




The Palaearctic steppe biome: a new synthesis

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Abstract The Palaearctic steppes range from the Mediterranean basin towards China, forming one of the largest continuous terrestrial biomes. The literature on steppe ecology and conservation is vast but scattered and often not available in English. We provide a review of some key topics based on a new definition of steppes, which includes also Mediterranean steppes and alpine rangelands of the Asian Highlands. Revisiting the terrestrial ecoregions of the world, we estimate that the Palaearctic steppe biome extends over ca. 10.5 million km². Major chorological regions differ in their macroclimatic niche with a clear distinction between Middle Asia with its winter precipitation and the Central Asian summer-rain regions of the Mongolian plateau and of Tibet. Steppe soils store large amounts of carbon, yet the sequestration potential is debated and depends on land use.

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Major physiognomic-ecological steppe types include forest-, typical-, desert-, and alpine-steppe, which vary in the importance of grasses, mainly C3 species. The steppes host a specialised fauna, and Middle Asia, Tibet, and especially Mongolia, have large herds of migrating ungulates. The share of pristine and protected sites is low in the steppe regions, with conversion into croplands being the most important land use impact in Europe, Middle Asia, and the Mediterranean, while grazing has a severe impact in some parts of Mongolia and Tibet. There are major gaps in our knowledge on: (1) the effects of climate change on the crucial seasonal patterns; (2) the role of steppe soils in the global carbon budget; and (3) the ecology and distribution of most animal groups except vertebrates.

Keywords Biogeography · Climate change · Grazing · Palaearctic · Protected area · Steppe biome

Abbreviations

BP	Years before present
cal BP	Calibrated years before present
QR	Range between quartiles
s.lat.	Sensu lato (in the wide sense)
s.str.	Sensu stricto (in the narrow sense)
TEOWs	Terrestrial ecoregions of the world (Olson et al. 2001)

Introduction

The Palaearctic steppes are among the largest continuous biomes on earth. They form a vast belt across the mid-latitudes of Eurasia and represent a large proportion of the global temperate grasslands. Steppes extend from a few outliers and many more secondary steppe-like grasslands in Central and Eastern Europe across the entire continent to Manchuria in north-eastern China (Coupland 1993; Lavrenko and Karamysheva 1993). Their northern limit is defined by the (boreal) forest belt, while the Eurasian-African drylands demarcate the southern margin. In spite of their spatial extent, steppes are physiognomically surprisingly similar (Fig. 1; Supplementary Material Online Resource 1), being dominated by herbaceous life-forms, especially graminoids.

Much of the ecological importance of the Palaearctic steppes is a consequence of the massive size of the biome. They harbour a large, though not disproportionately large flora of herbaceous plants; plot-level plant biodiversity may be high (Kuzemko et al. 2016; Polyakova et al. 2016). Palaearctic steppes have the most extensive ungulate migrations outside Africa (Batsaikhan et al. 2014) and provide habitat for specialised small mammals (Lavrenko and Karamysheva 1993). Steppe soils store large amounts of carbon (Lal 2004; Li et al. 2009), and the temperate rangelands of the Tibetan plateau have global climate relevance as the main heating zone fuelling the East Asian monsoon system. The cultural relevance is also high, and steppes are home to some of the Earth's last intact pastoral communities (Janzen 2005; Wang et al. 2014).

The world's temperate grasslands have been exposed to severe human impact, including conversion into croplands and overgrazing. In consequence the percentage of pristine and protected habitat is lower in temperate grasslands than in any other major ecosystem type (Henwood 1998; Hoekstra et al. 2005). Palaearctic steppes are no exceptions, and additional challenges to their conservation have emerged in the last decades including mining,

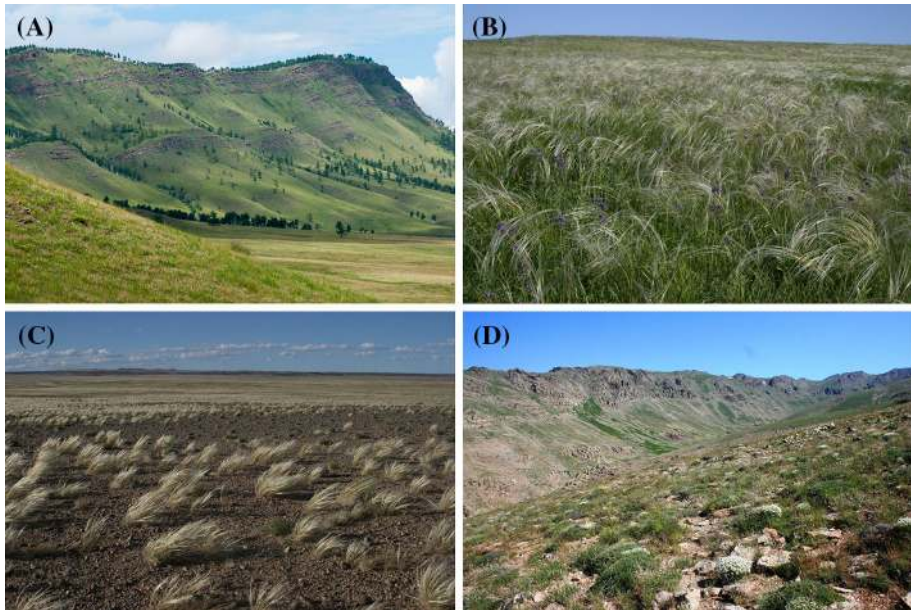


Fig. 1 Physiognomy of steppes. **a** Forest steppe in the Middle Asian region, northern Khakassia, Siberia, Russia. **b** Typical (tall-grass) steppe in the European region, Lower Don basin, Russia. **c** Desert steppe in the Central Asian region west of Bayankhongor, Mongolia. **d** Alpine steppe in the Mediterranean region; Sivas, Turkey. A wider range of steppe regions, types and edaphic variants is shown in Supplementary Material Online Resource 1 *Photos* J. Dengler, O. Demina, K. Wesche, D. Ambarlı

sedentarisation of pastoral communities and perhaps even undergrazing (Batsaikhan et al. 2014; Ptackova 2011; Robinson et al. 2003). Global climate change may add to these stressors.

The literature on steppe and associated rangelands is vast but scattered. This is partly a consequence of the extraordinary spatial extent, which crosses political realms and also scientific disciplines. Much of the relevant literature is in Russian, Chinese, or German. The 1990s brought a string of syntheses in English (e.g. Coupland 1993; Karamysheva and Khrantsov 1995; Lavrenko and Karamysheva 1993; Zhu 1993), but more recent treatments are few and hardly cover the entire Palaearctic steppe biome, with Werger and van Staaldouin (2012) being a major exception.

Here we first revisit some of the fundamental topics in steppe biogeography and provide:

- (1) an updated definition of ‘Palaearctic steppes’ and a proposal to distinguish main chorological and ecological subtypes;
- (2) a new estimate of the spatial extent of the Palaearctic steppe biome and of the core niche of steppe types in climate and altitudinal space; and
- (3) synoptic overviews of steppe flora, vegetation and fauna.

With respect to current challenges in steppe management and conservation, we summarise recent studies with the aim of highlighting key patterns of:

- (1) land-use changes and effects on steppe vegetation and soils;

- (2) temperature and precipitation change and the potential ecological consequences; and.
- (3) levels of formal protection in steppe regions.

Throughout, our aim was not a complete overview, but rather providing some solid ground and highlighting gaps in current knowledge meriting further exploration.

What are Palearctic steppes? An updated definition

The English term “steppe” is derived from the Russian *step* (*Степь*) originally used to describe the grasslands of the plains of European Russia and adjacent areas (Bone et al. 2015). Today, it is often used in a much wider sense (e.g. Bone et al. 2015). Many divergent definitions exist. Providing a full review of the complicated terminology is beyond our scope. Here we adopt a pragmatic view, which applies across the Palearctic realm.

Steppes are zonal (i.e. macroclimate-driven) vegetation types dominated by herbs, mainly grasses and other graminoids, sometimes with a significant admixture of chamaephytes, in climates that are too dry to sustain the growth of closed taller woody vegetation and that are—at least occasionally—affected by frost.

This definition separates steppes from forests and shrublands, where phanerophytes (shrubs and trees) have a cover of more than ca. 30 %, and from semi-deserts, and deserts where the vegetation cover falls below ca. 10 %. The two other groups of zonal grasslands found globally are differentiated from steppes by climatic parameters: *Savannas* occur in the tropics and are thus never affected by frost; and *Arctic-alpine grasslands/tundras* occur under climates where low temperature or long winters prevent growth of tall woody species. Our definition of steppes does not cover grasslands that occur in forest climates, either as a successional stage after natural disturbances (successional grasslands) or driven by edaphic peculiarities (e.g. salinity, water logging). The last types are considered *azonal*, or *extrazonal grasslands* if they resemble the climate-driven steppes (Dengler et al. 2014). We also exclude secondary grasslands, which originate from human land use (i.e. grazing, mowing or burning; Dengler et al. 2014). In contrast to broader concepts (e.g. Baumbach and Pfützner 2013; Werger and van Staalduinen 2012), we distinguish extrazonal or semi-natural grasslands of nemoral Central Europe and term them *steppe-like grasslands* if they have a high proportion of true steppe species.

Our steppe definition is thus similar to that of *indigenous temperate grasslands* issued by IUCN-associated specialists (Peart 2008): “Temperate grasslands are ecosystems, where seasonal climates and soils favour the dominance of perennial grasses and other graminoids; these ecosystems occur mainly in the middle latitudes and also in areas of tropical and temperate high mountains”. This corresponds with a recent attempt to define the world’s grasslands (Dixon et al. 2014) by using the following criteria: (1) not wetland; (2) at least 10 % vascular vegetation cover; (3) graminoids have >25 % cover or are at least the dominant life form; and (4) shrubs have <25 % cover, and trees have <10 % canopy cover and are <5 m tall in temperate grasslands (thresholds for tropical regions are tree cover below <40 % and height below <8 m).

Our definition of steppes as climate-determined broad-scale vegetation units allows comparison to global classification systems, where they correspond mainly to the *semi-arid part of the Continental zoniobiome (Zoniobiome VII; Walter and Breckle 1999)*, the *Steppes and deserts of the temperate zone (Richter 2001)* or the *Dry mid-latitudes (Schultz 2002)*.

