping temperatures and renewed increase of humidity towards modern levels	Aridity increased, Chenopodiaceen steppe expanded	Climate and vegetation approaching modern levels
<b>Middle Holocene</b> (8.2–4.2 ka)	Dry interval, vegetation changed towards steppe	<i>Artemisia</i> steppes during wet phases, Chenopodiaceen steppe during dry phases	Deserts retreated to NW (arid climate), steppe dominating in NE (semi-arid climate)
Middle and Late Atlantic – First half of Subboreal	Steppe replaced by forest-steppe, boreal woodland expanded	Taiga forests in the Gobi Altai	Increase in moisture and temperature in dryland belt, Helan Mts. range (along 106°E longitude) became meteorological divide
<b>Early Holocene</b> (11.7–8.2 ka)			
Preboreal – Boreal – Early Atlantic	Increasing temperature and humidity interrupted by some cold/dry reversals	Warm and humid period interrupted by short term cold/dry reversals	At the end of the LGM dry land belt from W to E, desert and steppe vegetation widespread

For references see text.

#### 9.5.4.2 Eastern Europe

The modern zonal steppe in Europe stretches from the Ukrainian Black Sea coast over southern Russia further east to western Siberia. It was already Kleopov in the 1930ies who argued that the modern steppes of the Ukraine derived from ‘near glacial’ steppes in the beginning of the Holocene (Korotchenko, Peregrym, 2012). This view is currently widely accepted, not only for the Ukraine. Just recently, Pokorný et al. (2015) emphasized “that there is no doubt that the modern zonal steppes of Ukraine, Russia, Kazakhstan, Mongolia and northern China represent direct continuation of the Pleistocene glacial steppe”. Biome reconstructions of the LGM biomes from pollen and macrofossil data compared with modern biomes support this view (Tarasov et al., 2000b; Binney et al., 2017).

The modern zonal forest-steppe in Europe adjoining the zonal steppe belt to the North, is confined to the Pannonian Basin, the lower course of the Danube, and a belt stretching from southeast of the Carpathians to the southern Urals. Contrasting views

about the history of the European forest-steppe have been put forward, especially for central-eastern Europe: continuous persistence of steppe species since the Pleistocene versus their post-glacial immigration due to anthropogenic impact during the Holocene. Starting at the assumption that during the last Pleistocene glacial interval landscapes in the mid-latitudes were characterised by a more or less open vegetation, convincing evidence accumulated to believe that in central and eastern Europe trees had a much wider distribution than previously assumed. The assumption of a nearly tree-less last-glacial landscape in eastern Europe and north of the Pyrenees, Alps and Carpathians was mainly based on pollen data. Emerging evidence from various fossil proxies, including plant macrofossils, macrofossil charcoal and dated pollen spectra, from palaeoclimate and biome modelling, and from genetic studies now begin to question this traditional view. It would appear that the central and eastern European landscape was partly covered by Taiga/montane woodland, which in some regions also contained isolat-

ed pockets of temperate trees (Willis, Van Andel, 2004). Trees grew as far north as Hungary including species of *Pinus*, *Picea*, *Betula*, *Juniperus*, *Salix*, and *Larix*. Thermophilic trees as *Carpinus betulus*, *Quercus*, *Corylus*, *Ulmus*, and *Tilia* survived in favourable sites (Willis et al., 2000). Last pleniglacial pollen sequences from the Carpathian Basin and adjacent east Carpathians have been interpreted as reflecting a partially wooded boreal forest-steppe landscape (Magyari et al., 2014). Evidence for uninterrupted occurrence of forest-steppe since the late Pleistocene is also provided for the great Hungarian plain by Magyari et al. (2010), for northern Bohemia, Czech Republic, by Pokorný et al. (2015), and by Feurdean et al. (2015) for Transylvania. It is hypothesised that eurythermic steppe species survived the LGM *in situ* whereas thermophilic southern continental, Pontic and sub-Mediterranean steppe species immigrated in post-glacial time (Magyari et al., 2010). Thus, it would appear that many species of the central-eastern European forest-steppe persisted continuously since the late Pleistocene whereas others, mostly thermophilic ones are post-glacial immigrants.

