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The edge of two worlds: A new review and synthesis on Eurasian forest-steppes

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Abstract

Aims: Eurasian forest-steppes are among the most complex non-tropical terrestrial ecosystems. Despite their considerable scientific, ecological, and economic importance, knowledge of forest-steppes is limited, particularly at the continental scale. Here we provide an overview of Eurasian forest-steppes across the entire zone: (i) we propose an up-to-date definition of forest-steppes, (ii) give a short physiogeographic outline, (iii) delineate and briefly characterize the main forest-steppe regions, (iv) explore forest-steppe biodiversity and conservation status, (v) and outline forest-steppe prospects under predicted climate change.

Location: Eurasia (29°-56° N, 16°-139° E).

Results and Conclusions: Forest-steppes are natural or near-natural vegetation complexes of arboreal and herbaceous components (typically distributed in a mosaic pattern) in the temperate zone, where the coexistence of forest and grassland is enabled primarily by the semihumid to semiarid climate, complemented by complex interactions of biotic and abiotic factors operating at multiple scales. This new definition includes lowland forest-grassland macromosaics (e.g. in Eastern Europe), exposure-related mountain forest-steppes (e.g. in Inner Asia), fine-scale forest-grassland mosaics (e.g. in the Carpathian Basin), and open woodlands (e.g. in the Middle East). Using criteria of flora, physiognomy, relief, and climate, nine main forest-steppe regions are identified and characterized. Forest-steppes are not simple two-phase systems, as they show a high level of habitat diversity, with forest and grassland patches of varying types and sizes, connected by a network of differently oriented edges. Species diversity and functional diversity may also be exceptionally high in forest-steppes. Regarding conservation, we conclude that major knowledge gaps exist in determining priorities at the continental, regional, national, and local levels, and in identifying clear target

states and optimal management strategies. When combined with other threats, climate change may be particularly dangerous to forest-steppe survival, possibly resulting in compositional changes, rearrangement of the landscape mosaic, or even the latitudinal or altitudinal shift of forest-steppes.

Keywords
Habitat complexity; Landscape heterogeneity; Meadow steppe; Prairie; Semiarid vegetation; Steppe; Vegetation mosaic; Wooded-steppe; Woodland

Nomenclature
Catalogue of Life (www.catalogueoflife.org; accessed on 15 Apr 2017)

Abbreviation
asl=above sea level

Running head
Eurasian forest-steppes

Introduction

Mosaic vegetation complexes consisting of woody and herbaceous patches are in the spotlight of current ecological research (e.g. Breshears 2006; Innes et al. 2013; Prevedello et al. 2018). Forest-steppes belong to the most complex ecosystems outside the tropics in terms of composition, structure, and function (Walter & Breckle 1989, Erdős et al. 2014). While also present in North America (e.g. Leach & Givnish 1999) and South America (e.g. Kitzberger 2012), the largest forest-steppes are found in Eurasia.

Eurasian forest-steppes have outstanding ecological and conservation importance. They occupy large areas and appear in a wide variety of types and sub-types on various terrains (plains, hills, mountain ranges, plateaus), from the sea level up to 3500 m asl and from sub-Mediterranean to ultracontinental to monsoon climates (Berg 1958; Walter & Breckle 1989; Wesche et al. 2016). Forest-steppes have a very high net primary production compared to other non-tropical systems (Zlotin 2002; Schultz 2005; Pfadenhauer & Klötzli 2014), as well as a considerable biomass and carbon sequestration capacity (Müller 1981; Schultz 2005). Species diversity is also high, with many taxa of special conservation interest such as endemics, endangered species, and wild relatives of cultivated plants (Bannikova 1998; Olson & Dinerstein 1998; Chibilyov 2002; Zlotin 2002). Furthermore, forest-steppes are important from an economic perspective, as they are often used as pastures and provide livelihoods for many people (e.g. Chibilyov 2002; Smelansky & Tishkov 2012; Pfadenhauer & Klötzli 2014; Ambarlı et al. 2016). Unfortunately, forest-steppes are among the most threatened ecosystems due to habitat loss, fragmentation, and an inadequate network of protected areas (Hoekstra et al. 2005).

The scientific knowledge on Eurasian forest-steppes is relatively scattered (Bone et al. 2015). Although the number of studies has increased recently, syntheses are scarce, with several limitations we outline here. First, most reviews have been conducted at national (e.g. Korotchenko & Peregrym 2012; Molnár et al. 2012), or regional scales (e.g. Milkov 1950, 1951, 1977; Krasheninnikov 1954; Berg 1958; Golubev 1965; Dokhman 1968; Lavrenko 1980; Chibilyov 2002; Makunina 2016 a), while continental scale studies are almost entirely lacking (but see Walter & Breckle 1989). Second, most syntheses have focused on the steppe biome, discussing forest-steppes only as a marginal topic (e.g. Nosova 1973; Lavrenko 1980; Lavrenko et al. 1991; Rachkovskaya & Bragina 2012; Wesche et al. 2016). Third, the few regional and continental overviews usually neglect the forest-steppes of the Middle East and the Tian Shan-Pamir ranges (e.g. Lavrenko 1969; Wendelberger 1989), resulting in an incomplete view of the ecosystem.

Our aim in this paper was to provide a synthetic overview of Eurasian forest-steppes, by collecting diffuse knowledge of the entire area covered by forest-steppes. First we provide a formal definition of forest-steppes, identifying inherent difficulties in producing an exact definition and delineation. We briefly discuss spatial extents and gradients. A substantial part of our review focuses on the delineation and brief description of the main forest-steppe regions. Then we review forest-steppe diversity in terms of habitats, species, and functional traits, and outline the conservation status of forest-steppes. Finally we explore the future prospects of forest-steppes under predicted climate change.

Defining forest-steppes

Forest-steppes are known by different names in the literature and across different regions. In most of Eastern Europe and Northern Asia, the terms “forest-steppe” or “wooded-steppe” are used, compared to “steppe forest”, “open woodland”, and “sparse arid woodland” in southwestern Asia. In this paper, we treat these terms as synonyms.

The majority of researchers mention one or more of the following points as decisive characteristics in defining forest-steppes: (i) the transitional spatial position (between closed forests and treeless steppes), (ii) semihumid to semiarid climatic features, and (iii) a mosaic-like vegetation pattern. (iv) Special soil characteristics as key drivers for vegetation may be considered a fourth criterion (soil is a basic part of nearly all steppe definitions; see for example: Dokuchaev 1899; Allan 1946; Berg 1958; Walter & Breckle 1989; Chibilyov 2002). We henceforth discuss the suitability of each of the above four points for defining forest-steppes.

(i) Standard forest-steppe definitions usually begin with an emphasis on the transitional spatial position of forest-steppes between closed forests (nemoral forests, taiga, or Mediterranean forests) and mostly treeless true steppes (e.g. Berg 1958; Lavrenko 1980; Müller 1981; Walter & Breckle 1989; Kleopov 1990; Pócs 2000; Bredenkamp et al. 2002; Chibilyov 2002; Illyés et al. 2007; Magyari et al. 2010), a description which does not apply to all regions. For example, the definition is problematic in both the Carpathian Basin and the Russian Far East, due to the lack of a southern steppe border (Ivanov 2002; Fekete et al. 2014). Furthermore, forest-steppes occur not only near the northern edge of the steppe zone, but also in the steppe region of the Middle East, without necessarily forming a transition towards the closed forests (Wesche et al. 2016). For instance, in some Iranian and Afghan mountain ranges, open woodlands can be found between low elevation semidesert-like steppes and high-mountain thorn cushion communities (Zohary 1973; Breckle 2007; Sagheb-Talebi et al. 2014). In the Qilian Mts, forest-steppes have developed above the lower (arid) timberline, but the closed forest zone is lacking due to the proximity of the upper (cold) timberline (Walter & Breckle 1989). A simplistic definition of forest-steppe as a transitional zone between treeless steppe and closed forest may therefore be inadequate, and other factors such as topography or soil grain size should be considered.