We also include the transitions (zono-ecotones) towards the nemoral (VI) and boreal (VIII) zonobiomes (forest steppes), to the alpine zones (alpine steppes) and to the Mediterranean zonobiome (Walter and Breckle 1999). We deviate from the global classification systems, in including the zono-ecotone between the Mediterranean (IV) and the subtropical-tropical arid (III) zonobiomes. In contrast to European sources, African authors also call such grasslands steppes to distinguish them from tropical savannas (Le Hou  rou 2009: *Perennial grass and dwarf shrub Mediterranean steppe*). For more information on the equivalence of different biome classifications, see Supplementary Material Online Resource 2.

Spatial extent and main divisions

Drawing boundaries between steppes and neighbouring habitats relies on arbitrary decisions, and estimates on the extent of the Palaearctic steppe biome diverge substantially, stretching from 8 to over 13 million km² (Dengler et al. 2014). Some detailed country-level and supranational vegetation maps have been produced (e.g. Bohn et al. 2003; Lavrenko et al. 1991; Lavrenko and 1979; Noirfalise 1987; Vostokova and Gunin 2005). However, definitions and survey methods vary markedly among countries and authors. Global approaches as reviewed above are superior in this respect, but are typically coarse and spatially less explicit. Inspired by a recent map of the world's grasslands (Dixon et al. 2014), we took advantage of the widely used *Terrestrial Ecoregions of the World* (TEOWs; Olson et al. 2001). Although the sources for the associated spatial layers are heterogeneous, the TEOWs currently remain the best attempt that is both spatially explicit and follows a unified approach. Olson et al. (2001) assigned a range of Palaearctic ecoregions to their biome *Temperate grasslands, savannas and shrublands*, but this assignment misses many ecoregions covered by our definition. Similarly, Dixon et al.'s (2014) collection of putative grassland ecoregions partly contains TEOWs with a low fraction of natural grasslands (e.g. *Alps conifer and mixed forests*) or with azonal grasslands (e.g. *Yellow Sea saline meadow*). We thus reassessed the TEOWs of the Palaearctic based on personal knowledge or descriptions from the literature (see Supplementary Material Online Resource 3 for correspondence with assignments of Olson et al. 2001; Dixon et al. 2014). We account for uncertainty by classifying the TEOWs into three broad classes of zonal grassland coverage (Fig. 2), i.e. 90–100 % steppe cover (e.g. Mongolian-Manchurian grassland), around 10 % steppes (e.g. Central Afghan Mountains xeric woodlands), and an intermediate class of ca. 50 %.

According to our assessment, the Palaearctic steppe biome covers ca. 10.3 million km², comprising ca. 8.9 million km² of steppes, corresponding to 6.9 and 5.9. % of the global terrestrial surface, respectively (Table 1, Supplementary Material Online Resource 4). The compilation by Dixon et al. (2014) yielded an estimate of 10.2 million km² for the Palaearctic grasslands. The Palaearctic steppe biome s.lat. can be subdivided both chorologically-climatically and ecologically-physiognomically (Table 1; Fig. 2; Supplementary Material Online Resources 1, 4).

The geographical centre of the Palaearctic steppe biome is formed by the steppes of southern Central Siberia, Kazakhstan, and adjacent regions west of the Tian Shan/Altai mountains. They were termed Middle Asia (*Srednyaya Aziya*) in European and Russian (bio-) geography (Cressey 1960), and have much in common with the European and Mediterranean grasslands (see climate and vegetation below). We thus advocate maintaining the term Middle Asia in the biogeographic context, which is synonymous with the

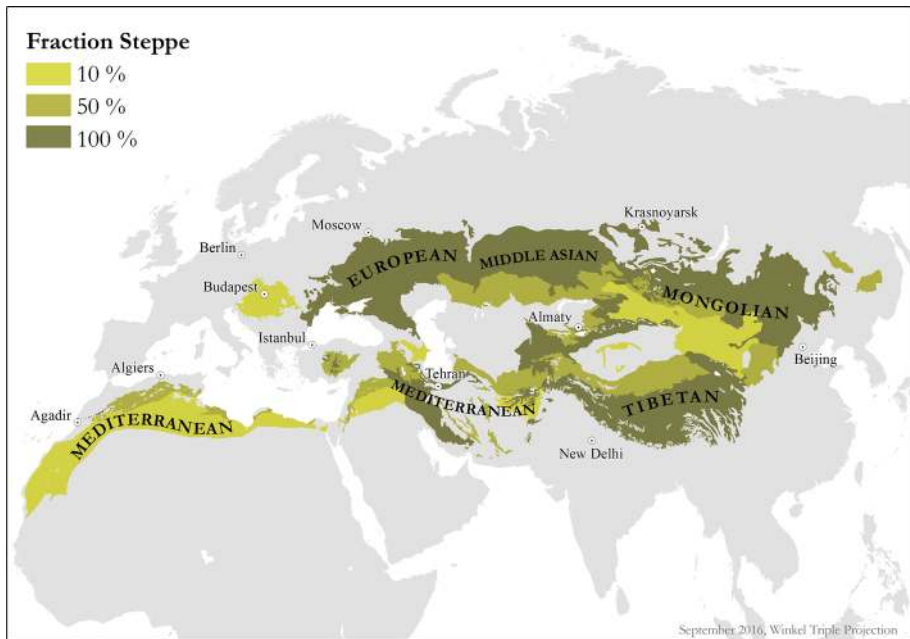


Fig. 2 Range of the Palearctic steppe biome based on the terrestrial ecoregions of the world. Colors represent the approximate fraction the steppe biome s.l.a.t. covers within them (referring to the potential extent of steppes in a given region; TEOWs according to Olson et al. 2001). (Color figure online)

Table 1 Approximate spatial extent of the Palearctic steppe biome sensu lato, its main chorological-climatic subtypes (regions) and ecological-physiognomic subtypes (zones), based on individual assessments of the terrestrial ecoregions of the world (TEOWs; Olson et al. 2001)

Unit	Area biome (million km ²)	Area grassland (million km ²)
Chorological-climatic subtypes		
European region	1.8	1.4
Middle Asian region	2.3	2.0
Mongolian region	2.7	2.3
Tibetan region	2.4	2.4
Mediterranean region	1.1	0.8
Ecological-physiognomic subtypes		
Forest steppe	2.9	1.5
Typical steppe	3.1	3.1
Desert steppe	1.5	1.5
Alpine steppe	2.8	2.8
Total	10.3	8.9

core part of the Irano-Turanian region (Djamali et al. 2012). In this view, Central Asia (*Tsentralnaya Aziya*) includes Mongolia as well as northern and western China (*Mongolian Region*) and also the Tibetan Plateau, which forms another subunit due to its elevation

(*Tibetan Region*). The *Middle Asian Region* and the two Central Asian subunits cover over ca. 2.5 million km² each, while the *European region* covers ca. 1.8 million km². At a total of approx. 1.1 million km², the *Mediterranean Region*, as defined here, comprises steppes at the southern margin of the distribution of extra-tropical natural grasslands. In global biome classifications, these grasslands have not or only partly been included in the steppe biome. Because of their broadly similar climate, we include steppes from Anatolia to the Hindu Kush in the Mediterranean region, although they form a transition to Middle Asia (Djamali et al. 2012).

We also classified subtypes of the steppe biome s.lat. along ecological-physiognomic principles (*ecological zones*; Fig. 1; Table 1; Supplementary Material Online Resources 1, 4). We consider *typical steppes* those that have a herbaceous vegetation cover of 25–100 % (including chamaephytes), but essentially no shrubs or trees except in special edaphic conditions (e.g. riverbeds, disturbed sites). They form the most extensive ecological subtype (3.1 million km², Table 1). *Desert steppes* have a more open vegetation cover of only 10–25 %, often with a larger proportion of dwarf and low-growing shrubs. They cover 1.5 million km² at the transition towards temperate or subtropical deserts. On the other hand, *forest steppes* mark the transition zones (ca. 2.9 million km²) to the adjacent forest biomes. Those at the northern border form a well-defined band with macro-mosaics comprised of forests and relatively moist grasslands. The latter are sometimes called meadow steppes and have a high cover of herbs and less drought-tolerant grasses (Bohn et al. 2003; Ermakov et al. 2012). The forest steppes in the Mediterranean region, by contrast, are rather open woodlands, where individual trees are widely scattered within a grassland matrix (Schroeder 1998). In *alpine steppes* phanerophytes are excluded both by drought and by low temperature/short growing season. They can be considered an intermediate type between steppes and arctic-alpine grasslands and cover extensive areas (ca. 2.8 million km²) mainly on the Tibetan Plateau. Special edaphic conditions lead to further steppe communities that deviate from the main zonal types. Common variants include saline/halophytic, sandy/psammophytic, rocky/petrophytic and gypsaceous steppes (for examples see Supplementary Material Online Resource 1).

Climate niche

We used WorldClim data (Hijmans et al. 2005) to estimate spatial and temporal variability in climate. These data are based on spatial extrapolation, which may cause artefacts in regions with a low density of climate stations. Thus care has to be taken when interpreting single values. We therefore summarised data as medians and lower and upper quartiles (QR; Table 2) and produced coarse-scale maps (Figs. 3, 4). Steppes have a wide temperature niche (QR of mean annual temperatures -1 °C to $+7$ °C), while annual mean precipitation values are rather low at 230–450 mm. Regional subdivisions are mainly due to seasonality in both temperature (continentality) and precipitation.

Steppes in Central and Middle Asia are associated with Köppen climate BSk (cold arid steppe, Kotték et al. 2006) and are relatively homogeneous with respect to mean temperature and precipitation (Figs. 3, 4). The Tibetan region has broadly similar precipitation, but tends to be colder (Table 2, Köppen ET). The Mediterranean is the warmest part of the steppe biome (mainly Köppen Csb, some Csa), while the European steppe region is characterised by intermediate values for both precipitation and temperature (Köppen Cfb, partly Cfa). Elevation introduces differentiations. Tibetan grasslands display extreme median elevations of 4600 m a.s.l. (QR 3800–5000 m a.s.l., Table 2), while the Mongolian region is still at 800–1700 m a.s.l.