### 9.5.5 Synopsis of the Holocene climate and vegetation history of the Euro-Siberian steppe region

A synopsis of climate and landscape changes and vegetation histories of the Euro-Siberian steppe region during the Holocene is presented in Table 11, based mainly on following literature.

References for eastern Europe: Lang (1994), Velichko (1999), Velichko et al. (1999), Tarasov et al. (2000b), Magyari et al. (2010, 2014), Feurdean et al. (2015) Pokorný et al. (2015), and Binney et al. (2017). References for West Siberian Plain and Kazakhstan: Tarasov et al. (1997), Velichko (1999), Arkhipov et al. (1999), Rudaya et al. (2012), Andreev and Tarasov (2013), and Zhilich et al. (2017).

### 9.6 Azonal steppe islands in Central Europe

The western-most outposts of Euro-Siberian steppe grassland are found in Central Europe: in the dry valleys of the Central Alps, in the upper Rhine valley in southwest Germany and adjacent Alsace, in central and southern Germany, and also in northern Bohemia, and in Lower Austria. These ‘Steppenheide’ (Gradmann, 1933) and ‘Waldsteppeninseln’ (Wendelberger, 1956) in middle and southeastern Europe are small mosaics of open dry grassland, shrubs and sparse woodland. They show many “forest-steppe” plants typical for the

forest steppes of eastern Europe, however in different combinations and under different environmental and edaphic conditions than the true zonal forest steppe, and clearly represent azonal vegetation types within the zonal nemoral deciduous forest belt of Central Europe.

Origin of the extra-zonal small steppe islands in Central Europe is much debated. Gradmann (1933) thought that the roots of the Central European ‘Steppenheide’ reach back to the ‘Dilluvium’ (Pleistocene), and Wendelberger (1956) also argued that the Pannonian ‘Waldsteppeninseln’ house relics of the Pleistocene cold steppes (e.g., *Eurotia ceratoides* = *Krascheninnikovia ceratoides*). Hejcman et al. (2013) basically share this view when writing that originally “they represent relicts of Pleistocene steppes”.

Present vegetation in Central Europe is the result of anthropogenic transformation of the early Holocene woodlands into a cultivated landscape (Ellenberg, Leuschner, 2010). The opening of the forests by human activities started about 7000 years BP. One of the outcomes are different grassland communities, commercial grasslands (in terms of phytosociology, the class of the *Molinio-Arrhenathera* grasslands), and the fescue steppes and brome grasslands (*Festuco-Brometea*). The *Festuco-Brometea* is a poor grassland vegetation characterized by more or less basiphytic plant species in dry, warm areas on loess and sandy soils, often on carbonate rocks or steep slopes and similar exceptional habitats. They are composed either of mainly submediterranean-mediterranean geoelements (order *Brometalia erecti*) or of mainly pontic-sarmatic geoelements (order *Festucetalia valesiacae*, continental-subcontinental steppe grassland) (Pott, 1992). The origin of the *Festucetalia valesiacae* grasslands is interpreted as relicts of the glacial steppes but their species composition and present locations are undoubtedly strongly influenced by human impact (Pott, 1995, 1996). Whether the concerned plants of the *Festucetalia valesiacae* are relicts of the glacial cold steppe as Pott argues for, or rather are relicts of a former continuous belt of continental steppe during the postglacial warm period as advocated by Ellenberg and Leuschner (2010), stands for question.