(ii) Climate is a key defining element for forest-steppes in many scientific publications (e.g. Walter & Breckle 1989; Kleopov 1990; Chibilyov 2002; Schultz 2005). In the temperate zone, aside from edaphic variations, humid environments are able to support forests, while primary grasslands are typical under more arid conditions (Dengler et al. 2014). Where climate is transitional (i.e. semihumid to semiarid, close to neutral moisture balance), a mosaic of forests and grasslands can develop, as neither of them has a decisive advantage over the other (Berg 1958; Budyko 1984; Walter & Breckle 1989; Kleopov 1990; Lavrenko & Karamysheva 1993; Borhidi 2002; Bredenkamp et al. 2002; Chibilyov 2002; Djamali et al. 2011).

(iii) An obvious feature of forest-steppes is their mosaic-like pattern. Definitions usually refer to the macromosaic feature, i.e. the spatial alternation of large forest patches and extensive grasslands (e.g. Müller 1981; Walter & Breckle 1989; Bredenkamp et al. 2002; Chibilyov 2002). However, fine-scale mosaics become typical as Mediterranean climatic influences increase (Donită 1970, Wendelberger 1989, Zólyomi & Fekete 1994, Varga et al. 2000, Wesche et al. 2016). Here, individual patches may be very small. In some cases, the grassland matrix is scattered with solitary trees, which may be regarded as small forest patches (cf. Erdős et al. 2015 a). In sum, forest-steppes may appear as macro- or micromosaics, thus restricting the definition to macromosaics is not justifiable. Another recurring element of forest-steppe definitions is that the grassland component is represented by meadow steppes (e.g. Lavrenko 1980; Müller 1981; Kleopov 1990; Lavrenko & Karamysheva 1993; Chibilyov 2002; Zlotin 2002), i.e. rather mesic tall grasslands with numerous forbs. Several cases, most notably in regions with considerable Mediterranean influences, demonstrate that the grassland component is in fact a dry grassland with short grasses, and limited number and cover of forbs. Tragacanthic species are typical, especially in the mountains of the Middle East (Zohary 1973; Akhani 1998).

(iv) Generally, the steppe component of forest-steppes frequently grows on chernozem soils, and the forest component on grey forest soil (Knapp 1979; Rychnovská 1993; Zamotaev 2002; Zech et al. 2014). Different chernozem varieties may also occur under forest patches (Berg 1958; Wallis de Vries et al. 1996). Solonetz and solonchak soils are quite usual under the steppe component (Sochava 1979 a; Müller 1981; Walter & Breckle 1989; Lavrenko & Karamysheva 1993), and solonetz occasionally occurs under forests (Horvat et al. 1974; Molnár & Borhidi 2003). Planosols may support *Betula* stands, while podzols can be found under *Pinus* stands (Berg 1958; Rachkovskaya & Bragina 2012). On chestnut soils, both forest patches and steppes can develop (Berg 1958; Zhu 1993; Shahgedanova et al. 2002; Tamura et al. 2013). Gley soils are typical of *Larix* forests of Inner Asian mountains with permafrost (Walter & Breckle 1989; Shahgedanova et al. 2002). Under a strong Mediterranean climatic influence, in the Middle East (e.g. Turkey, Iraq, Iran), sierozems are widespread (Singh & Gupta 1993; Kürschner & Parolly 2012). For more detail on soil types in the forest-steppes, see also Schultz (2005) and Zech et al. (2014).

Based on the reviewed criteria we argue that a broad yet accurate definition of forest-steppes requires both climatic (semihumid to semiarid) and physiognomic (a mosaic of arboreal and herbaceous components) features. In the climatic range where neither closed forest nor treeless grassland is favored, both have a roughly equal chance to develop. Competition outcomes usually depend on local factors such as aspect, microclimate, or soil (e.g. Mayer 1984; Walter & Breckle 1989; Borhidi 2002; Liu et al. 2012; Anenkhonov et al. 2015; Hais et al. 2016). When the distribution of forest-steppe is determined primarily by macroclimate, the forest-steppe is zonal. However, forest-steppes may also develop outside this transitional climatic range, provided that local factors modify water availability so that neither component has a competitive advantage. For example, in a region of sufficient humidity to support forests, soils with an extremely low water retention capacity or steep south-facing slopes with a warm microclimate may result in a forest-grassland mosaic. In this case, the forest-steppe is considered extrazonal.

Many additional drivers contribute to the dynamics of the forest-grassland coexistence. The interplay of climate, competition, facilitation, fire, grazing and browsing in maintaining the vegetation mosaic is as yet not fully understood for complex forest-grassland ecosystems (e.g. Stevens & Fox 1991; Scholes & Archer 1997; House et al. 2003; Sankaran et al. 2004).

An exact definition and the accurate delineation of forest-steppes is complicated by inherent ambiguity. The grassland-forest continuum ranges from totally treeless grasslands to closed forests (Breshears 2006). Based on the physiognomy, forest-steppes lie somewhere between the two extremes, but the proportion of grasslands and forest patches varies widely (Illyés et al. 2007). The middle of the continuum (i.e. 50% arboreal and 50% grassland vegetation) is clearly a forest-steppe, but the designation of lower and upper thresholds is necessarily arbitrary and often difficult (e.g. Berg 1958; Chibilyov 2002).

An additional question is whether a mosaic of grasslands and shrubby vegetation should be regarded as forest-steppe. If low shrubs occur only, such as *Prunus tenella*, the complex may be termed shrub-steppe and classified among steppes (Berg 1958; Lavrenko & Sochava 1956; Lavrenko et al. 1991). In contrast, 2-6 m tall *Pistacia* spp., *Juniperus excelsa*, or *Quercus pubescens* individuals or small stands in a grassland matrix are usually classified among forest-steppes.

Considering the arguments outlined above, our definition of forest-steppes is as follows: Forest-steppes are natural or near-natural vegetation complexes of arboreal and herbaceous components (typically distributed in a mosaic pattern) in the temperate zone (excluding the Mediterranean), where the coexistence of forest and grassland is enabled primarily by the semihumid to semiarid climate, complemented by complex interactions of biotic (e.g. grazing, land-use) and abiotic (e.g. soil, topography) factors operating at multiple scales. The arboreal cover (with a minimum height of 2 m) is 10-70% across the entire landscape mosaic. The vascular vegetation cover within the grassland is at least 10% (corresponding with the grassland definition of Dixon et al. 2014 and the steppe definition of Wesche et al. 2016).

Our forest-steppe definition therefore rests on physiognomic features and the underlying environmental factors, the most important of which is climate. This broad understanding of forest-steppes includes lowland forest-grassland macromosaics (e.g. in Eastern Europe and the southern parts of West Siberia), exposure-related mountain forest-steppes (e.g. in Inner Asia), fine-scale forest-grassland mosaics (e.g. in the Carpathian Basin), and open woodlands (e.g. in the Middle East).

Are forest-steppes a biome?

Whether forest-steppe is a biome in its own right or only a transition between two neighboring biomes may be considered a merely semantic question. However, it should be pointed out that forest-steppes differ considerably from both closed forests and treeless steppes in terms of numerous features, including physiognomy, habitat complexity, ecological functions and abiotic parameters, as has been shown for a number of forest-grassland mosaic ecosystems (e.g. Wendelberger 1989; Scholes & Archer 1997; Bannikova 2003; Breshears 2006; Erdős et al. 2014).

Based on the biogeographical view of Lomolino et al. (2010) and Cox et al. (2016), who define biomes based on their climate and physiognomy (i.e. vegetation structure), we may conclude that forest-steppes satisfy the criteria to be considered a biome as they have a specific climate and a characteristic physiognomy. Here we have to emphasise that this concept includes latitudinal as well as altitudinal vegetation zones, which fits well with our understanding of forest-steppes. However, the recognition of forest-steppes as a biome is a subject of scientific controversy. Some of the well-known global classification systems treat forest-steppes as a mere contact area between two adjacent biomes or zones (rather than a separate biome or zone in its own right). For example, in the classification of Walter (1979), our forest-steppe definition is equivalent to those of zonoecotone VI/VII (transition between nemoral forest and steppe), zonoecotone VII/VIII (transition between taiga and steppe), and zonoecotone IV/VII (transition between the Mediterranean and steppe), complemented by some parts of the Tibetan subzonobiome (within zonobiome VII) and areas from mountain orobiomes (e.g. Crimean Mts, Caucasus, Kopet Dag, Pamir-Alai, Tian Shan). Regarding the scheme of Schultz (2005), our forest-steppe definition is included in the ecozone "dry midlatitudes" and the contact zone between the ecozones "subtropics with winter rain" and "dry tropics and subtropics". In the system of Pfadenhauer and Klötzli (2014), our forest-steppes are included mainly in the dry nemoral subzone, but considerable parts belong to the subtropical subzone with winter rain.