Table 2 Elevation and macro-climatic characteristics of the Palaearctic steppe biome s.lat. and the five chorological regions (based on Fig. 1 and Hijmans et al. 2005)

Parameter	Quartile	European	Middle Asian	Mongolian	Tibetan	Mediterranean	All regions
Elevation (m a.s.l.)	25 %	80	150	800	3790	900	210
	Median	140	280	1220	4570	1390	900
	75 %	190	530	1680	4960	1990	2230
Mean annual temperature (°C)	25 %	4.7	1.8	−2.0	−5.3	9.7	−0.6
	Median	6.5	3.1	0.2	−2.8	13.3	2.8
	75 %	8.7	6.1	2.7	0.1	16.8	6.8
Continentality (K)	25 %	35.4	46.4	46.4	34.4	34.3	37.6
	Median	38.7	47.8	50.3	37.1	37.6	43.0
	75 %	42.3	48.9	53.1	39.8	39.8	48.6
Mean annual precipitation (mm)	25 %	440	240	180	170	220	230
	Median	520	300	280	280	300	330
	75 %	560	370	400	440	420	450
Precipitation of warmest quarter (mm)	25 %	140	50	120	90	0	70
	Median	170	100	190	160	10	130
	75 %	190	140	250	240	30	190
Precipitation of coldest quarter (mm)	25 %	140	50	10	0	80	10
	Median	170	50	10	10	120	50
	75 %	190	70	10	20	160	90
Share coldest quarter of total precipitation (%)	25 %	30	15	2	2	30	3
	Median	32	18	3	3	38	15
	75 %	35	24	4	9	50	23

Medians, lower (25 %) and upper (75 %) quartiles are given (calculated across all respective raster cells)

In the Mediterranean, steppes are also associated with mountains and occupy a similar elevation range. In contrast, steppes of Middle Asia and Eastern Europe mainly occur at lower elevations; 150–500 and 100–200 m a.s.l., respectively.

Annual mean numbers have limited value in describing steppe climates with their pronounced seasonality. Temperature seasonality increases eastwards, with the Mongolian region being exposed to mean monthly winter temperatures below -25°C , while summer temperatures may be above $+20^{\circ}\text{C}$ or even $+30^{\circ}\text{C}$. Even alpine Tibet still experiences summer temperatures well above $+10^{\circ}\text{C}$ (Miehe et al. 2001). This is reflected in high values of a simple continentality index (difference between maximum temperature of the warmest month and minimum temperature of the coldest month, Table 2; Supplementary Material Online Resource 5). With a median of around 50 K, values in Central and Middle Asia are broadly similar, whereas in the other regions including Tibet, values are well below 40 K.

Seasonal patterns in precipitation are even more decisive: Djamali et al. (2012) highlight winter precipitation as the key factor controlling main phytogeographic patterns in Middle Asia (Irano-Turanian region) while finer subdivisions are controlled by temperature

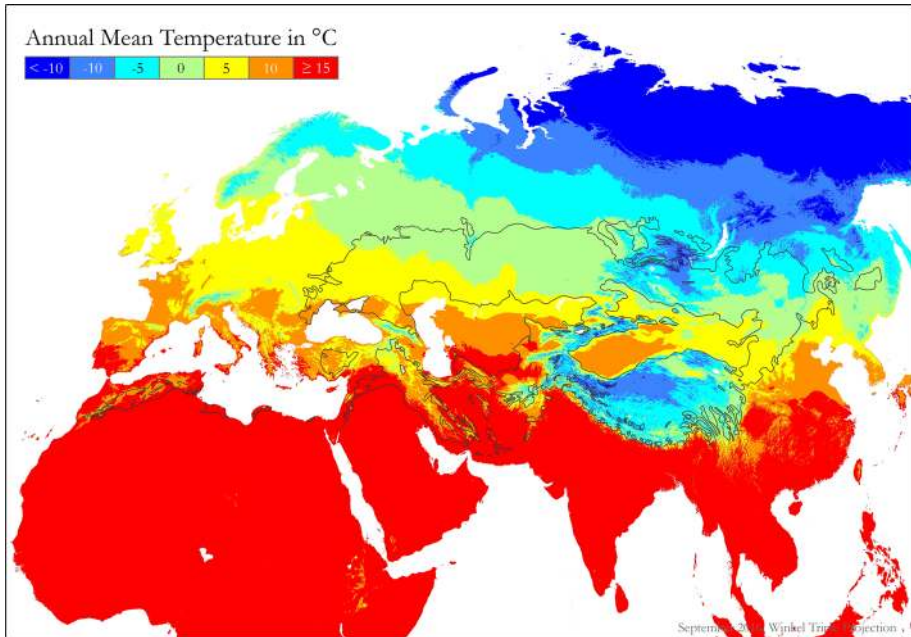


Fig. 3 Modelled mean annual temperature (adopted from Hijmans et al. 2005) in the Palearctic. *Black lines* delimit those terrestrial ecoregions whose share of the steppes is supposed to be at least 50 %. The legend refers to the lower limit of the given interval unless stated otherwise. (Color figure online)

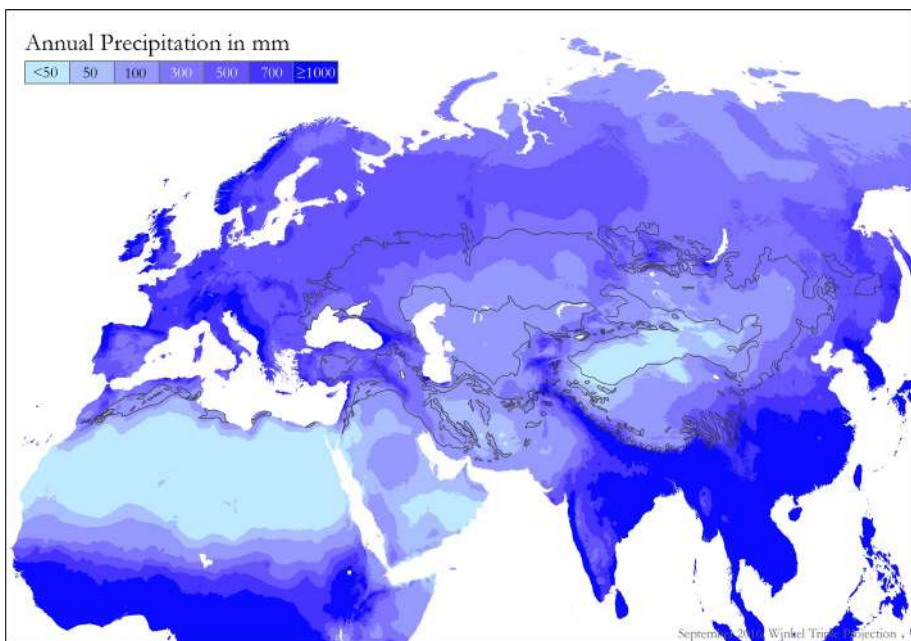


Fig. 4 Modelled annual mean precipitation in the Palearctic. *Black lines* delimit ecoregions whose share of the steppes is supposed to be at least 50 % (adopted from Hijmans et al. 2005). (Color figure online)

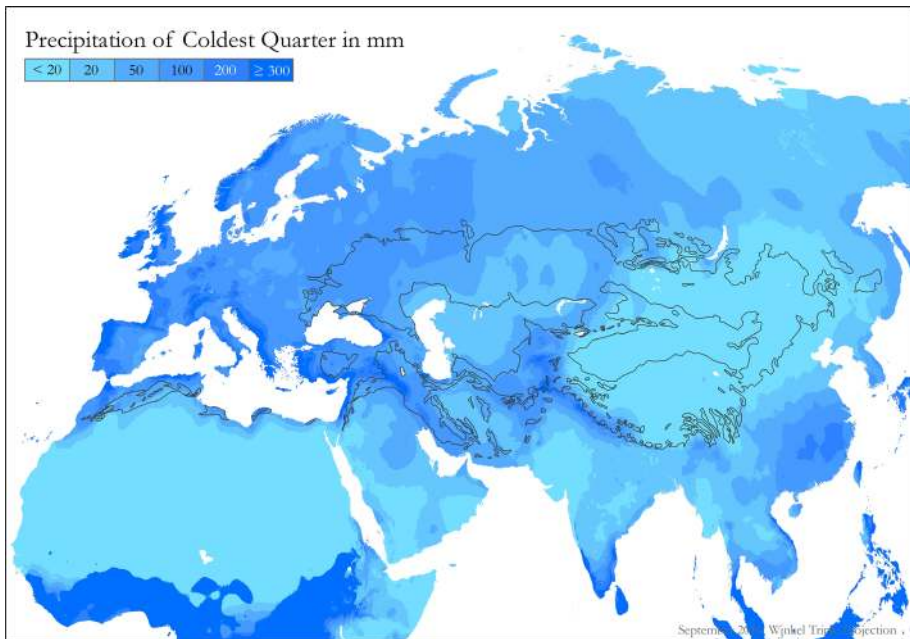


Fig. 5 Modelled mean precipitation of the coldest quarter of the year in the Palearctic. *Black lines* delimit ecoregions whose share of the steppes is supposed to be at least 50 % (adopted from Hijmans et al. 2005). (Color figure online)

seasonality. Steppes in the Mediterranean and in Europe receive appreciable winter rains (Fig. 5; Table 2), which reach across Middle Asia to the Tien Shan and the Dzungarian Gobi. Even these dry steppes still receive winter precipitation of 50–70 mm (December–February, Table 2). The Altai and the Tien Shan demarcate the main climate divide towards the Mongolian and Tibetan regions with monsoonal precipitation regime. There the limited rains are confined to the thermal growing season, which still receives decent precipitation of 120–250 mm (Table 2, Supplementary Material Online Resource 5). This is not very different from European steppes and allows for relatively lush plant growth compared to winter rain environments with the same annual precipitation total where >30 % of it may fall in thermally unfavourable seasons. Palearctic steppes thus show, as the prairies of North America, a large-scale gradient from oceanic, Mediterranean-type climates to highly continental summer rain regimes (Bone et al. 2015).