## 10. Glacial and interglacial refuge areas

### 10.1 General Aspects

The literature on ‘refugia’ is vast and has a long history. In the last two decades, debate on the refugia terminology has come up and led to an increase

Table 11

## Holocene climate and vegetation history in the Euro-Siberian steppe region

Series/ Subseries Blytt – Sernander classification	Eastern Europe	West Siberian Plain and Kazakhstan
<b>Late Holocene</b> (4.2 ka – to present)  Second half of Subboreal – Subatlantic	Modern vegetation: forest-steppe with <i>Quercus</i> forests in between <i>Tilia–Quercus</i> forests, wet steppe, dry steppe, desert steppe, deserts  Increase of thermophilic trees during warmings, decrease during coolings, vegetation approaching modern one  Cooling trend to modern values, with warmings and coolings	Modern vegetation: forest-steppe with <i>Betula–Pinus</i> forests, wet steppe, dry steppe, desert steppe, deserts  Dominance of forest-steppe in west Siberia, Kazakh upland and western Altai, dry and semi-desert steppe in northern Kazakhstan lowlands  Cooling trend to modern values, with warmings and coolings
<b>Middle Holocene</b> (8.2–4.2 ka)  Middle and Late Atlantic – First half of Subboreal	At the beginning <i>Pinus–Betula</i> forest vegetation, increase of thermophilic trees ( <i>Tilia</i> , <i>Ulmus</i> , <i>Quercus</i> ) up to Holocene Optimum  Forest-steppe from Pannonian Basin to southern Urals and further east, perhaps locally since late Pleistocene	At Holocene Optimum, forests with thermophilic trees extended, thereafter temperature decrease, <i>Betula–Pinus</i> open forests spread  During Atlantic, <i>Betula</i> forests expanded, forest-steppe emerged in west Siberia, <i>Pinus</i> immigrated into steppes of Kazakhstan
<b>Early Holocene</b> (11.7–8.2 ka)  Preboreal – Boreal – Early Atlantic	Steppe from Ukrainian Black Sea coast to southern Russia and further east, continuously since late Pleistocene	Steppe in West Siberian Plain and Kazakhstan, continuously since late Pleistocene
Warming trend to Holocene Optimum, several warming and cooling		

For references see text.

of refuge-related terms, a debate which often appears rather academic. Initially, the term ‘refugia’ was coined by biogeographers to describe localities where temperate species existed during glacial conditions and is thus synonymous with the common term ‘glacial refugia’ (Willis, Whittaker, 2000). The cyclic changes of the Pleistocene between cold (glacials) and warm (interglacials) periods resulted in expanding cold-adapted species during glacials and retracting during interglacials, and vice versa (warm-adapted, i.e. temperate species retracting during glacials and expanding during interglacials). Accordingly, ‘cold stage refugia’ (syn. glacial refugia) for warm-adapted taxa, and ‘warm stage refugia’ (syn. interglacial refugia) for cold-adapted taxa have been distinguished (e.g., Bennett, Provan, 2008; Stewart et al., 2010). Whereas glacial refugia attracted attention since long and continue to

be widely discussed, interglacial refugia have long been neglected.

Many more different types of refugia have been proposed, as for instance ‘palaeorefugia and neorefugia’ (Nekola, 1999), ‘macro- and microrefugia’ (Rull, 2009), and ‘nunatak, peripheral and lowland refugia’ for mountain species (Holderegger, Thiel-Egenter, 2009). We refer to Tzedakis et al. (2013) who critically commented on these terms. To avoid terminological debate and to be in line with the terminology used in older literature, we will only use the terms ‘glacial’ and ‘interglacial’ refugia in its broadest sense referring “to an area, of any size, in which a taxon persisted, at any population density, during a cold [or warm] stage” (Bennett et al., 1991).

*Glacial refugia* – In Europe, classic southern glacial refugia for many plants (namely trees) and animals are supposed to be the Iberian, Italian and

Balkan peninsulas, which has been substantiated by palaeontological, palaeoclimatological and genetic data (Frenzel, 1968b; Bennett et al., 1991; Willis, 1996; Taberlet et al., 1998; Hewitt, 1996, 1999, 2000; Petit et al., 2002). In addition to these southern refugia, it has become obvious that temperate species in Europe survived cold stages also north of the Pyrenees – Alps – Balkan mountain ranges in sheltered habitats with favourable microclimates. These refuge areas of warm-adapted species north of the classical southern glacial refugia have been termed ‘cryptic refugia’ (Stewart, Lister, 2001; Magri et al., 2006; Magri, 2008; Petit et al., 2008; Provan, Bennett, 2008; Tzedakis et al., 2013). Evidence for cryptic northern refugia comes from plant macrofossils, pollen records and genetic data. The original formulation of this hypothesis referred to temperate species but has taken on a wider meaning including boreal and hemiboreal species as well (see Stewart et al., 2010).