Physiogeographic setting

Forest-steppes cover vast areas in Eurasia (2.9 million km^2 according to Wesche et al. 2016, although the figure may be higher, depending on the defining criteria). The altitudinal range of forest-steppes extends from sea level (e.g. Turkey-in-Europe and Crimea) up to some 3500 m asl (Qilian Mts), including lowlands, hilly areas and mountain ranges. Forest-steppes form two distinct latitudinal belts (Fig. 1): northern (ranging from the Carpathian Basin to the Russian Far East), and southern (ranging from Central Anatolia to the Tian Shan). The northernmost reaches of the forest-steppe zone are found in Russia, north of the city of Yekaterinburg in the Ural Mts (56° N) and north of the Kuznetski Alatau Mts (56° N). The southernmost extensions are in Iran, in the Zagros Mts near Shiraz (29° N). The longitudinal extension of the forest-steppe zone is 9000 km, stretching from the westernmost parts of the Carpathian Basin (near Vienna, Austria, 16° E) to the Amur Lowlands in Russia (139° E).

The most important latitudinal climatic gradient is along the increase in aridity to the south (Zlotin 2002). Plant species richness usually decreases toward the steppe zone (Zlotin 2002; Liu & Cui 2009), although the most obvious change is the reduction of tree abundance (Schultz 2005). In forest-steppe areas within the proximity of the closed forest zone, steppes are limited to small patches (Walter & Breckle 1989). As aridity increases towards the south, grasslands become more extensive, while forest patches become smaller. Within the southern forest-steppe belt, forest patches are almost always very small.

Concerning longitudinal gradients, continentality generally increases towards Inner Asia (Zhu 1993; Chibilyov 2002; Zlotin 2002; Wesche et al. 2016). This means that mean annual precipitation decreases (summer precipitation increases, while winter precipitation decreases), mean annual temperature simultaneously decreases, while yearly temperature range increases (summers remain hot, but winters are long and extremely cold). These changes are accompanied by pronounced changes in cardinal vegetation characteristics (Lavrenko 1942, 1970 a, b; Berg 1958; Lavrenko et al. 1991; Bannikova 1998; Liu et al. 2000, 2012; Chibilyov 2002; Zlotin 2002): with increasing continentality, species richness usually decreases, especially for shrubs and trees, while the root/shoot ratio increases. There are deviations from the described general patterns, depending on the scale of the study and whether it concerns forest or grassland (Palpurina et al. 2015; Lashchinskiy et al. 2017).

Box 1 Eurasian forest-steppes: A fact-sheet

Definition: natural or near-natural vegetation complexes of arboreal and herbaceous components (typically distributed in a mosaic pattern) in the temperate zone, where the coexistence of forest and grassland is enabled primarily by the semihumid to semiarid climate, complemented by complex interactions of biotic and abiotic factors operating at multiple scales. The arboreal cover (height >2 m) is 10-70% across the entire landscape mosaic, while the vascular vegetation cover within the grassland is at least 10%.

Forest-steppes as a transitional zone or a separate biome: as biome definitions usually rest on climate and physiognomy, it may be concluded that forest-steppes satisfy the criteria to be considered a biome. However, this is a subject of scientific controversy, and some well-known global vegetation classification schemes treat forest-steppes as a mere contact area between two adacent biomes, rather than a separate biome in its own right.

Geographic extent: 29°-56° N, 16°-139° E.

Main regions: Southeast Europe, East Europe, North Caucasus and Crimea, West Siberia and North Kazakhstan, Inner Asia, Far East, Middle East, Central Asia and southwestern Inner Asia, Eastern Tibetan Plateau.

Dominant life forms: mainly phanerophytes and hemicryptophytes, but also chamaephytes and therophytes, in places many geophytes.

Dominant taxa: Anacardiaceae, Apiaceae, Asteraceae, Betulaceae, Cupressaceae, Cyperaceae, Fabaceae, Fagaceae, Lamiaceae, Pinaceae, Poaceae, Ranunculaceae, Rosaceae, Salicaceae.

Forest-steppes on a coarse scale: major divisions

A north-south divide bisects forest-steppes into a western and an eastern part. The transition zone is considered to be either near Lake Baikal (Berg 1958), or near the Altai Mts and the Yenisei River (Lavrenko 1969, Lavrenko et al. 1991). Phytogeographic ranges of forest-steppe species lend support to both of these propositions, suggesting a blurred boundary (Popov 1963; Nimis et al. 1994; Hilbig et al. 2004). However, given that the main floristic and vegetation changes begin in the western part of the Altai Mts, classifying the Altai-Sayan-Baikal area to the eastern forest-steppe section appears well-founded. In terms of climate, plant species composition and syntaxa, a major boundary exists at the northwestern foothills of the Altai Mts (Lashchinskiy et al. 2017), which also appears for edaphic grasslands in the forest-steppe biome (Ermakov et al. 2006). Hilbig & Knapp (1983) and Lavrenko & Karamysheva (1993) subsequently place the border to the western foothills of the Altai Mts. Similarly, Pott (2005), in agreement with Wesche et al. (2016), regards the Altai Mts as forming the boundary between western and eastern steppes and forest-steppes.

Another major division must be made between northern and southern forest-steppes, the border running from the Sea of Marmara along the main ridge of the Caucasus and through the arid lands east of the Caspian Sea to the Tian Shan. Generally, northern forest-steppes are relatively mesic, steppes are typically closed and forest patches are often large, although exceptions do exist, especially in extrazonal situations. Southern forest-steppes are more arid, with open grasslands and usually solitary and widely spaced trees (Zohary 1973; Memariani et al. 2016). The position of forest-steppes between the neighboring vegetation belts differs strongly between northern and southern forest-steppes. While northern forest-steppes occupy space between mesic steppes and forests, southern forest-steppes usually appear in a transitional zone (i) between forests and semidesert-like steppes, (ii) between forests and alpine communities, or (iii) between steppes and alpine/subalpine communities.

Main forest-steppe regions

We here provide a basic description of the main regions (Fig. 1). Our delineation rests on a combination of floristic and physiognomic characteristics, as well as relief and climate features. We relied on previously published material and expert knowledge, complemented by climatic data of selected stations located within forest-steppe areas. Climate data, as well as information about the remaining forest-steppe areas and current land-use practices are given in Table 1.

Region A – Southeast Europe (Fig. 2a): Carpathian Basin, Lower Danube Plain, and Inner Thrace (Northeast Austria, Southeast Czech Republic, Hungary, South Slovakia, Northeast Croatia, Romania, North and Northeast Serbia, South Moldova, Soutwest Ukraine, North and Southeast Bulgaria, Northeast Greece, Turkey-in-Europe) (Bodrogközy 1957; Zólyomi 1957; Niklfeld 1964; Szodfridt 1969; Donită 1970; Horvat et al. 1974; Mayer 1984; Wallnöfer 2003; Tzonev et al. 2006; Bölöni et al. 2008; Chytrý 2012; Molnár et al. 2012)

Forest-steppes in this region are under considerable Mediterranean climatic influences, with increasing continental effects towards the northeast. Thrace is transitional towards the Anatolian forest-steppes (Region G). Forest-steppes typically occupy plains (from the sea level to 250 m asl), but some hills and mountains (often on south-facing slopes) also host similar forest-grassland mosaics. Mean annual temperature is 9-12.5 °C (up to 13.5 °C in

Thrace). Summers are hot, winters are mild. Mean annual precipitation is 420-600 mm, with a maximum in early summer, a secondary maximum in autumn, and a semiarid period in between.