Soils

Soil conditions depend heavily on the microscale abiotic and biotic environment. There are, however, some large-scale patterns, often associated with macro-climatic gradients (Acton 1992; Zech et al. 2014). Chernozems with their thick (mollic) topsoil horizon rich in organic matter are mainly found in the European and northern Middle Asian steppes. At drier sites, notably in the Mongolian region and in the Kazakh steppes, Kastanozems are the dominant soils. They have a mollic top soil, yet C contents are lower than in the Chernozems. In the Mediterranean, Luvisols and Cambisols are common and often have colourful reddish (chromic) horizons. Soils of the Tibetan region are Cambisols or, at drier

sites, Arenosols, often underlain by permafrost (gelic conditions, Yang et al. 2013). Soils of moist eastern Tibet have a thick organic (felty) topsoil, consisting of a dense turf formed by the local *Kobresia* spp. (Kaiser et al. 2008).

Steppe soils play an important role in the global carbon budget, and there are hopes that steppe soils can sequester a large share of globally emitted C (Lal 2004; Schierhorn et al. 2013). However, a study for Middle Asia (Sommer and de Pauw 2010) yielded sobering estimates indicating that the soils there are barely capable of sequestering the (limited) C emission from the region itself. Much of the tremendous uncertainty is related to land-use effects. Conversion of steppes to farmland typically leads to massive losses of soil C (Kämpf et al. 2016a). Whether improved farming techniques or fallowing can result in reversal of these flows has been questioned (e.g. Kurganova et al. 2014; Wiesmeier et al. 2015). Similar uncertainty pertains with respect to grazing as shown for the Tibetan case, where soils of alpine meadows are generally seen as modest C sinks (Fu et al. 2009; Ingrisch et al. 2015). Measurements, however, reveal complex patterns in response to changing climate (Yang et al. 2013) and land use, and both positive and negative effects of grazing have been reported (e.g. Wen et al. 2013 vs. Hafner et al. 2011).

Nitrogen and phosphorus are known to control ecosystem processes across a wide range of ecosystems (Elser et al. 2007). In many steppes, collection of dung for fuel purposes (Rhode et al. 2007) results in nutrient withdrawal. Nutrients are also translocated by grazers, which release them with faeces (Clark and Woodmansee 1992), often near resting places. This results in removal of nutrients from open grasslands and accumulation in spatially limited nutrient hotspots (Holst et al. 2007; Stumpp et al. 2005). Several fertilisation studies demonstrated nutrient deficiency in typical steppes (Gong et al. 2011; Niu et al. 2009), while data from drylands are much sparser due to a general focus on water rather than nutrient limitation (Austin 2011; Xia and Wan 2008). Nutrient availability may, however, constrain steppe biomass production at well below 200 mm annual precipitation (Ronenberg and Wesche 2011). More studies on nutrient budgets across the entire steppe biome are required, taking into account effects of grazer density and species composition (Bagchi and Ritchie 2010), deposition of N emissions (Kinugasa et al. 2012), and interaction with small-scale vegetation patterns such as the formation of fertile islands (Allington and Valone 2014).

Flora and vegetation

Although the literature on the biogeography of the steppe flora does not reach consensus in all details, it is certain that the region of interest is part of the temperate zone of the Palaeartic/eastern Holarctic flora kingdom (Meusel and Jäger 1992; Schroeder 1998; Takhtajan 1986; Table 3). The European region falls within the Southern-Euro-Siberian flora region, while Middle Asia on one side and the Mongolian and Tibetan regions on the other constitute subregions of the Irano-Turanian flora region (sometimes considered as regions of their own). Middle Asia's southern ecotone to the Mediterranean is demarcated by drylands from Anatolia to Afghanistan, which still host Middle Asian species, but are climatically similar to the Mediterranean (Djamali et al. 2012). These regions are part of the Irano-Turanian region, while the Mediterranean s.str. represents an own flora region. Eastern Asia is biogeographically distinct, and this term should be reserved for the oceanic Sino-Japanese region.

The dominant plant family in steppes are grasses, mainly with C3 photosynthesis. Unlike for example the North American prairies, steppes lack dominant C4 grasses, with

Table 3 Major flora regions of the Palearctic realm that are relevant for the steppe belt (Meusel and Jäger 1992; Schroeder 1998; Takhtajan 1986), and summary of respective key climate characteristics (*P* precipitation, *T* temperature; see Djamali et al. 2012)

Steppe region	Flora region	Climate
European	Southern Euro-Siberian	Moderate T, low P seasonality, relatively large share of winter P
Middle Asian	Irano-Turanian, Middle Asian subregion	Moderate T with high T seasonality, low P, large share of winter P
Mongolian	Irano-Turanian, Central Asian subregion	Low T with high T seasonality, low P, mainly in summer
Tibetan	Irano-Turanian, Central Asian subregion	Low T due to high altitudes, low P in East, more mesic in West, P mainly in summer
Mediterranean	Mediterranean; Anatolia to Afghanistan: Irano-Turanian	High T, moderate P, large share of winter P

Cleistogenes spp. (Middle and Central Asia) and *Botriochloa ischaemum* being among the few exceptions. Feather grasses of the genus *Stipa* are typical elements of the Palearctic steppes from Eastern Europe to Mongolia, but also occur with several species in the Mediterranean (Hamasha et al. 2012). Spring geophytes can form colourful spring aspects in Middle Asia, Europe and the Mediterranean. Several genera from this region are of ornamental importance in gardening (e.g. *Crocus*, *Eremurus*, *Tulipa*; Bone et al. 2015). Those plants are scarce in Mongolia and China. The Near East from Anatolia to the Caucasus is the richest part of the Irano-Turanian phytogeographical region (Takhtajan 1986) in terms of non-arboreal xerophytes (species of *Astragalus*, *Onobrychis*, and *Acantholimon*; Kürschner 1986; Zohary 1973). Centres of endemism with 20–100 endemic species on 10,000 km² are found in Anatolia and the Kopet Dagh (Kier et al. 2009; Medail and Quezel 1997).

The major disjunction along the Tien Shan–Altai line is also reflected in steppe vegetation, where the western Pontik-Kazakh steppes are distinguished from the eastern Siberian-Inner Asian steppes (Lavrenko et al. 1991). Phytosociologically, the characteristic steppes of the West belong to the class *Festuco-Brometea*, while those of the East mainly are *Cleistogenetea squarrosae* (Ermakov et al. 2006).

According to Bohn et al. (2003), the *European steppe region* forms a continuous band increasing in width towards the East, being limited to the North by a band of 200–400 km forest steppes. Separated from this extensive steppe area (usually called Pontic steppes) are smaller outposts of forest steppe to the West, the largest being in the Pannonian Basin (Hungary) with approx. 37,000 km² (Molnár et al. 2012, Supplementary Material Online Resource 1) and smaller ones along the Lower Danube (Romania) and in Turkey-in-Europe (Bohn et al. 2003). The natural vegetation of the Pannonian forest steppes is a mosaic of grasslands on sandy, loess and saline soils mixed with drought-adapted shrublands and woodlands (Molnár et al. 2012). In the Pontic subregion, vegetation changes along the precipitation gradient from north to south: (1) meadow steppes rich in meso-xerophytic forbs in the forest-steppe zone; (2) true steppes (with *Stipa pennata*, *S. tirsia*, *S. daysphylla*, *S. ucrainica*, *Festuca valesiaca*, *Koeleria macrantha*) and (3) desert steppes (with *Stipa lessingiana*, *S. sareptana*, *Festuca valesiaca*, *Artemisia* spp; Bohn et al. 2003; Walter and Breckle 2004). Phytosociologically the majority of the European steppes belong to the

class *Festuco-Brometea*, the types on sandy soils to the *Koelerio-Corynephoretea*, and those in saline depressions to the *Festuco-Puccinellietea* (Mucina et al. 2016).

The steppes of *Middle Asia* form a broad belt in southern-central Siberia and northern Kazakhstan and extend south-eastwards as a narrow band between the Tien Shan–Himalayan mountains and the Central Asian desert. Comprehensive vegetation studies and maps are available (Rachkovskaya 2006; Rachkovskaya and Bragina 2012; Smelansky and Tishkov 2012). In the forest steppe zone of northern Middle Asia, forests (*Betula pendula*, *Populus tremula*, *Pinus sylvestris*) intermingle with meadow steppes. These are rich in forbs (e.g. *Filipendula vulgaris*, *Fragaria viridis*) and mesophytic grasses (*Phleum phleoides*, *Helictotrichon schellianum*). Further south, forests become confined to moist spots (with small birch groves, *kolki*, in depressions) surrounded by a matrix of typical steppes (Smelansky and Tishkov 2012), dominated by grasses such as *Stipa lessingiana*, *S. zaleskii*, *S. tirsia*, *Koeleria cristata*, and several ephemeroïds (e.g. *Tulipa* spp.). The desert steppes surrounding the Middle Asian (semi)-deserts have an open cover of *S. glareosa*, *S. krylovii*, *S. sareptana*, and (dwarf) shrubs, most notably *Artemisia* species (*A. lessingiana*, *A. semiarida*, *A. gracilescens*). The tall mountain ranges host mountain steppes with a high number of petrophytic species (e.g. *Festuca valesiaca*, *Thymus* spp.). Their upper limit is demarcated by *Larix* or *Picea* forests, while above the treeline, Tibetan-type alpine steppes and pastures occur.

The *Mongolian and Tibetan steppes* of Central Asia constitute the largest of the main steppe regions. Major subregions can be distinguished (Grubov 2010; for vegetation maps see Lavrenko and 1979; Vostokova and Gunin 2005; Zhang et al. 2014). In the *Mongolian steppe region*, the desert steppes of the Dzungarian basin form the western transition zone, as indicated by the presence of spring ephemeroïds (e.g. *Carex physodes*, *Eremurus* spp.). The iconic grass steppes of the Mongolian plateau mainly stretch eastwards from the Altai to NE China, with plant height increasing towards tall grass steppes (height >80 cm, akin to tall-grass prairies) in the East, which demarcate a transition to the Manchurian forest region. These typical steppes are characterised by a number of dominant and often endemic bunch grasses (Supplementary Material Online Resource 6), interspersed with shrubs on disturbed substrates (Karamysheva and Khramtsov 1995; Hilbig 1995). The transition to the Central Asian drylands (“Gobi”; Sternberg 2015) is demarcated by desert steppes with an increasing share of summer geophytes (e.g. *Allium* spp.) and chenopods (i.e. *Anabasis* and *Salsola* spp.).