*Interglacial refugia* – In the Northern Hemisphere, cold-adapted species persist through interglacials in high-latitude regions known as ‘polar refugia’. Classical polar refugia in Eurasia are located in the northernmost parts of continental Eurasia and in several islands as, for instance, Greenland, Svalbard and Wrangel Island (Stewart et al., 2010). Interglacial refugia at lower latitudes are termed ‘cryptic southern refugia’ in parallel to the cryptic northern refugia although their present ranges are well known (in contrast to the original sense of cryptic refugia; Stewart et al., 2010). Refugial areas for those cryptic southern refugia are often mountains as the Alps and Pyrenees.

It should be kept in mind that a refugium is an area where distinct genetic lineages have persisted through a series of Tertiary or Quaternary climate fluctuations, and their locations are determined by complex historical and environmental factors. The modern structure of genetic diversity was shaped over multiple glacial-interglacial cycles rather than solely by the influence of the last glaciation period (e.g., Lavrenko et al., 1952; Bennett, Provan, 2008; Médail, Diadema, 2009).

## 10.2 Refuge areas of the Eurasian mid-latitudes

For a deeper understanding of the history of the mid-latitude eastern European and Asian fauna and flora (steppe biomes) we review present knowledge of refuge areas in these geographical regions. Early in the last century, the principal refugia in eastern Europe and Central Asia have been outlined by Lavrenko (1930) and Lavrenko et al. (1952). The

most important centres from West to East were supposed to be the Carpathians, the uplands of the Ukraine and central (European) Russia, the southern Urals, and the Altai-Sayan mountain ranges. Meanwhile, this has been substantiated by many palaeobotanical data, biome reconstructions, modelling of palaeoenvironments, and by genetic studies, yet with main focus on forest tree. There are still considerable gaps in knowledge about grassland, especially steppe refugia.

### 10.2.1 Forest tree refugia

There is no doubt that many European trees survived the LGM in mountainous regions of the Iberian, Italian and Balkan peninsulas (the so-called southern refugia). The Carpathian Mts. as a northern cryptic glacial refugium for temperate trees has been corroborated by many studies (Lang, 1994; Birks, Willis, 2008; Magyari et al., 2014; see also chapter 9.5.4.2). Northern forest refugia have been also reconstructed in the uplands of European central Russia and Ukraine, in the Crimea and in the Caucasus (Markova et al., 2002, 2009). Climatologically, they were all suitable for boreal tree species (Svenning et al., 2008). Nemoral tree species were largely restricted to the Black Sea region (Tarasov et al., 2000b; Markova et al., 2002, 2009; Svenning et al., 2008). The southern Urals as another cryptic cold-stage refugium for boreal and hemiboreal forest vegetation has also been confirmed (Ermakov, 1998; Birks, Willis, 2008; Chytrý et al., 2010).

A hemiboreal forest vegetation is also reported for the more humid and relatively warm foothills of the northern Altai Mts. (north of Lake Teletskoye) and for the mountain regions in the Kemerovo Region, Russia (Ermakov, 1998). Endemic to this region is *Tilia sibirica*, which is sometimes treated as a subspecies of *T. cordata*. In these linden-forests, several herbs typical for European temperate deciduous forests occur, separated by a gap of ca. 2000 km from their eastern limit of their continuous distribution range in the southern Urals (Ermakov, 1998). In the Russian literature, *Tilia sibirica* has since long been considered as a relict of Tertiary deciduous forests (Ermakov, 1998, and literature cited therein). A recent molecular study of *Tilia sibirica* confirmed the close relationship of *T. sibirica* to *T. cordata* and suggested middle Pleistocene divergence, ca. 450 kya (Logan et al., 2018). It is argued that the hemiboreal *Tilia sibirica*-forests can be considered as an analogue of a glacial refugium of temperate trees in Late Pleistocene (Novák et al., 2004; Hais et al., 2015; Logan et al., 2018).