Both forest and grassland patches are mostly xeric. Forest patches are usually small and have an open canopy, with a high number of oak species (among others: *Quercus cerris*, *Q. frainetto*, *Q. petraea*, *Q. pubescens*, *Q. robur*). Other tree species such as *Acer tataricum*, *Carpinus orientalis*, *Fraxinus ornus*, *Populus alba*, and *Tilia tomentosa* are also typical. Grasslands are usually characterized by *Chrysopogon gryllus*, *Festuca rupicola*, *F. valesiaca*, *F. vaginata*, *Stipa capillata*, *S. pennata*, and *S. pulcherrima*. Important herbs include *Astragalus austriacus*, *A. dasyanthus*, *A. onobrychis*, *Fragaria viridis*, *Salvia austriaca*, *S. nemorosa*, and *S. nutans*.

Region B – East Europe (Fig. 2b): southern part of the East European Plain (Northeast Romania, Moldova, Southeast Poland, Ukraine, Southwest Russia) (Milkov 1950; Krasheninnikov 1954; Berg 1958; Soó 1957; Jakucs et al. 1959; Borhidi 1966; Dokhman 1968; Lavrenko 1980; Walter & Breckle 1989; Kleopov 1990; Chibilyov 2002; Molnár et al. 2007; Safronova 2010; Korotchenko & Peregrym 2012; Kuzemko et al. 2014; Semenishchenkov 2015)

Stretching from Podolia and the eastern foothills of the Carpathians to the southern foothills of the Ural Mts, forest-steppes of this region occupy lowlands and hilly areas between ca. 90 and 500 m asl. Climate is temperate continental, with some Mediterranean influence in the westernmost parts. Mean annual temperature is approximately 9 °C in the west, and ca. 3 °C in the east. Summers are warm, winters are moderately cold. Mean annual precipitation varies between 400-600 mm (up to 660 mm in Podolia), with a peak in June (-July) and a semiarid period in late summer.

Large and mesic forest patches are formed mainly by broad-leaved deciduous trees (*Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*, *Ulmus glabra*), although *Populus tremula* and *Betula pendula* are also common. The grassland patches are mesic, hence the names "meadow steppe" and "steppified meadow" (the two differ regarding the role of xeric species, although the distinction is used mainly by Russian and Ukrainian authors; e.g. Kuzemko 2009; Semenishchenkov 2009; Averinova 2010). Important species of the grassland patches include *Festuca valesiaca*, *Filipendula vulgaris*, *Fragaria viridis*, *Koeleria macrantha*, *Phlomoides tuberosa*, *Poa angustifolia*, *Ranunculus polyanthemos*, *Salvia pratensis*, *S. nutans*, *Stipa capillata*, *S. pennata*, *S. pulcherrima*, *S. zalesskii*, *Teucrium chamaedrys*, and *Trifolium montanum*, as well as different *Tulipa* and *Iris* species.

Region C – North Caucasus and Crimea (Fig. 2c) (Southwest Russia, Crimea) (Berg 1958; Walter & Breckle 1989; Serebryanny 2002; Volodicheva 2002)

Forest-steppes occupy substantial areas from sea level up to ca. 600 m asl. The whole region is under marked Mediterranean climatic influence. Mean annual temperature is 9.5-12 °C. Mean annual precipitation varies from 300 to 600 (-770) mm, with the maximum in summer.

In the North Caucasus, mesic forest patches are composed of *Acer campestre*, *Carpinus betulus*, *Quercus petraea*, *Q. robur*, and *Tilia dasystyla*. In the Crimea, forest-steppes are more xeric and show remarkable similarities with those of the Middle East (Region G) and the Lower Danube Plain (in Region A) (Donită 1970). In the northwestern part of the Crimean Mts, the most characteristic tree species are *Pyrus communis*, *P. elaeagrifolia*, *Quercus petraea*, *Q. pubescens*, *Q. robur*, and *Ulmus procera*, while *Arbutus andrachne*, *Juniperus excelsa*, *Pistacia atlantica*, and *Quercus pubescens* are typical in the southern parts of the Crimean Mts. Some of the most common and characteristic species of the grassland patches in the region are *Adonis vernalis, Festuca rupicola*, *Paeonia tenuifolia*, *Phleum phleoides*, *Stipa capillata*, *S. pennata*, *S. pontica*, and *S. pulcherrima*.

Region D – West Siberia and North Kazakhstan (Fig. 2d) (South Russia, North Kazakhstan) (Berg 1958; Lavrenko & Karamysheva 1993; Rachkovskaya & Bragina 2012; Makunina 2016 a; Korolyuk & Yamalov 2015; Mathar et al. 2016; Bátori et al. 2017; Lashchinskiy et al. 2017; Lebedeva et al. 2017; Tölgyesi et al. 2017)

The majority of the forest-steppes of this region occur in lowlands (100-200 m asl), but some, mainly in Kazakhstan, occupy hills (ca. 300-400 m asl). The climate is continental, with mean annual temperatures of 1-4.5 °C. Summers are warm, winters are very cold. Mean annual precipitation is 270-610 mm. Most precipitation falls during the summer months.

Large mesic to semi-dry forest patches alternate with extensive, mostly mesic grasslands. The forest patches are composed of small-leaved deciduous trees (*Betula pendula*, *B. pubescens*, *Populus tremula*) and *Pinus sylvestris*. Principal steppe species include *Artemisia glauca*, *A. pontica*, *Filipendula vulgaris*, *Festuca rupicola*, *F. valesiaca*, *Fragaria viridis*, *Gypsophila paniculata*, *Helictotrichon hookeri*, *Lathyrus pisiformis*, *L. pratensis*, *Poa angustifolia*, *Phleum phleoides*, *Phlomoides tuberosa*, *Pimpinella saxifraga*, *Potentilla incana*, *Ranunculus polyanthemos, Scorzonera ensifolia*, *Stipa capillata*, *S. pennata*, *S. tirsa*, *S. zalesskii*, *Vicia cracca*. The large amount of various halophytic communities is characteristic within the forest-steppes of this region.

Region E – Inner Asia (Fig. 2e): Altai Mts and their northern foothills, Sayan Mts and their northern foothills, Baikal area, Transbaikal Mts, Tarbagatai Mts, Saur Mts, Khangai Mts, Khentei Mts, Inner Mongolia (South Russia, East Kazakhstan, Mongolia, North and Northeast China) (Hilbig & Knapp 1983; Hou 1983; Karamysheva & Khramtsov 1995; Wallis de Vries et al. 1996; Korotkov & Krasnoshchekov 1998; Korolyuk & Makunina 2000; Liu et al. 2000; Shahgedanova et al. 2002; Bannikova 2003; Dulamsuren et al. 2005 b; Namzalov & Baskhaeva 2006; Rachkovskaya & Bragina 2012; Makunina 2010, 2013, 2014, 2016 b, 2017; Hais et al. 2016)

The region includes Inner Asian mountain ranges. (The Tarbagatai-Saur range as well as the westernmost extensions of the Altai Mts are transitional towards Region H and Region D, respectively. They are consequently sometimes treated as belonging either to the northern Tian Shan, or to the West Siberian-North Kazakhstan forest-steppes.) Mountain forest-steppes, extending as high as 2400 m asl, are typically situated between the steppe and forest elevational belts. Forests are usually found on north-facing slopes (often with permafrost), whereas the steppe component occupies mainly south-facing slopes and intermountain depressions. In more arid parts, only small forest patches occur amid dry grasslands. In valleys, forest-steppes can be found as low as 200 m asl. The climate here is ultracontinental.

Mean annual temperature is between -6 °C and +2 °C (up to +5 °C in southern Inner Mongolia). Summers are warm, winters are extremely cold. Mean annual temperature amplitude may exceed 50 °C. Mean annual precipitation is 210-550 mm; winters are dry, most precipitation falls during summer (July-August).

Forest patches are composed of *Betula pendula*, *B. platyphylla*, *Larix sibirica*, *L. gmelinii*, *Pinus sylvestris*, and *Ulmus pumila*. The most common plant species of the grasslands include *Achnatherum sibiricum*, *Agropyron cristatum*, *Artemisia frigida*, *Carex pediformis*, *Cleistogenes squarrosa*, *Cymbaria daurica*, *Filifolium sibiricum*, *Festuca valesiaca*, *F. lenensis*, *Koeleria macrantha*, *Leymus chinensis*, *Nepeta multifida*, *Poa attenuata*, *Pulsatilla patens*, *Stellera chamaejasme*, *Stipa baicalensis*, and *S. krylovii*.