The *Tibetan steppes* are differentiated by the extreme elevations, yet show large precipitation gradients (Liang et al. 2012). The moister East hosts relatively dense alpine pastures (known as alpine meadows in the local literature) formed by sedges of the *Kobresia* group (now included in *Carex*, Global Carex Group 2015). Most notable is the tiny *K. pygmaea*, which forms one of the largest alpine ecosystems worldwide and is highly tolerant to both extreme climate and intense grazing (Miehe et al. 2008; Seeber et al. 2015). The eastern Tibetan steppes are more similar to Mongolian desert steppes formed by *Stipa* spp. and onions (Supplementary Material Online Resource 6; Miehe et al. 2011).

The *Mediterranean steppes*, as treated here, form a discontinuous belt from Morocco in the West through Anatolia and North Iran to Afghanistan. According to Walter and Breckle (2004), the steppes of North Africa cover about 630,000 km², of which the driest parts should probably be considered as semi-deserts under our steppe definition. However, vegetation types dominated by species such as *Stipa tenacissima*, *Lygeum spartum*, and *Artemisia herba-alba*, largely fall under our definition. In the Atlas Mountains of Morocco, they mainly occur at elevations of 1400–2400 m a.s.l. (Finckh and Poete 1987). These landscapes, which have been under severe human impact for millennia, would naturally be

very open woodlands, with trees such as *Juniperus phoenicea* scattered in a grass-forb matrix (Walter and Breckle 2004). The steppes of the Near East extend from Anatolia to south of the Caucasus, while the Middle East steppes mainly cover mountainous parts of Syria and northern Iraq. In Iran, steppes mainly occur on the southern slopes of the Alborz Mts. at elevations of ca. 1000–4000 m a.s.l. (Akhami et al. 2013; Mahdavi et al. 2013). Under arid conditions, the vegetation is dominated by *Artemisia* spp. (N Caucasus: *A. taurica*, S Caucasus: *A. lerchiana*; Mesopotamia and Syria: *A. aucheri*; Anatolia and Albroz Mts.: *A. sieberi*; Geerken et al. 2005), mixed with desert species such as *Salsola* spp. and ephemeroïds such as *Poa bulbosa* (Edgell 2006; Nakhutsrishvili 2013; Zohary 1973). The total plant species richness is low (Nakhutsrishvili 2013) and wormwood communities may have replaced primary grass steppes after heavy grazing (Walter and Breckle 1985; Zohary 1973). Steppes dominated by perennial grasses are heavily fragmented today. In the sub-humid climate of the Caucasus, *Botriochloa ischaemum-Stipa* grasslands occur, often as a replacement of forest communities (Atamov 2002; Nakhutsrishvili 2013). In central Anatolia and Iran, *Bromus tomentellus* becomes more abundant under xeric conditions, while scattered trees of *Quercus*, *Juniperus*, and *Pistacia*, as well as shrubs (e.g. *Berberis vulgaris*, *Rosa canina*) occur locally under higher precipitation regimes as remnants of original woody vegetation (Frey and Probst 1986). Montane steppes are characterised by perennial grasses of the genera *Festuca*, *Bromus* and *Stipa*, dwarf shrubs, such as *Thymus* and thorny cushions (*Astragalus* spp., *Acantholimon* spp., *Onobrychis cornuta*; Atamov 2002). In Albroz Mts. steppes with *Stipa hohenackeriana* and *Astragalus microcephalus* at 1400–2000 m a.s.l.; *Stipa arabica*, *Festuca sclerophylla* and *Dactylis glomerata* occur up to 2900 m a.s.l., followed by thorn cushion communities up to 3400 m a.s.l. In Afghanistan mountain forelands and deep valleys host desert steppes with Middle Asian affinities (Breckle et al. 2010), while mountain slopes support Mediterranean forest steppes and woodlands. High altitude grasslands and shrublands occur in the subalpine ecotone; many of these may owe their existence to human impact. Lack of summer rains, however, restricts tree growth at least in the drier central and eastern parts of Afghanistan. Alpine steppes show affinities to the Tibetan region located eastwards.

Fauna

Palaeartic grassland plants have evolved with grazing herbivores, and large herds of wild ungulates still roam several steppe regions. The wild Przewalski's horse (*Equus ferus przewalskii*) became extinct in the wild in the twentieth century (Wakefield et al. 2002), but has since been re-introduced to Mongolia and Northern China (van Dierendonck and Wallis de Vries 1996; Wakefield et al. 2002); and recently to Kazakhstan (Astana Times 2014) and neighbouring Russia (The Guardian 2016). Wild Ass survived from the Near East to eastern Mongolia (*Equus hemionus* group) and Tibet (*Equus kiang*; Kaczensky et al. 2008; Mallon 2016; Ward et al. 1999). Large wild grazers have almost disappeared from the European steppes, with a small population of Saiga antelope (*Saiga tartarica*) remaining in European Russia (Mallon 2016). Saiga is still present (Kamp et al. 2016) across the steppes of Kazakhstan. The Mongolian and Tibetan steppes host a rich mammal fauna (Batsaikhan et al. 2014; Mallon 2016; Mallon and Zhigang 2009; Schaller 1998). Goitered gazelles (*Gazella subgutturosa*) and Mongolian gazelles (*Procapra gutturosa*) form large herds in parts of Kazakhstan and in eastern Mongolia (Fig. 6), and the

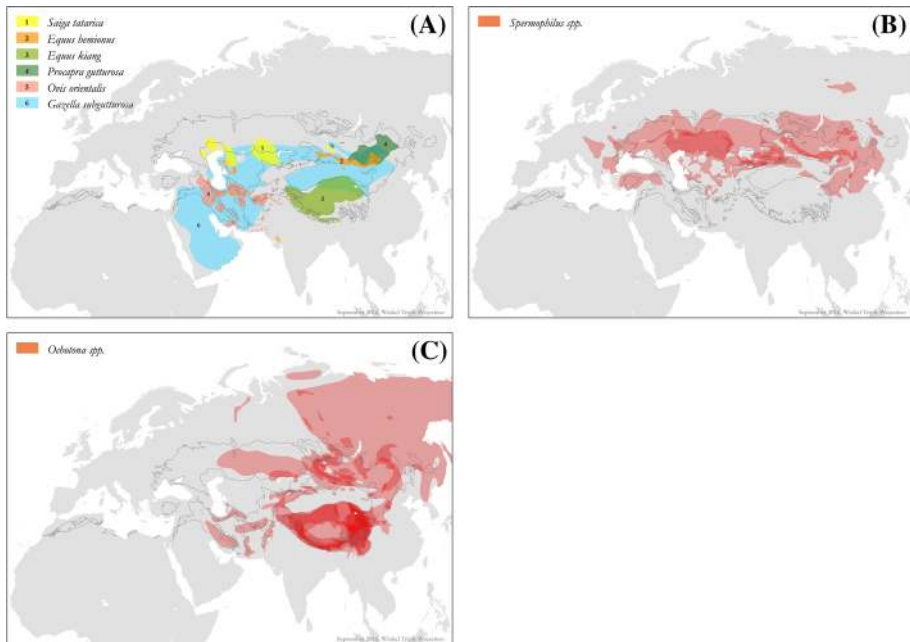


Fig. 6 Approximate distribution ranges of key steppe mammal species. **a** Large herbivores. **b** Species richness of ground squirrels (“susliks”). **c** Combined range of pika—*Ochotona* spec. **d** Data after IUCN’s red list database (<http://www.redlist.org>; see Supplementary Material Online Resource 8). (Color figure online)

Mongolian gazelles represent one of the very few remaining extensive ungulate migration systems outside of Africa (Olson et al. 2009). Wild camels (*Camelus bactrianus*) are largely restricted to Mongolia and China (Guoying et al. 2002; Kaczensky et al. 2014), while Yak (*Bos mutus*) is an endemic of Tibet (Qiu et al. 2015). The Mouflon (*Ovis orientalis*) occurs in western Asia, but experienced strong population declines (status now vulnerable; IUCN 2016) due to habitat loss as well as poaching. Other threatened large herbivores, such as *Gazella cuvieri* and *G. gazella*, *Nager dama* and *Ammotragus lervia*, are distributed mainly across the steppes of the Near East.

Small mammals, especially burrowing herbivorous species, fulfil key ecosystem roles across the region (Fet and Atamuradov 2012; Lavrenko et al. 1991; Zlotin and Khodshova 1980). Their burrows and mounds provide habitat for plants and animals and increase grassland heterogeneity and landscape diversity. They influence soil fertility and the nitrogen cycle and so increase forage quality for large herbivores (Davidson et al. 2012; Wesche et al. 2007). Across the steppes, small mammal diversity is high including a large number of regional endemics (Ognev 1967). Characteristic taxa are Marmots (*Marmota* spp.), nocturnal Jerboas (Allactagini) in Kazakhstan and Siberia as well as Ground squirrels (*Spermophilus* spp.; Figure 6) and Pikas (*Ochotona* spp.) across the region. Keystone roles have been demonstrated, for instance in *O. curzoniae* in Tibet (Lai and Smith 2003; Smith and Foggin 1999) and *O. pallasii* in Mongolia (Wesche et al. 2007). However, much research on these small mammals is published in Russian, rendering access difficult for an international readership.

Bird species richness is usually low due to comparatively low productivity and uniformity of the steppe habitat. The dominant birds of the steppe region are larks (Alaudidae), which show high species richness and abundance (e.g. Kamp et al. 2012). Several species occur both in the steppes west of the Altai and in Mongolia and China, while others form vicariant pairs, e.g. White-winged lark (*Melanocorypha leucoptera*) in Kazakhstan, Mongolian lark (*Melanocorypha mongolica*) in Mongolia (Mainjargal et al. 2013). Birds of prey, such as the Steppe eagle (*Aquila nipalensis*), Cinereous vulture (*Aegypius monachus*), and Saker falcon (*Falco cherrug*), are widespread across the steppes, as they benefit from high numbers of small mammals and carrion of wild and domestic ungulates. The Kazakh steppes host a comparatively large number of biome-restricted bird species, such as Sociable lapwing (*Vanellus gregarius*; Kamp et al. 2009) and Black lark (Lameris et al. 2016). Furthermore, they are a stronghold of several open-country birds (termed ‘farmland birds’ in Europe), which are declining across Western and Central Europe (Kamp et al. 2015).