### 10.2.2 Steppe refugia

The term 'steppe' becomes problematic in the context of steppe refugia. Present-day steppe vegetation consists of cold-adapted and warm-adapted (thermophilic) species. Theoretically, one may argue that the cold-adapted species are presently in a warm-stage refugium (interglacial refugium) whereas the warm-adapted species are in expansion and question arises as to their cold-stage refugium (glacial refugium). This is further complicated by the fact that cold-adapted species often show high temperature tolerances and in reality should better be characterized as eurythermal instead of cold-adapted. It has already been discussed that cold-adapted or eurythermal species may have survived in *in situ* refugia whereas temperate-adapted species supposedly are immigrants from *ex situ* refugia. This is well investigated for the Carpathians and the Pannonian basin (see chapter 9.5.4.2).

As mentioned above, the principal refugia have been already outlined early in the last century. Some of these regions obviously are not only glacial but also interglacial refugia. Two examples will be given, one from eastern Europe, the other from the Altai-Sayan mountain region.

*Eastern Europe* – A conspicuous eastern European association of steppe plants confined mainly to calcareous outcrops (*Schivereckia*, Brassicaceae, and its associates) and its discontinuous distribution area (Urals, uplands of European Russia and the Ukraine) have since long attracted botanists. *Schivereckia* and its associates have been interpreted as relics of a formerly continuous distribution belt of periglacial steppe vegetation (Litvinov, 1902; Kozó-Poljanski, 1928, 1929; Gajewski, 1934) and thus would represent an interglacial refugium of LGM steppe vegetation.

*Altai-Sayan Mts.* – The southeastern Russian Altai harbours many Pleistocene relic species (e.g., Horsák et al., 2015 for plants and snails; Pavelková-Řičánková et al., 2015 for mammals). Increasing evidence based on these findings and on fossil record argues for a modern analogue of the full-glaciated tundra-steppe ecosystem in the intermontane basins (e.g., Kurai and Chuya basins) and high mountain plateaus (e.g., Plateau Ukok) in the Altai-Sayan mountain country. It is likely that in some regions the present steppe biome is not only an analogue but also, at least partly, an *in situ* relic of the LGM tundra-steppe (reviewed in Chytrý et al., 2018). This assumption seems to be corroborated by modelling the spatial distribution of habitats during the LGM. The models projected the LGM predominance of desert steppe across most of the non-glaciated area

of the Russian Altai, and it is argued that these desert steppes also supported the cold-adapted open-landscape biotas (Hais et al., 2015). However, Pleistocene relict species are presently concentrated in areas, which presumably were glaciated during the LGM or were flooded by ice-dammed lakes (e.g., Rudoy, 2002; Lehmkuhl et al., 2011; Blomdin et al., 2016). It is suggested that the LGM biota survived in nearby unglaciated or unflooded areas and returned to the deglaciated or dried areas during the late Glacial or Holocene.

Knowledge about cold-stage (glacial) refugia for thermophilic steppe plants is limited. As shown in Figure 2, during the LGM, steppe and desert steppe vegetation spread over interior regions of the Middle East and of Central Asia (Grichuk, 1992; Tarasov et al., 2000b; Andreev, Tarasov, 2007) and is also recorded from the region between the Black and Caspian Sea (Grichuk, 1992; see also Magyari et al., 2010). These biomes grow there also today. It is largely unknown which of the Euro-Siberian continental-subcontinental steppe species (mainly pontic-sarmatic geoelements from the order Festucetalia valesiacae) are cold-adapted, which are thermophilic, and which are eurythermal. In essence, the range of climatic tolerances of steppe plants is widely unknown. Apart from that, it stands for question whether the range of climatic tolerances of a living species allows conclusions about its temperature tolerances tens of thousands years ago. It is not without problems, therefore, to locate glacial refugia for thermophilic steppe species, except probably for submediterranean-mediterranean geoelements from the order Brometalia erecti.