Region F – Far East (Fig. 2f): West Manchuria (=Northeast China Plain), southern parts of the Greater Khingan Range, eastern parts of the Chinese Loess Plateau, Amur Lowland, Southwest Sihote Alin, Khanka Lowland (Northeast China, Southeast Russia) (Berg 1958; Hou 1983; Rychnovská 1993; Zhu 1993; Ivanov 2002; Qian et al. 2003; Liu et al. 2015)

Forest-steppes of this region occur across a wide range of terrains and altitudinal gradients. Examples of occurrence at low altitudes include the Amur Lowland (ca. 50 m asl), and West Manchuria of China (120-150 m asl). Some forest-steppes have developed on low hills, while forest-steppes of the Chinese Loess Plateau and the Greater Khingan Range are found between 800 and 2500 m asl. Regional climate is influenced by the monsoonal circulation, particularly in the east, while continental influence positively correlates to increasing distance from the ocean. The northeast-southwest direction of the forest-steppe zone in Manchuria, the greater Khingan Range and the Chinese Loess Plateau can be explained by the diminishing effects of the monsoon; the main vegetation zones run more or less parallel with the coast. Mean annual temperature ranges between -1 and +14 °C. Mean annual precipitation is 360-650 mm. Winters are cold and dry, summers are warm (western Manchuria of China, Greater Khingan Range, Chinese Loess Plateau) to cool (Amur and Khanka Lowlands, Sihote Alin). Most precipitation falls during the summer months. Forest-steppes of the Amur Lowland are also known as “Amur prairies”, while those of the Amur and the Khanka Lowlands are sometimes referred to as “East Asian savannas”.

The most typical tree species of the forest patches is *Quercus mongolica*, although *Betula dahurica*, *B. platyphylla*, and *Tilia amurensis* are also frequent. Grasslands are steppe and meadow steppe ecosystems with different sub-types occurring in dry and more mesic environments. Typical species include *Arundinella hirta*, *Bothriochloa ischaemum*, *Calamagrostis epigejos*, *Cymbaria daurica*, *Filifolium sibiricum*, *Leymus chinensis*, *Miscanthus sinensis*, *Poa pratensis*, *Stipa baicalensis*, *S. bungeana*, *S. grandis*, and *S. pennata*.

Region G – Middle East (Fig. 2g): the peripheral areas of Central Anatolia, East and Southeast Anatolia, South and East Caucasus, Abdulaziz Mts, Zagros Mts, Persian Plateau, Alborz Mts, Kopet Dag, Badkhyz Mts, Central Afghan Mts (Turkey, South Georgia, Armenia, Azerbaijan, Southwest Russia, Northeast Syria, Northeast Iraq, Iran, South Turkmenistan, Afghanistan) (Zohary 1973; Assadi 1988; Popov 1994; Akhani 1998; Merzlyakova 2002; Volodicheva 2002; Çolak & Rotherham 2006; Breckle 2007; Kürschner

& Parolly 2012; Uğurlu et al. 2012; Nakhutsrishvili 2013; Naqinezhad et al. 2015; Ambarlı et al. 2016; Memariani et al. 2016; Ravanbakhsh & Moshki 2016; Ravanbakhsh et al. 2016)

The forest-steppes of the Middle East occur on hills and mountains from ca. 200 m (foothills of South and East Caucasus, southwest Iran) to 3000 m asl (Central Afghan Mts). Other names include “southern forest-steppes”, “arid open woodlands”, “savannoid vegetation”, “semisavanna”, “pseudosavanna”, “steppe-forests” and “light forests”. “Wild orchards”, i.e. grasslands with scattered wild fruit trees, are structurally similar to forest-steppe landscapes, but have probably developed from oak woodlands through selective cutting (Kramer 1984; Mayer 1984; Woldring & Cappers 2001). Mean annual temperature ranges between 10.5 and 17 °C. Mean annual precipitation varies between 270 and 860 mm. Summers are hot and arid, winters are cold. Forest-steppes are under considerable Mediterranean climatic influences. The Central Afghan Mts form a transitional zone towards the Pamir and the Tian Shan (Region H), with scattered trees in a semidesert-like steppe matrix.

The region has been under human influence for so long that it is very difficult to infer its pre-human vegetation (Frey & Probst 1986; Asouti & Kabukçu 2014; Wesche et al. 2016). Trees in the forest-steppes of this region either form small groves or occur as scattered individuals. The most common tree species are *Juniperus excelsa*, *J. foetidissima*, *Pinus nigra*, *P. sylvestris*, *Pistacia atlantica*, *P. vera*, *Prunus dulcis*, *Pyrus elaeagrifolia*, *Quercus brantii*, *Q. infectoria*, *Q. ithaburensis*, *Q. macranthera*, *Q. petraea*, *Q. pubescens*, *Q. robur*. Some of the most common taxa of the grasslands are *Agropyron cristatum*, *Astragalus angustifolius, A. lycius*, *Bothriochloa ischaemum*, *Chrysopogon gryllus*, *Festuca valesiaca*, *Koeleria macrantha*, *Poa bulbosa*, *Seriphidium fragrans*, *S. sieberi*, *Stipa arabica*, *S. barbata*, *S. capillata*, *S. lessingiana*, *S. pulcherrima*.

Region H – Central Asia and southwestern Inner Asia (Fig. 2h): Pamir Mts, Alai Mts, Tian Shan, Qilian Mts, Helan Mts (Southeast Kazakhstan, Kyrgyzstan, Tajikistan, East and Southeast Uzbekistan, Northwest China) (Berg 1958; Wu 1980; Walter & Breckle 1989; Rychnovská 1993; Tian 1996; Jiang et al. 2000; Wang et al. 2001; Merzlyakova 2002; Sang 2009; Pang et al. 2013; Bone et al. 2015)

Forest-steppes are present in altitudes between ca. 800-3500 m asl. Climatic influences in the region vary, resulting in significantly different precipitation and temperature records among both individual mountain chains and among slopes of differing aspects. The climate is mostly continental, with Mediterranean influences in the western areas. Mean annual temperature is 0-12 °C. Mean yearly precipitation varies between 380-600 mm, with a maximum occurring during spring (in the west) or summer (in the east).

In the western part of the region (Pamir and Alai Ranges, western and northwestern Tian Shan) forest-steppes are characterized by scattered fruit trees (*Juglans regia*, *Malus sieversii*, *Pistacia* spp., and *Punica granatum*) and *Juniperus* species, embedded in a dry steppe or even a semidesert-like matrix (*Bothriochloa ischaemum, Ferula tenuisecta, Hordeum bulbosum*, *Poa bulbosa*, and *Thinopyrum intermedium*). The complex is also known as “open woodland”, “desert with scattered wooded patches”, “orchard”, and “wooded field”. While this type shows clear similarities towards the open woodlands of the Middle East (Region G), in the eastern parts of the region (northern and eastern Tian Shan, Qilian Mts, Helan Mts), forest-steppes are similar to those on the mountains of Region E. Such cases are usually located at higher elevations than the fruit tree woodlands. Here, forest patches are found on north-facing slopes, and are formed primarily by *Picea schrenkiana* and *P. crassifolia*, with additional species such as *Betula pendula*, *Larix sibirica*, *Picea asperata*, *Populus tremula*, and *Ulmus glaucescens*. Montane steppes occupy south-facing slopes, with the most common species being *Agropyron cristatum*, *Ajania fruticulosa*, *Artemisia frigida*, *A. lagopus*, *Cleistogenes squarrosa*, *Festuca rupicola*, *Koeleria macrantha*, *Medicago falcata*, *Oryzopsis chinensis*, *Ptilagrostis pelliotii*, *P. purpurea*, *Stipa capillata*, *S. breviflora*, and *S. przewalskyi*.