In spite of the cold winters, the herpetofauna is relatively rich, with lizards and snakes occurring in all regions, while tortoises are not known from Mongolia and Tibet (Middle Asia: one species). Amphibians are generally rarer due to lack of water bodies (and cold winters, Terbish et al. 2006).

Taxonomic baseline information is available for most invertebrate groups, but their ecology has rarely been studied, and synoptic reviews are lacking. Steppes host many rare and biome-restricted species of Lepidoptera, such as *Agrodiaetus* spp. in the Near East, a species-rich group of blues particularly well represented in Turkey and Iran (Ambarlı et al. 2016). Grasshoppers and crickets (Orthoptera) have a large impact on ecosystems in terms of herbivory and nutrient cycling, especially in years of population outbreaks (Kang et al. 2007; Zhong et al. 2014). Several species, such as *Calliptamus italicus* and *Locusta migratoria*, are considered cropland pests in the Kazakh steppes, where land abandonment and a lack of control allowed mass gradations during the 1990s and 2000s (Tolubayev et al. 2007).

Land use and its change

Nomadic pastoralism is the traditional form of land use in steppes, where semi-arid conditions render arable farming difficult. Seasonality triggers regular migrations of herders along slopes in mountain regions or across the plains (Fernandez-Gimenez 1999; Zemmrich et al. 2010). Rains are unreliable from year to year, and herders conduct long-distance movements across hundreds of kilometres in response to drought. This requires exchange of information and adapted land management rules (Addison and Greiner 2016; Upton 2005). Although the role of mobility for sustainable land use seems obvious, recent land use policies have aimed at sedentarisation. The environmental effects have not received attention until recently, mainly under socio-economic perspectives (Conte and Tilt 2014; Kreutzmann 2013; Li and Huntsinger 2011; Ptackova 2011).

Sheep and goats are the key livestock species (Bedunah and Harris 2002; Berger et al. 2013; Wang et al. 2010), followed by cattle and horses. They were domesticated in the region (for sheep and goats dating back to 11,000 cal BP, pigs 10,500 cal BP, cattle 10,000 cal BP; Zeder 2008). Locally, horses, camels, and yaks are also important. Pastoral livelihoods are not necessarily older than arable farming because herders usually depend on grain traded with farmers in exchange for milk products and other commodities such as

salt. In Tibet, pastoral livelihoods spread after 3600 BP, when farming societies were already established in the more mesic sites on the plateau and in the neighbouring regions (Chen et al. 2015a). Early Neolithic remains date back to 6000 BP, and the domestication of the Yak has recently been dated at 7300 BP (Qiu et al. 2015), so pastoral and sedentary livelihoods may have developed simultaneously.

Given that steppes have been exposed to wild migratory grazers over evolutionary time-scales, pastoralism did not introduce fundamentally new pressures. The question of degradation is therefore not a question of grazers’ presence, but of their density. Unfortunately, “natural” ungulate numbers before human interventions are largely unknown in all temperate grasslands (e.g. Lauenroth 1998). Adjusting local stocking rates to a natural reference point is practically impossible and theoretically difficult given the temporal and spatial variability inherent to the steppes. Complete grazing exclusion, as advocated in many conservation policies, is questionable and may be seen as a form of “disturbance” in view of the evolutionary grazing history of steppes. Low or moderate intensity grazing often seems the best option for biodiversity and carbon sequestration (Han et al. 2016; Shao et al. 2013).

We have summarised land use impacts crudely in Fig. 7, acknowledging the uncertainty of assessments. More detailed and reliable data are available for the European steppes and those in, for instance, Russia and Ukraine (Supplementary Material Online Resource 7). Conversion of steppes to cropland, rather than grazing intensification, has been the most important threat in mesic steppes in Europe, Middle Asia and partly in the Mediterranean. In the *European steppes*, conversion has been particularly widespread (Deák et al. 2016). Pristine steppes lacking a dense tree cover have only been preserved if they were unsuitable for agriculture (Molnár et al. 2012). Such grasslands are often azonal saline grasslands (Eliáš et al. 2013), as in the Carpathian basin (Zólyomi and Fekete 1994). Zonal steppes, such as those in the Pontic region of Ukraine, were mostly ploughed, and only fragments survive at road verges or on kurgans (Sudnik-Wójcikowska and Moysiyeenko 2012). Similar trends are reported from European Russia (Smelansky and Tishkov 2012), central Anatolia in Turkey (Ambarlı et al. 2016) and the Pannonian forest steppes in Hungary (Deák et al. 2016; Molnár et al. 2012).

In recent decades, however, land abandonment increased in post-communist countries (Alcantara et al. 2013) such as Russia, where almost 260,000 km² of arable land were abandoned in the last two decades (Smelansky and Tishkov 2012), or in Turkey, where rural workers migrated to Turkish cities or even Europe (Ambarlı and Bilgin 2014).

Unit	Conversion		Rangeland degradation		classes
	Extent	Evidence	Extent	Evidence	
European region	↔	WE	↔	WE	low
Middle Asian region	↔	WE	↔	EI	moderate
Mongolian region	↔	WE	↑	EI	high
Tibetan region	↔	WE	↑	IC	very high
Mediterranean region	↓	EI	↓	IC	

Fig. 7 Impact of steppe conversion (mainly to cropland) with respect to the former/natural extent of grasslands in the steppe regions, and effects of grazing degradation in the still extant grasslands. Impact classes low, moderate, high, very high. Based on our knowledge, we estimated trends 1990–2020 as *increasing, declining, largely unchanged* (see *arrows*). Confidence of estimated impact *WE* well established, *UR* unresolved, *EI* established but incomplete, *IC* inconclusive (see IPBES confidence levels, IPBES 2016). See Supplementary Material Online Resource 7 for more detailed information on selected countries

Spontaneous recovery of steppe-like grasslands was reported where local seed rain was sufficient (Ruprecht 2006; Török et al. 2011).

Large secondary *steppe-like grasslands* have been created in Europe outside the steppe biome by tree cutting and are maintained by traditional grazing or hay-making (Fischer and Wipf 2002; Hejzman et al. 2013; Poschlod et al. 2009). Many of these are now affected by the twin threats of intensification in favourable sites such as lowlands, and abandonment in marginal sites with shallow soils or at high altitudes (Dengler et al. 2014; Habel et al. 2013). The latter results in increased cover of shrubs and trees (Vassilev and Apostolova 2013), increased litter accumulation, and increases in unpalatable grasses. Severe grazing intensification, on the other hand, has led to an increase of degraded loess grasslands (e.g. Pannonian region, Zólyomi and Fekete 1994; western Pontic steppes in Bulgaria, Tzonev et al. 2006; Vassilev and Apostolova 2013; Anatolian steppes, Adak et al. 2005). In Ukraine and Russia, arson and illegal burning are a problem today (Korotchenko and Peregrym 2012; Smelansky and Tishkov 2012). While prescribed burning with longer fire return periods (at least 2–3 years) is beneficial for biodiversity conservation through removing accumulated litter, irregular or frequent burning is detrimental to grassland biodiversity (Valkó et al. 2014). In several regions, steppe and forest-steppe grasslands are also threatened by afforestation (Korotchenko and Peregrym 2012; Molnár et al. 2012; Smelansky and Tishkov 2012). Mining and oil/gas drilling are recent pressures reported from Russia.

In the *Middle Asian steppes* of Western Siberia, arable agriculture was already practised 3500 BP (Zakh et al. 2010); yet 2500 BP sedentary and semi-nomadic animal husbandry prevailed, and there is little evidence for crop cultivation at that time. Agriculture again became widespread with the Russian expansion in the eighteenth century (Ramankutty and Foley 1999) but remained patchy and unproductive until the 1950s. The Soviet ‘Virgin Land Campaign’ of 1953–1960 (McCauley 1976) resulted in the conversion of 460,000 km² of steppes into cropland across Kazakhstan and adjacent parts of Russia (Durgin and Frank 1962). After 1991, the transition to a market economy rendered crop production unprofitable over large areas, and the state farm system collapsed (Kamp et al. 2011). About 310,000 km² of cropland were abandoned across Russia (Schierhorn et al. 2013) and 120,000 km² in Kazakhstan (Kamp et al. 2011; Kraemer et al. 2015). Species richness (Kamp 2014; Kamp et al. 2011) and carbon stocks (Propastin et al. 2008; Schierhorn et al. 2013) recovered on ex-arable land. Successions are, however, slow, and it is uncertain how close to pristine steppe the resulting vegetation communities will ever be (Brinkert et al. 2016; Kämpf et al. 2016b). Since about 2000, ca. 50 % of the abandoned cropland has been recultivated in Kazakhstan and other parts of Middle Asia (Chen et al. 2013b; Petrick et al. 2013). In contrast, cropland recultivation in Western Siberia has remained insignificant (Kühling et al. 2016). Where, when and how much cropland will eventually be recultivated is unclear (Meyfroidt et al. 2016).

In Central Kazakhstan, traditional pastoralism with horses and sheep changed in the nineteenth century when Russian colonists started to settle. Nomadism collapsed with collectivisation in the 1930s. At least 1 million people (40 % of Kazakhstan’s population) died from hunger, and hundreds of thousands fled to Mongolia and China (Yesdauletova et al. 2015), leading to a strong decline in livestock numbers. Livestock recovered in Soviet times due to a well-implemented pasture management, including animal movements between summer and winter pastures, albeit over much shorter distances than in the nineteenth century (Robinson and Milner-Gulland 2003). Livestock numbers collapsed again after 1991, with declines of up to 80 % in cattle and sheep (Kazakhstan: Kamp et al. 2016; W Siberia, Kühling et al. 2016). Biomass accumulated, increasing the frequency of

wildfires (Dubinin et al. 2011, 2010) and changing ecosystem properties (Brinkert et al. 2016). In the period 2000–2015, livestock numbers remained at very low levels in Western Siberia (Kühling et al. 2016), but have increased significantly in Kazakhstan (Kamp et al. 2016; Kerven et al. 2016). However, most of these animals are now owned privately, and due to lack of transport, they are concentrated within 10 km of settlements, leading to local overgrazing at few sites, while others remain ungrazed (Kamp et al. 2012). There are incentives to revive the commercial livestock industry, but these have so far been of limited efficiency (Kamp et al. 2016). Developments in steppes of the southern lowland of Middle Asia have been different. In Turkmenistan livestock numbers increased from 5.6 million in 1991 to 15.5 million in 2004, causing increasing pressure on the few productive steppe pastures (Kaplan et al. 2014). Since 1971 the area irrigated for agriculture has increased (Saiko and Zonn 2000), with continuous growth after 1991 (Kaplan et al. 2014). After a few years, salinisation often leads to abandonment (Löw et al. 2015) and the need to convert new grassland areas (Kaplan et al. 2014).