In the Mongol-Chinese steppe region, vegetation during the LGM consisted to a large extend of steppe and desert biomes, periglacial tundra and steppe were nearly absent except for mountain regions (Fig. 2). Thus, LGM biota were similar to the preceding interglacial (Fig. 1) and to present-day conditions. Nevertheless, despite the absence of major Quaternary glaciations, significant climatic oscillations impacted the evolution of the biota. Climatic cycles consisted of dry glacial and humid interglacial periods, and plant species may have experienced glacial-time (arid periods) retreats and interglacial (humid periods) recolonizations. This is evidenced by several phylogeographic studies, summarized by Meng et al. (2015).

It is obvious that the florogenesis of present-day steppe vegetation is much more complicated than would be anticipated by mere shifting of vegetation belts. Geographical position of cold- and warm-stage refugia, *in situ* survival and immigration fa-

cilities from *ex situ* refugia, and competition have definitely influenced steppe florogenesis.

## 11. Summary and outlook

### 11.1 The Eurasian steppe, Status Quo

The term ‘steppe’ is of ambiguous meaning. In vegetation science and plant geography, ‘steppe’ is characterized as the naturally treeless climax formation of the semiarid regions within the cool-temperate (nemoral) vegetation zones, i.e. steppe and prairie in the Northern Hemisphere and pampas in the Southern Hemisphere. However, a ‘treeless steppe’ may also depend on various kinds of physical disturbances like grazing and fire. There are many attempts to fit the steppes into a global vegetation classification system, e.g., systems based on the zonal climax vegetation; or the WWF ecoregions and EUNIS (European Nature Information System) classifications.

Classification and nomenclature of steppe formations is rather vague and far from being standardized. Three main classification approaches can be recognized, the physiognomic approach, the dominant species approach, and the floristic approach. The dominant species approach is most successfully applied in Russian literature and is somehow in between the other two approaches. All classification principles have their advantages and disadvantages, and none alone is sufficient to cope with the steppe reality.

The Eurasian steppe belt can be divided into two subregions, the Euro-Siberian and Mongol-Chinese steppe. These two subregions differ in floristic, climatic and edaphic respects. The Altai Mountain Country and adjacent Tuva is the contact zone between the Euro-Siberian and Mongol-Chinese steppes, and comprise species of diverse floristic regions of different biogeographic origin.

Since thousands of years, the steppe biome is highly influenced, disturbed and transformed by human activities as agriculture and pastoralism. Today, natural or semi-natural steppe vegetation remains only in nature reserves, in gullies and ravines, on the slope of river valleys, on the edges of fields, and along roadsides. Steppes have become one of the most endangered terrestrial biomes but belong to the least protected areas worldwide. Main destructive threats are conversion of steppe into cropland, overgrazing, expanding mines, oil- and gasfields, urban encroachment, and afforestation. Magnitudes of these threats vary between regions. On top of all these threats come the effects of climate change. The

impact of climate change is profound as evidenced by increased fire risks, for instance in Russia, and vanishing permafrost in Mongolia.

### 11.2 Origin and evolutionary history of the Eurasian Steppe

During the Palaeogene (Palaeocene to Oligocene) and at the beginning of the Neogene (Miocene) major reorganizations of climate, mountain ranges and oceans in northern Eurasia had major impacts on the origin and evolutionary history of the steppe. At the end of the Oligocene grass-dominated habitats appeared and became dominant biomes during the Neogene. The first steppes in Eurasia are recorded from Central Asia in the Palaeogene/early Miocene and later in Europe. Steppe habitats obviously are of multiple origins, originating at different places and at different times. A continuous Eurasian steppe belt established at the end of the Miocene/early Pliocene as evidenced by the Hipparion (Pikermi) faunal complex. The Miocene landscape was the ‘precursor’ of the present day zonal landscape structure.