Region I – Eastern Tibetan Plateau (Southwest China) (Wu 1980; Chang 1981; Zhao et al. 2011)

Forest-grassland mosaics of the eastern areas of the Tibetan Plateau may only tentatively be classified among forest-steppes owing to the ambiguity of the primary cause underlying the mosaic pattern. From the southeastern periphery to the central parts of the Plateau, forests gradually give way to meadows and steppes, with a broad transitional zone. The opening up of the forest is a result of a combination of decreasing temperature and decreasing precipitation, although temperature appears as the primary driver in most cases. The elevation is 3200-4000 m. Mean annual temperature is between -3 and +7 °C. Mean annual precipitation is 300-700 mm.

Forest patches are composed of *Abies fabri*, *A. fargesii*, *A. recurvata*, *A. squamata*, *Picea asperata*, *P. brachytyla*, *P. likiangensis*, *P. purpurea*, and *P. wilsonii*. The most typical grassland species are *Kobresia* species (*Kobresia capillifolia*, *K. humilis*, *K. littledalei*, *K. royleana*, *K. tibetica*, and *K. vidua*). Other important species are *Argentina stenophylla*, *Carex atrofusca*, *Gentiana algida*, and *Thalictrum alpinum*.

Biodiversity features

Forest-steppes are characterized by a high level of habitat diversity. Forests, scrubs, and grasslands have strongly different physical environmental conditions, resulting in plant communities that differ in terms of vegetation structure and floristic composition (e.g. Berg 1958; Hilbig & Knapp 1983; Bannikova 1985; Walter & Breckle 1989; Hilbig et al. 2004; Erdős et al. 2014; Anenkhonov et al. 2015; Hais et al. 2016). Moreover, forest, scrub and grassland patches have a number of different types (usually aligned along micro-topographic gradients), further increasing the habitat diversity of forest-steppes (Wallis de Vries et al. 1996; Dulamsuren et al. 2005 a; Namzalov & Baskhaeva 2006; Namzalov et al. 2012; Bátori et al. 2014; Makunina 2014, 2017; Tölgyesi et al. 2016 a, b). In addition, differently sized patches of the same type may also possess dissimilar environmental and vegetation characteristics. For example, small, medium and large forest patches differed considerably in tree size class distribution and seedling composition (Erdős et al. 2015 a), while the species composition of grasslands also appears to relate to size (Molnár 1998). Forest-steppes harbor an extensive network of boundaries between different patches, which may be regarded as distinct plant communities, deviating from the communities of habitat interiors (Molnár 1998; Erdős et al. 2013, 2015 b). Edges with different orientations may also represent slightly different habitats, showing dissimilar environmental conditions and vegetation features (Erdős et al. 2013). Consequently, forest-steppes should by no means be conceived as simple two-phase systems. Instead, they are characterized by multi-level spatial heterogeneity, where forest, scrub and grassland patches of many types and different sizes, connected by a network of differently oriented edges, form an intricate and highly complex system. An integrated view of these complex ecosystems, including all components, is a prerequisite for the efficient conservation and sustainable use of forest-steppes (cf. Luza et al. 2014).

Forest-steppes have been recognized as important biodiversity hotspots (Bannikova 1998; Zlotin 2002; Oprea et al. 2010; Habel et al. 2013; Kamp et al. 2016; Makunina 2016 a). Habitat diversity, together with vegetation history, is a key determinant of species diversity in forest-steppes (cf. Dengler et al. 2012; Feurdean et al. 2015; Novenko et al. 2016). The grassland component of the forest-steppe may have very high fine-scale plant species richness (Chytrý et al. 2015; Dengler et al. 2016; Lashchinskiy et al. 2017). For example, meadow steppes that typically form the grassland component of the forest-steppes in Russia may contain on average 64 plant species per 100 m^2 (Korolyuk et al. 2008). In the forest component, up to 114 species per 100 m^2 have been registered within the forest-steppe landscape of the northern Altai Mountains, suggesting that those forests are probably the most species-rich forests in non-tropical Eurasia (Chytrý et al. 2012). Diversity and composition of the shrub and herb layers are influenced by variations in canopy cover. If the canopy is relatively open, many xeric steppe species may survive under the trees (Erdős et al. 2015 b). Under a closed canopy, mesic conditions develop, providing suitable habitats for plants adapted to more humid conditions (Walter & Breckle 1989). Forest edges are typically of higher biodiversity than habitat interiors, and provide habitat for several species that are rare or absent in the patch interiors of the studied forest-steppe system (e.g. *Achillea seidlii*, *Cervaria rivini*, *Geranium sanguineum*, *Hieracium umbellatum*, *Polygonatum odoratum*, *Ranunculus polyanthemos*, *Tragopogon pratensis*) (Wendelberger 1986; Varga 1989; Molnár 1998; Erdős et al. 2013, 2015 a).

Forest-steppes provide habitats for many rare, endemic and threatened plants, including IUCN red-listed species (e.g. *Artemisia pancicii*, *Astragalus wolgensis*, *Colchicum arenarium*, *Malus sieversii*, *Pistacia vera*, and *Prunus tenella*) (Zlotin 2002; Oprea et al. 2010; Habel et al. 2013; Kamp et al. 2016).

Owing to their high structural heterogeneity, forest-steppes host a high diversity of life-forms as well. Forests are dominated by phanerophytes (trees and shrubs). In their herb layer, geophytes, hemicryptophytes, and/or therophytes are typical, depending on local site conditions. Shrubs are the most characteristic life-form in forest edges and steppe thickets. The steppe component is characterized by hemicryptophytes (both graminoids and forbs) and usually chamaephytes. In the steppes of Europe, West Siberia and the Middle East, geophytes play an important role, while therophytes are frequent in dry areas and around disturbed sites (Berg 1958; Walter & Breckle 1989; Rychnovská 1993; Schultz 2005; Tzonev et al. 2006; Breckle 2007; Kürschner & Parolly 2012; Rachkovskaya & Bragina 2012; Erdős et al. 2014; Wesche et al. 2016).

The functional diversity of forest-steppes is exceptionally high. Although usually not very tall, forests are multi-layered, with evergreen or deciduous woody species (usually both of them in the same place). The steppe component also has multiple layers, with both tall and short herbs, mosses and sometimes even lichens. Both tussock and rhizomatous graminoids are typical. The amount of N-fixing species is considerable (e.g. *Astragalus*, *Medicago*, and *Vicia* species). The flowering time of forbs is variable, starting in early spring and lasting till autumn. Steppe plants have evolved numerous strategies to withstand drought, cold, grazing, fire or other natural disturbances, further enhancing the diversity of functional types (Berg 1958; Walter & Breckle 1989; Schultz 2005; Korotchenko & Peregrym 2012; Kürschner & Parolly 2012).

Conservation status

Forest-steppes and steppes have been transformed by human activity more than any other part of Northern Eurasia (Chibilyov 2002), although there are regional differences concerning the level of anthropogenic impacts (Table 1). The proportion of destroyed or severly degraded forest-steppes generally decreases towards the east, where agriculture began later (Zlotin 2002). Forest-steppes have largely persisted in many Asian landscapes east of the Ural Mts (Lavrenko & Karamysheva 1993; Smelansky & Tishkov 2012). However, the situation is much worse in the western parts of the forest-steppe zone.

A large proportion of the steppe patches has been converted into croplands or plantations of non-native species such as *Robinia pseudoacacia*, while many forest patches have been logged or replaced with plantations (e.g. Berg 1958; Walter & Breckle 1989; Parnikoza & Vasiluk 2011; Molnár et al. 2012; Ambarli et al. 2016). The remaining forest-steppe areas are usually edaphic ones (e.g. on rocky surfaces), and/or small fragments with varying levels of degradation (Smelansky & Tishkov 2012). As an extreme case of fragmentation, small areas of anthropogenic habitats, such as field margins (Cizek et al. 2012), railway embankments (Dudáš et al. 2016), river dikes (Bátori et al. 2016), kurgans (Deák et al. 2016), and road verges (Heneberg et al. 2017) may serve as the last refuges for steppe and forest-steppe species.