Land use impact varies tremendously across the *Mongolian steppe region*. With more than 800,000 km² of steppes and drylands, Mongolia hosts one of the world's largest intact rangeland systems (Batsaikhan et al. 2014). Pastoral livelihoods continued to be the main form of land use during the socialist economy, when a system of permanent settlements supplied necessary services (e.g. medical care, education) to essentially still mobile small-scale herder groups (Fernandez-Gimenez 1999). In times of drought, even long-term migrations were supported. In the drier steppes, livestock numbers fluctuated in line with the non-equilibrium model of rangeland science (Ellis et al. 2002; Fernandez-Gimenez and Allen-Diaz 1999), yet country-level livestock numbers remained stable over much of the twentieth century (Janzen 2005). Numbers increased tremendously after transformation in the early 1990s, which was partly a consequence of a series of moist years (Retzer and Reudenbach 2005). Recurrent droughts since 2000 enforced fluctuations, yet livestock, especially Cashmere goat numbers (Berger et al. 2013), still showed a net increase to a current all-time high. This triggered an extensive discussion about widespread degradation (Hilker et al. 2014; Liu et al. 2013; Sneath 1998). Consensus is emerging that degradation is unevenly distributed, being pronounced in the central part of the typical steppes, while the dry southern parts and the vast tall grass steppes in eastern Mongolia are in a better state (Addison et al. 2012; Eckert et al. 2015; Gao et al. 2015; von Wehrden et al. 2015).

While conversion into cropland is almost negligible in Mongolia, >10 % of steppes of Chinese Inner Mongolia have been ploughed (mainly in mesic tall grass steppes; John et al. 2009; White et al. 2000). This was paralleled by sedentarisation of herders and assignment of land use rights. These governmental interventions were partly a response to steppe degradation. Many of today's extensive sand semi-deserts may once have been dry steppes (Brogaard and Li 2006; Wang et al. 2008; Zheng et al. 2006), and massive restoration schemes have been implemented (Hao et al. 2005, 2014; Jiang et al. 2010; Zhang et al. 2013). Success was, however, limited (even unwanted effects like soil desiccation occurred; Deng et al. 2016). Recent studies also suggest that sedentarisation and individual land use rights reduce flexibility and force herders to unsustainable grazing practices on their limited land (Conte and Tilt 2014; Liang et al. 2012). Whether larger pasture user groups would graze more sustainably is still an open question (Hua et al. 2015).

The complexity of grazing effects in the Chinese steppes is captured by a recent review (Wang and Wesche 2016). Grazing effects depend on vegetation composition, soil nutrient content, local grazing intensity and—on a large scale—climate and productivity. Impacts on soil carbon and nitrogen contents generally tend to be negative, but with large variance. These facts also hold for the Tibetan steppes and pastures. In spite of claims of widespread

degradation, evidence of grazing impact is not based on standard assessment methods and is often unbalanced and biased (Cui and Graf 2009; Harris 2010; Yang et al. 2005). In view of the apparent complexity of grazing effects, governmental efforts to reduce livestock numbers in general are questionable. Pasture user rights were contracted to individual households or communities, and since the 1990s pastures became fenced. This was accompanied by sedentarisation schemes, and now migrations have been reduced in the larger part of Tibet (Li et al. 2012; Ptackova 2011; Wang et al. 2014). Since 2002, so-called grassland retirement programmes have been implemented, forcing local herder communities to seek alternative sources of income (mainly collection of the fungus *Ophiocordyceps sinensis*; Cannon et al. 2009; Winkler 2008). The Tibetan grazing systems are now undergoing a similar change as Inner Mongolia experienced decades ago. In a striking parallel, first studies start to question governmental policies and highlight the threat of increased grazing degradation under sedentary rather than traditional mobile livestock keeping on the Tibetan plateau (Cao et al. 2011; Shang et al. 2014; Wang et al. 2014).

The areas of the *Mediterranean steppe region* in North Africa, Anatolia, Mesopotamia, and Iran are among those that have been longest inhabited by highly developed human cultures. Thus human impact on landscape and vegetation dates back several millennia. It is very hard to reconstruct the “natural vegetation” there, which is probably one of the reasons why the opinions to which extent steppes are natural in this region and to which extent they have replaced dry forests deviate. For the North African and Anatolian part of the Mediterranean steppe region, estimates assume that at least 50 % of the original vegetation were ploughed during the last century (Supplementary Material Online Resource 7). Livestock grazing, at suitable sites often linked with arable farming, is the main livelihood. Sedentary husbandry of sheep, goats and cattle is practised around villages with nearby water sources, while transhumance prevails in highlands (e.g. Akasbi et al. 2012). In contrast to European steppes, fires are not commonly employed for steppe management. Overgrazing is the major cause of land degradation in steppes of many countries such as Turkey and Iran (Ambarlı et al. 2016; Farahpour et al. 2004). Land abandonment has occurred regionally due to armed conflicts and poor income options. Successions are much slower in Anatolia compared to European grasslands (Ambarlı and Bilgin 2014).

Climate change

Given the broad climatic niches occupied by steppes (Table 2), climate change effects are likely to differ between and even within major steppe regions. Not surprisingly, many of the continental parts experience increases of annual mean temperature that exceed globally averaged trends. These are, however, less important than changes in certain seasons or interactions with other key elements such as precipitation.

Mean annual temperatures in Southern, Central, and Eastern *Europe* are projected to increase by up to 2 K, with slight regional differences, until the year 2035 (Kovats et al. 2014; Stocker et al. 2013). For precipitation, seasonal shifts are projected with a decrease of growing-season precipitation and an increase in the winter period. The dry lowlands of the Pannonian regions are least vulnerable in Europe with respect to climate change because their species are highly adapted to drought and heat. Pronounced species turnover is, however, expected with conditions becoming more Mediterranean: Forest steppe

specialists and forest generalists may decrease, while drought-tolerant Mediterranean species are predicted to increase (Kovács-Láng et al. 2000; Thuiller et al. 2005). Drought-tolerant invasive plants may also extend their cover in steppes (i.e. *Asclepias syriaca* in sand steppes of the Pannonian subregion; Kelemen et al. 2016). Lower summer precipitation should result in increased probability of wildfires. These will affect tree cover, with a considerable reduction of sites suitable for forests and an increase of sites potentially suitable for true steppe vegetation (Czúcz et al. 2011; IPCC 2014b).

For *Middle Asia*, global scenarios predict an increase in mean annual temperature by 1.5–2 K by 2035 and an increase in drought frequency, but little precipitation change (IPCC 2013). Regional scenarios suggest that mean annual temperatures will increase even more (by 2.3–4.5 K until 2030), but especially in spring (Pilifosova et al. 1997). Degefe et al. (2014) predict changes in extreme events for the West Siberian forest steppe in the period 2021–2050, including an increasing frequency of droughts. For the West Siberian forests steppes, a shift of vegetation zones to the North due to warming has been proposed (Tchebakova et al. 2009). Middle-Asian wide analyses of trends in precipitation are generally inconclusive for the period 1990–2009, with regionally varying increases and decreases (Chen et al. 2013a). Droughts became more frequent in Kazakhstan in the period 2000 to 2008 (de Beurs et al. 2009; Lioubimtseva and Henebry 2009; Mohammad et al. 2013). While accumulated growing season precipitation decreased in this period, accumulated growing degree days increased (Wright et al. 2009). Pronounced climatic changes across the steppes of Kazakhstan between 1990–2006 include a: (1) mean annual temperature increase of 0.8 K, especially pronounced in winter (1.2 K) and spring (0.9 K); (2) weak, but non-significant increase in annual precipitation (ca. 4 %), and (3) significant increase of the absolute humidity of the near surface air.

In the *Mongolian steppes*, temperature increase in the last decades has exceeded the global average (Dagvadorj et al. 2009; Yue et al. 2013). Effects of increased temperatures on vegetation are complex and interact with both grazing (Spence et al. 2014) and local moisture conditions (Auerswald et al. 2012; Niu et al. 2008; Wu et al. 2014) as the key driver (Liang et al. 2015). Precipitation is highly variable in space and time, with coefficients of interannual variation often exceeding 30 % (von Wehrden et al. 2010; also data in Maussion et al. 2014). This variability renders detection of long-term trends difficult, and most stations in Central Asia lack clear temporal trends in precipitation (Klein Tank et al. 2006; von Wehrden et al. 2010; Yue et al. 2013). In consequence, climate modelling faces severe difficulties with low consensus among precipitation models across Central Asia (IPCC 2014b). Even though there is no evidence that annual precipitation totals are generally decreasing, increasing temperatures may result in higher physiological drought stress. It is unclear if this may offset effects of rising CO₂ levels and thus increased water use efficiency (Piao et al. 2015; Soussana and Luscher 2007). Seasonal trends are even more difficult to derive, but are of outmost relevance (Guo et al. 2012; Yang et al. 2015). Several studies describe a shift from summer to winter or spring precipitation (Dagvadorj et al. 2009; Peng et al. 2010; Zhao et al. 2014). Snow in deep winter would evaporate without any favourable effects on plant growth and may instead pose serious problems for overwintering livestock and larger mammals (Middleton et al. 2014; Shang et al. 2012). An increase in spring precipitation would, however, extend the growing season as shown by a correlation between snow cover and growth in Chinese grasslands (Peng et al. 2010). The Mongolian region recently witnessed a series of extreme climate events (Nandintsetseg and Shinoda 2013), but these do not necessarily result in reduced growth in the drier rangelands as shown for North America (Heisler-White et al. 2009). Extreme rain events also are a

precondition for successful plant reproduction in the Central Asian drylands (Gunin et al. 2003; Ronnenberg et al. 2008).