At the end of the Pliocene, vegetation cover in Eurasia consisted of forests in the North, forest steppe in southeastern Europe and the West Siberian Plain, and true steppes in Middle and Central Asia. Significant cooling at the end of the Pliocene marks the transition to the Pleistocene macrocycles of cold and warm periods. Waves of deep cooling and warming coupled with increased severity and duration of cold stages since the Middle Pleistocene had profound effects on the biota and the physical landscape and transformed the zonal landscape structure. Development of permafrost, formation of large continental ice sheets and loess deposition were intensified. During the cold stages (glacials), a cold steppe vegetation spread over northern Eurasia, and forests stretched from the Atlantic Ocean to the Ochotskoye Sea during the warm stages (interglacials). The cyclic changes of the Pleistocene between cold (glacials) and warm (interglacials) periods resulted in expanding cold-adapted species during glacials and retracting during interglacials, and vice versa. Accordingly, ‘cold stage refugia’ (syn. glacial refugia) for warm-adapted taxa, and ‘warm stage refugia’ (syn. interglacial refugia) for cold-adapted taxa have been distinguished.

Severity of continental climate reached a maximum in the Late Pleistocene when periglacial tundra and steppe dominated the higher northern and middle latitudes. Landscape zones shifted southwards by 10° latitude. Repeated transgressions of

the Caspian Sea and ice-dammed lakes caused longitudinal range splits of the cold steppe hyperzone. At the beginning of the Holocene, temperatures increased considerably and reached a maximum during the Mid-Holocene. With a shift to warmer and moister Holocene climates, the Pleistocene tundra-steppe hyperzone dispersed and was replaced by modern vegetation zones. The Altai Mountains became an important climate boundary. Wetter climate conditions prevailed west and north of the Altai Mountains whereas the eastern slopes of the Altai Mountains and Central Asia became arid during the Holocene. There have been major shifts in the distribution of animals and plants during the Holocene. Many Pleistocene environments, in which plant and animals coexisted in the late Pleistocene, were destroyed or fragmented, and possible relic areas have been proposed. This is an issue still under discussion.

### 11.3 Challenges and outlook

It would appear that the essential features of the origin and historical biogeography of the Eurasian steppe have been outlined in general. However, detailed knowledge and profound understanding are often limited or missing. Progress in Earth sciences and in palaeontological and geobotanical research, including the emerging ancient DNA studies, will definitely contribute to enhance our knowledge. We are also convinced of molecular-systematic approaches as a valuable tool for understanding the evolution of steppe. Contemporary genomes of steppe plants, up to a certain degree, document the evolutionary and biogeographical history of species, as has been shown by several studies. Testing the congruence of species phylogenies and landscape evolution has been greatly enhanced by molecular markers. Such studies analysed species histories for many parts of the world but are rare for steppe plants. We strongly propose to apply phylogeographic and biogeographic methods on steppe species to understand the geographic origin and the climate/landscape history of the Eurasian steppe belt.

Challenges of particular importance are the dynamics of steppe habitats in space and time, the evolution of the steppe flora (florogenesis), steppe refuge areas and the Holocene history of the European steppes.

*Dynamics of steppe habitats* – Palaeoclimatic oscillations, landscape history and tectonic processes led to repeated latitudinal shifts and longitudinal range splits of the steppe belt, which often caused range contractions and expansions of steppe habitats. Steppe habitats are of multiple origins. They

developed at different places and at different times. We lack detailed knowledge about these fundamental processes and are far away from an all-embracing synthesis of the evolutionary history of the Eurasian steppe.

*Florogenesis* – The flora of the Eurasian steppe is different between its individual regions, both at a macrogeographical and at a microgeographical scale. The present-day flora of each region, irrespective of its extent, may have its own history. Origin of their floral elements and possible immigration routes at the species and genus level may differ not only between the regions but also within it. Geographic position of cold- and warm-stage refugia, *in situ* survival and immigration facilities from *ex situ* refugia as well as competition have definitely influenced steppe florogenesis.