Forest-steppes are highly sensitive to even small changes in factors determining forest/grassland proportion and distribution (Kovács-Láng et al. 2000; Bartha et al. 2008). In many European forest-steppes, the main threats are the invasion of non-native species (e.g. *Asclepias syriaca*, *Elaeagnus angustifolia*, *Robinia pseudoacacia*) and the effects of current agricultural and forestry practices (Protopopova et al. 2006; Molnár et al. 2008; Smelansky & Tishkov 2012). In Turkey, forest-steppe ecosystems are negatively affected by agricultural intensification and conversion to croplands, deep ploughing, choosing non-native trees for afforestation, over-exploitation of wild plants and animals (e.g. collecting plants for firewood, poaching, and the illegal collection of bulbous plants), overgrazing, and road constructions (Ambarlı et al. 2016). Iranian pistachio-almond forest-steppe remnants are severely degraded due to firewood cutting (Djamali et al. 2009), while oak forest-steppes suffer from heavy overgrazing (Sagheb-Talebi et al. 2014). The *Pistacia vera* and *Juniperus excelsa* woodlands of Afghanistan are exploited for charcoal production (Breckle 2007). The biodiversity of the Kazakh forest-steppe is highly threatened by farming and collection of plants (Rachkovskaya & Bragina 2012). The rapid increase in the number of grazing livestock (especially goats) and logging negatively affect the flora and fauna of the Mongolian forest-steppes (Wallis de Vries et al. 1996; Liu et al. 2013 a). However, since the regime change in the eastern bloc around 1990, abandonment of former croplands has increased (Smelansky & Tishkov 2012; Alcantara et al. 2013; Schierhorn et al. 2013), providing a unique opportunity for the spontaneous recovery or planned restoration of the steppe component (Hölzel et al. 2002; Török et al. 2011; Sojneková & Chytrý 2015).

Forest-steppes have a long history of human presence, and have historically provided humans with countless ecosystem survices such as food sources (including crop progenitors), medicinal plants, grazing areas, as well as material for cooking, heating, construction, or leaf fodder (Mosaddegh et al. 2012; Asouti & Kabukçu 2014). Some forest-steppes in present-day Turkey, Iraq, and Iran are located in the region known as "the cradle of civilization" (Zohary 1973; Asouti & Kabukçu 2014; Poschlod 2015). Nomadic, semi-nomadic and sedentary herders of the forest-steppe belt continue to possess rich traditional ecological knowledge of the steppes, their forage species, and the spatial and temporal patterns of forage availability (Fernández-Giménez 2000; Molnár 2012, 2014). They have developed complex herding systems that utilize diverse pasture types and adapt to the unpredictability of grazing conditions and extremely harsh winters. At the same time, social rules and cultural taboos sometimes protect steppes and forest patches from destruction and over-exploitation. Herders living in forest-steppes, together with ecologists and conservationists, can effectively co-produce knowledge and develop tradition-based but conservation-oriented management systems (Zhang et al. 2007; Molnár 2013; Molnár et al. 2016).

Forest-steppe conservation requires addressing certain knowledge gaps. First of all, conservation targets at continental, regional, national and local levels must be identified. Second, more research is needed to decide where the conservation of the status quo is a realistic goal, and where inevitable changes must be accepted or even facilitated. Third, practitioners must be equipped with adequate knowledge to choose between non-intervention and active management strategies. It is not yet fully known where the re-establishment of traditional practices in forest-steppe landscapes is a useful strategy, and where land-use pressure should be reduced. While identifying optimal management is challenging, we believe that a thorough knowledge of local circumstances combined with trial-and-error may be the way to success.

Climate change

Although climate change is not yet considered the greatest threat to forest-steppes (Ambarlı et al. 2016; Kamp et al. 2016), these ecosystems, where both forests and grasslands are near the margin of their tolerances, may be particularly vulnerable. Although drought-adapted forest types such as those in forest-steppes may be able to withstand short (seasonal) droughts, they are threatened by long (multi-year) droughts (Allen et al. 2010).

In line with global trends, increasing temperatures have been detected in many Eurasian forest-steppe areas, including Eastern Europe (Matveev et al. 2017), Turkey (Ambarlı et al. 2016), Kazakhstan (Kamp et al. 2016), Siberia (Tchebakova et al. 2011), the Altai Mts (Lkhagvadorj et al. 2013), and Inner Mongolia (Zhang et al. 2011). Precipitation changes, both observed and predicted, are much more variable (Angerer et al. 2008; Tchebakova et al. 2011; Ambarlı e al. 2016; Matveev et al. 2017).

Vegetation responses to changing climate may include (i) changing species composition within patches but sustained patchwork of grassland and forest stands, (ii) altered pattern of grassland and forest patches, such as shrinkage or expansion of one patch type at the expense of the other, and (iii) complete disappearance of one patch type and thus a shift of biome boundaries.

In Trans-Baikalian and northern Mongolian forest-steppes, *Pinus sylvestris* may replace *Larix sibirica* in a drier climate due to its capacity to cope with drought stress (Dulamsuren et al. 2009; Anenkhonov et al. 2015). In the Carpathian Basin, species diversity in forest-steppe grasslands may decrease with increasing aridity, while interannual variability and the number of annual species may increase (Kovács-Láng et al. 2000; Bartha et al. 2008).

The response of forest patches to future climatic changes may mimic behavior along climatic gradients, where forest patch size and cover decrease with increasing aridity (Kovács-Láng et al. 2000; Xu et al. 2017). Xu et al. (2017) found that small forest patches had increased mortality and decreased regeneration after disturbances than larger patches. A recent field study in Inner Asia has already revealed widespread tree mortality and decreased tree growth at the most xeric sites in response to increased water deficit (Liu et al. 2013 b). Permafrost melting is likely to affect vegetation, including diminishing forest cover (Sharkhuu & Sharkhuu 2012). Continued warming and drying may lead to broad-scale biome shifts. Northward movement of vegetation belts is predicted for several parts of Eurasia (e.g. Angerer et al. 2008; Zhang et al. 2011; Ischii & Fujita 2013; Kamp et al. 2016). This would lead to an overall decline of forest-steppes in Mongolia (Angerer et al. 2008). Central parts of the Carpathian Basin may be replaced by treeless steppes in the long term (Hickler et al. 2012), with an increase in the proportion of Mediterranean species (Thuiller et al. 2005).

The non-linear nature of climate-change impacts renders detection difficult; systems may resist certain levels of environmental change, which may then be followed by a sudden and large-scale vegetation shift (Liu & Piao 2013). Extreme climatic events or disturbances may be catalysts of such changes (Kröel-Dulay et al. 2015).

Changing climate may affect ecosystems not only directly, but also in combination with other factors, such as land use or biological invasion. For example, in the forest steppe of the Mongolian Altai Mts, earlier snow melt resulting from warming climate caused reduced migration of pastoral nomads, which, in turn, led to an intensified use of local forest patches (Lkhagvadorj et al. 2013). Drought and associated insect damage resulted in severe forest mortality in Anatolian forest-steppes (Allen et al. 2010).

All these examples demonstrate that forest-steppe ecosystems are already responding to changing climate. With predicted further warming and changing precipitation regimes in the 21st century (IPCC 2014), climate change may become one of the most important threats to the biodiversity and integrity of numerous ecosystems (Sala et al. 2000), including forest-steppes. Moreover, it has been suggested that the interaction of climate change and habitat fragmentation may have disastrous consequences for biodiversity (Travis 2003), worsening forest-steppe prospects, given the high level of habitat loss in the biome (Hoekstra et al. 2005).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. GIS map (shp file) of Eurasian forest-steppes with the main regions.

Appendix S2. Methods and sources used for the delineation of the forest-steppe zone and the main forest-steppe regions as shown in Fig. 1.