In the *Tibetan steppe region*, temperatures have also strongly and almost uniformly increased (Chen et al. 2013a). Higher temperatures negatively affect growth of *Kobresia* pastures at their lower altitudinal limit (Klein et al. 2004), while effects in the core alpine range are complex (Dorji et al. 2013). Across most of Tibet, however, precipitation patterns are more relevant for ecosystem functioning than temperature (Chen et al. 2013a; Yang et al. 2010). Temporal trends in annual mean precipitation are heterogeneous across the plateau (Lehnert et al. 2016), resulting in declining vegetation cover in the southern part and increasing in the north-eastern part. In terms of seasonal patterns, snow precipitation increases, locally allowing for increased growth with conditions becoming warmer (Chen et al. 2015b; Wan et al. 2014), while other authors found a reduced growing season length (Yu et al. 2010). Moreover, climate effects interact with local grazing patterns (Li et al. 2011). Effects of climate change on soil C are even more complicated with losses due to permafrost degradation (Yang et al. 2013), being potentially compensated by increased growth and sequestration under warmer conditions (Chen et al. 2013a).

In the *Mediterranean region*, temperature increase has been especially pronounced in summer, and heat waves are projected to increase further (IPCC 2014a; Kovats et al. 2014). Total annual precipitation, in contrast, shows only slight changes. Although uncertainty is high, plant-available moisture is predicted to decline more than in any other of the main regions of the Palaearctic steppe biome. This is critical in view of the severe soil degradation in the entire Mediterranean region, which reduces soil water retention capacity and also increases runoff. In terms of crucial seasonal patterns (Lozano-Parra et al. 2014), there is a tendency towards drier summers and increased interannual variability (Kovats et al. 2014). In response to more frequent droughts, drought-sensitive perennials may decline, while annuals may be fostered (Ooi 2012). Among perennial grasses, functional types with high drought tolerance or with especially broad ecological niches will benefit (Porqueddu et al. 2016). The predicted turnover in species composition (Henkin et al. 2010) will be more important for forage quality than the limited changes observed within species (Dumont et al. 2015). General ecosystem properties are also affected by variability, and some grasslands may oscillate between being C sinks and C sources in response to droughts and moist phases (Aires et al. 2008). Although prospects with respect to overall alterations in species composition, habitat loss and degradation seem dim for the Mediterranean basin as a whole (Navarra and Tubiana 2014), specific overviews of the effect on its steppes and related grasslands are still needed.

Formal conservation and protected areas

The IUCN world database of protected areas provides a general overview of formal conservation (Fig. 8). In total reserves (as currently registered) cover 1.4 million km², being equivalent to some 14.1 % of the overall spatial extent of the Eurasian steppe biome. Thus levels appear to be higher than in other temperate grasslands, where protected areas account for 3.4 % as a global average and much less in regions such as North America (Henwood 1998, 2012). Care has to be taken with respect to the tremendous regional differences. Excluding a single complex of 11 reserves on the Tibetan plateau (total 0.8 million km²) would lead to an overall fraction of 6.5 %, which is close to earlier estimates by White et al. (2000), who reported 6.6 % of protected areas for Asian, 3.4 %

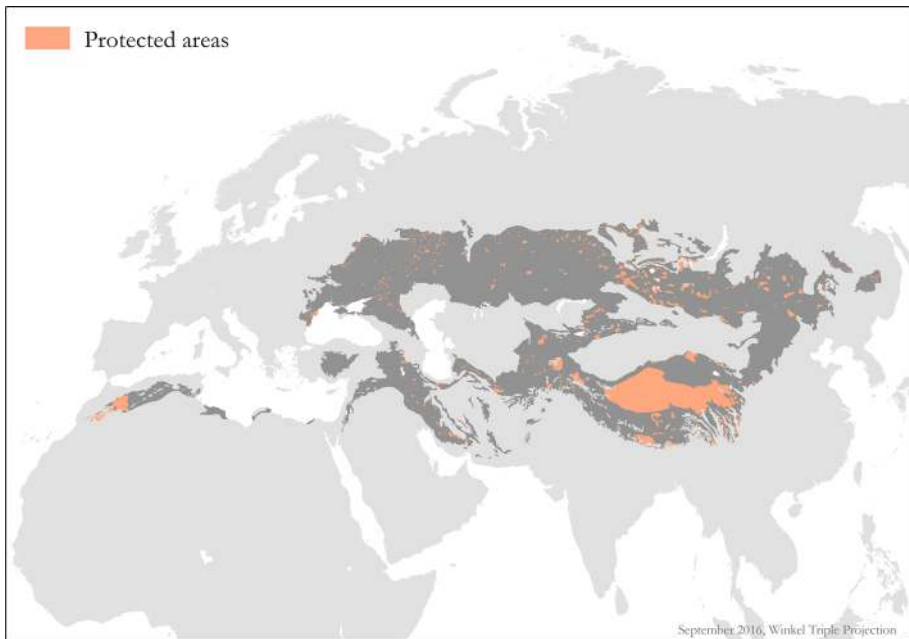


Fig. 8 Map of the Palaearctic steppe biome showing the main protected areas as registered in the IUCN, UNEP-WCMC world database of protected areas (<http://www.protectedplanet.net>), categories I–IV. (Color figure online)

for European and 7.5 % for North African grasslands. Moreover, conservation efforts in terms, for example, of grazing restrictions and the issuing of mining concessions differ tremendously.

In the *European steppes*, sizes and numbers of reserves increase from the western part towards the East in southern Ukraine and southern Russia (Bohn et al. 2003; Deák et al. 2016; Rachkovskaya and Bragina 2012). Outside of reserves, very few steppe sites remain, and conservation of the tiny fraction of extant European natural grasslands clearly is a high priority. Conservation efforts including further extension of reserves are thus urgently needed.

The first protected areas in the *Middle Asian steppes* were created as strict nature reserves ('Zapovedniks'), e.g. in Kazakhstan in 1926 (Aksu-Zhabagly, Tien Shan) and 1931 (Naurzum zapovednik, Central Kazakhstan). More recently, the designation of new protected areas in the steppes and semi-deserts of Kazakhstan resulted in an increase from 7700 km² in 1990 to 38,700 km² in 2013 (i.e. from 1.0 to 5.1 % of the steppe zone area; Kamp et al. 2016). These new protected areas are situated in the least productive steppes and semi-deserts and mostly aim at the conservation of the Saiga antelope (*Saiga tatarica*). In the near-natural steppes e.g. of the provinces Aktyubinsk and West Kazakhstan, nature reserves are still lacking. Systematic assessments are not available, yet the efficiency of the current set of protected areas might be high (birds: Schweizer et al. 2014; Saiga: Singh and Milner-Gulland 2011).

Coverage of protected areas in the *Mongolian steppes* is relatively high, partly as a consequence of massive reserve designation in Mongolia during the 1990s (Stubbe 1997). The largest reserves are, however, in the southern (semi-) deserts and in the forest steppes

of the North (Reading et al. 2006), while protection is much lower in typical steppes. Most of the parks, whose aims are similar to those of biosphere reserves, still allow some form of grazing. Formal conservation is high in the Hustai National Park, which is especially prominent as a reintroduction site of Przewalski horses (Wit and Vegten 1998). Fragmentation of other steppe areas due to road development is now becoming a problem in Mongolia (Batsaikhan et al. 2014; Olson et al. 2011), whereas steppes of Chinese Inner Mongolia are already severely fragmented. There typical steppes are confined to reserves; which are again larger in the desert steppes. Within Chinese reserves, land use controls are partly relatively strict, and reserves with prominent species such as Przewalski horses and Camels receive special attention in conservation (Xia et al. 2014).

The exceptionally high cover of protected areas in the *Tibetan steppes* reflects the aim to reduce grazing impact and to develop other sources of income including tourism. In spite of formal protection, most of the Tibetan steppes are currently under some form of grazing (Fox et al. 2009; Fox and Dorji 2009). Grazing is, however, subject to increasing governmental control as stated above. The largest reserves are found in the relatively dry north-western alpine steppes, which still host large herds of wild ungulates. They have been under modest pressure from traditional hunting, but more recently an increase of permanent settlements resulted in higher levels of poaching. Fencing is practised even in reserves and results in locally increased grazing pressure and—perhaps more importantly—in fragmentation of wild ungulate habitat.

Legally protected areas in the *Mediterranean* steppe region are insufficient to represent the steppe biodiversity. In addition to those shown in Fig. 8, there are 28 protected areas in the typical and forest steppe parts of Anatolia. They cover 1.5 % of the terrestrial land and represent only 16.2 % of threatened and near-threatened steppe species (Ambarlı et al. 2016). Iran has 253 protected areas (10.1 % of the territory), but it has been argued that only 2 % of them are effective (Kolahi et al. 2012). In Syria there are 14 rangeland protected areas (Barkoudah et al. 2000), but it is unclear how well they currently function. The Caucasus region benefits from transboundary conservation projects, which identified ca. 40 priority sites and three corridors to be conserved in steppes and semi-desert lands (Critical Ecosystem Partnership Fund 2004). Most of the protected areas in the IUCN database for the North African belt do not target steppe biodiversity as such, but have other goals (e.g. Ramsar sites).

Conclusions and the way forward

The Palearctic steppes share a number of unifying characteristics in climate, but also in the biota as a whole, although we have concentrated on the fauna and flora here. At the same time, there are major differences between steppe regions, and we strongly advocate to view data and management options against the backdrop of geographical and ecological subunits. Overgeneralisation should be avoided as shown by the example of livestock grazing, which may have negative effects in certain parts of the biome, while traditional mobile pastoralism may be the only sustainable land use option in others.

Obvious knowledge gaps nonetheless remain, including our understanding of climate change effects, especially potentially changing seasonal patterns. Related and equally needed is a comprehensive quantification of carbon pools in soils and their potential for C sequestration. We also lack data on ecology and distribution of most fungi (including lichen-formers) and invertebrate groups, for which we often have only taxonomical

information (and sometimes not even these as e.g. in case of soil organisms). Knowledge on vertebrates is much better, and data on flora and vegetation are especially rich. Here the challenge lies in synoptic approaches, which are urgently needed in the age of macroecology and global models. How this can work has recently been shown for the polar zonobiome (Walker et al. 2005, 2016). Ultimately a sound biome classification should take into account not only a single biome, but aim at a meaningful partitioning of the globe in a set of clearly defined such units—one of the tasks a new global working group is aiming at (Franklin et al. 2016).

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