*Steppe refuge centres* – Knowledge about steppe refuge areas is rather limited compared to tree refugia. This is especially true for possible ‘cryptic’ interglacial refugia and for glacial refugia of thermophilic species. Present-day steppe vegetation consists of cold-adapted and warm-adapted (thermophilic) species. Theoretically, cold-adapted species are presently in interglacial (warm-stage) refugia, whereas the thermophilic species are in expansion and question arises as to their glacial (cold-stage) refugia. This view, however, is complicated by the fact that cold-adapted steppe species often show high temperature tolerances and should better be characterized as eurythermal instead of cold-adapted species. Unfortunately, the range of climatic tolerances of Euro-Siberian continental-subcontinental steppe plants is widely unknown. In the Mongol-Chinese steppe, we find another situation. Despite the absence of major Quaternary glaciations, plants may nonetheless have experienced glacial-time (arid periods) retreats and interglacial (humid periods) recolonizations.

*Holocene history of the European steppe* – A long-standing issue concerns two opposing hypotheses: continuous persistence of steppe species since the Pleistocene versus post-glacial immigration during the Holocene Climatic Optimum caused by climate change and anthropogenic activities. Occurrence of chernozems in central Europe and molecular studies are often used as aid to decision-making to distinguish between the two hypotheses.

The interpretation of chernozems as steppe soils goes back to the 19<sup>th</sup> century Russian pedologist S.V. Dokuchaev. He argued that chernozems are climax soils above loess under the influence of steppe climates. Chernozems under forest-steppe are traditionally seen as a secondary phenomenon explained



by forest penetration into initial chernozem steppe (Wilhelmy, 1950). Following these classical views, the black earth soils in central Europe (in Germany, Czech Republic, Austria and Hungary) are regarded as a relic of early Holocene soil formation (Preboreal and Boreal) and seem to testify steppe or forest-steppe biomes at the beginning of the early Holocene. A critical review on pedogenesis of chernozems by Eckmeier et al. (2007), however, revealed that the central European chernozems are of different ages (and not of uniform early Holocene age), that chernozems formed not only under steppe but also under forest vegetation, and that not all soils classified as chernozems in central Europe are steppe soils. Thus, origin and age of chernozems in central Europe do not necessarily reflect past climate and vegetation.

In the light of the few relevant molecular studies so far available, the matter has become even more complicated. It seems reasonable to suspect that an unambiguous decision in favour of one or the other of the two hypotheses is not possible. It would appear that eurythermic steppe species survived *in situ*, i.e. are relics of the cold Pleistocene periglacial tundra steppe, whereas the thermophilic species immigrated in post-glacial time. This has to be substantiated by identification of source areas and migration routes.

*Outlook* – The challenges outlined above impose several basic questions:

Do palaeoclimate oscillations and landscape evolution influence phylogenies and genetic subdivisions across species ranges? Do molecular signals mirror biogeographic dynamics and colonization of steppe habitats from different source populations? Can we identify source areas and migration routes?

Molecular phylogeographic studies including dated phylogenies and ancestral area reconstructions and correlation with climate/landscape history at the species and population level are necessary to answer these questions.

### Acknowledgements

This work has been supported by the German Research Foundation (DFG; FR 1431/8-1 to NF; NE 314/15-1 to BN and HH; BL 462/18-1 to FB), by the Austrian Science Fund (FWF; Projekt 1 3002-B25 to KGB) and by Russian Science Foundation (RSCF, Project 19-14-00071). Financial support for fieldwork and excursions by the DFG, DAAD, Ministry of Science and Culture of Lower Saxony, and the University of Osnabrueck is greatly acknowledged. We thank M. V. Markov, Tver and Moscow, and Z. Jamsran and B. Oyuntsetseg, Ulaanbaatar, for organizing excursions.

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