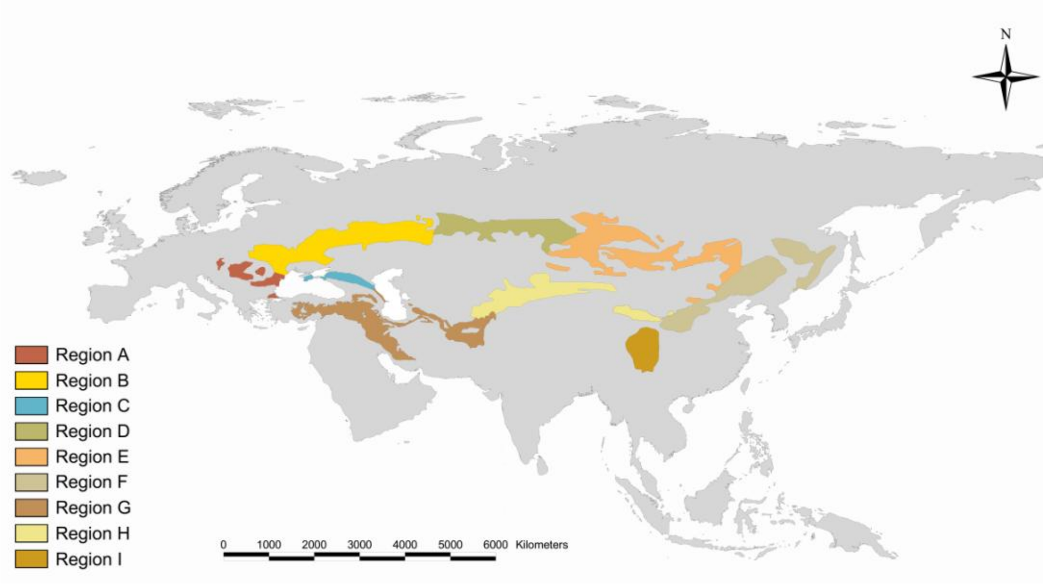

Fig. 1. The distribution of Eurasian forest-steppes and the main forest-steppe regions. Region A: Southeast Europe, Region B: East Europe, Region C: North Caucasus and Crimea, Region D: West Siberia and North Kazakhstan, Region E: Inner Asia, Region F: Far East, Region G: Middle East, Region H: Central Asia and southwestern Inner Asia, Region I: Eastern Tibetan Plateau.

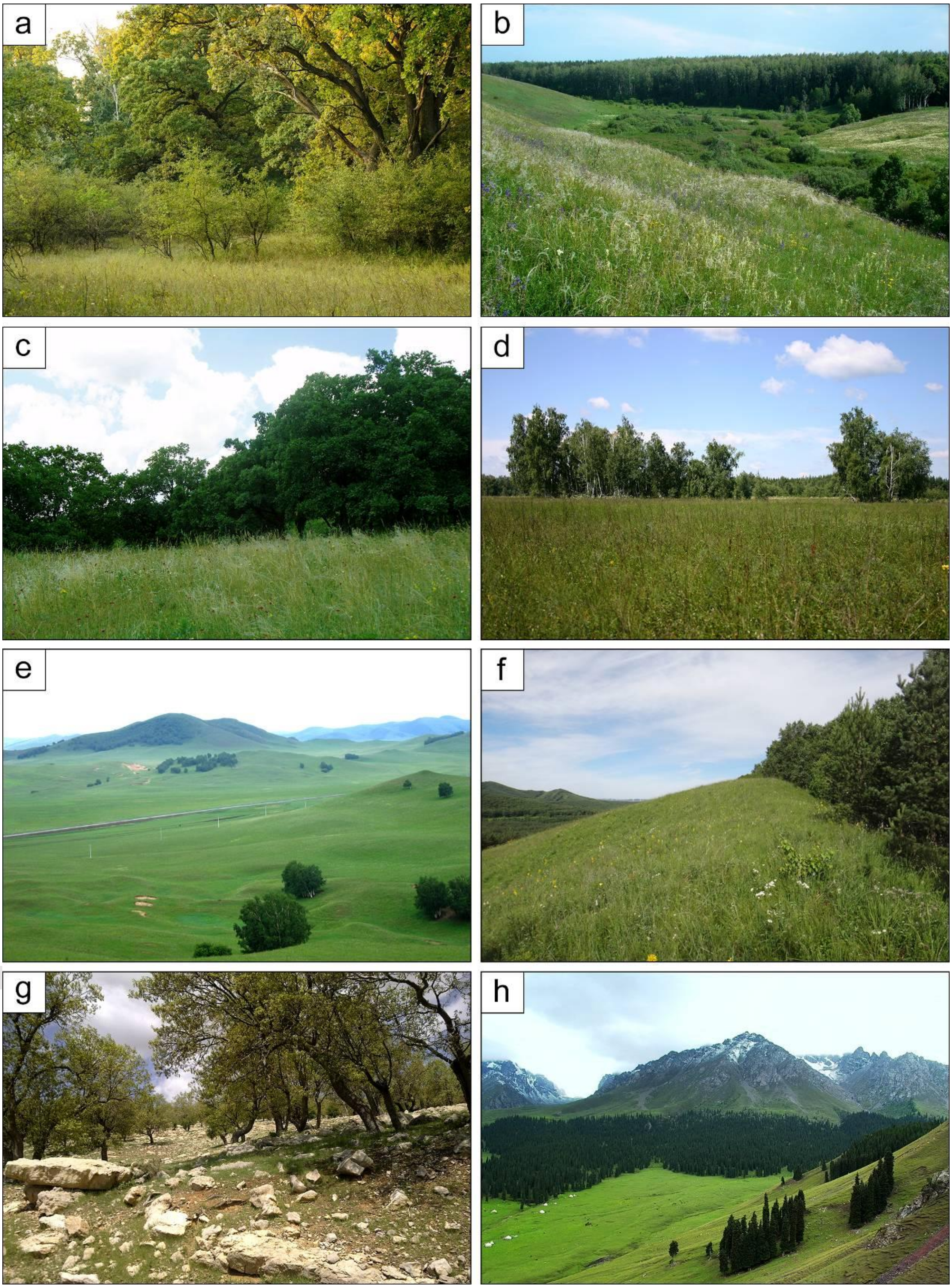

Fig. 2. Eurasian forest-steppe landscapes. **(a)** *Quercus robur* forest with grasslands of *Festuca rupicola*, *F. wagneri*, and *Stipa capillata* in the Kiskunság sand region of the Carpathian Basin, Hungary (photo Á. Molnár). **(b)** *Betula pendula*-*Quercus robur* forest and *Stipa pennata* steppe patch with *Salvia pratensis* in the Kulikovo Polye reserve, Tula region, Russia

(photo Yu. A. Semenishchenkov). **(c)** *Quercus pubescens* forest and *Stipa pontica* steppe in the Crimean Peninsula (photo Y. P. Didukh) **(d)** *Betula pendula* patches and *Festuca-Stipa* grasslands in the Kostanay Region, North Kazakhstan (photo Z. Bátori). **(e)** *Betula platyphylla* individuals and groves embedded in a *Leymus chinensis-Filifolium sibiricum* grassland in the Ulan Buton area of Inner Mongolia, China (photo H. Liu). **(f)** Forest-steppe landscape dominated by *Betula platyphylla* and *Stipa baicalensis* in the southern part of the Gretaer Khingan Range, China (photo H. Liu). **(g)** *Quercus brantii* woodland with *Bromus* spp. on calcareous and gypsiferous alluvium deposits in the Zagros Mts, Iran (photo A. Daneshi) **(h)** Mosaic of *Picea schrenkiana* forests and *Stipa capillata* steppes in the Tian Shan, Xinjiang Uygur Autonomous Region, China (photo H. Liu).

Table 1. Basic climatic parameters (to the nearest 0.5 °C and 10 mm), remaining areas (+: small, ++: medium, +++: large) and current land-use practices (-: absent or very rare, +: rare, ++ moderately widespread, +++: widespread) of forest-steppes.

Region	A	B	C	D	E	F	G	H	I
Mean annual temperature (°C)	9 – 13.5	3 – 9	9.5 – 12	1 – 4.5	-6 – 5	-1 – 14	10.5 – 17	0 – 12	-3 – 7
Mean January temperature (°C)	-3 – 3	-15 – -3	-4 – 1	-20 – -14	-28 – -12	-26 – 0	-5 – 4.5	-24 – -3	-12 – -2
Mean July temperature (°C)	19 – 25	18 – 22	21 – 24	19 – 22	14 – 20	20 – 27	22 – 31	18 – 26	8 – 16
Mean annual precipitation (mm)	420 – 600	400 – 660	300 – 770	270 – 610	210 – 550	360 – 650	270 – 860	380 – 600	300 – 700
Mean summer precipitation (mm)	100 – 210	160 – 260	160– 230	100 – 240	150 – 290	220 – 400	1 – 170	40 – 400	230 – 490
Proportion of summer precipitation (%)	17 – 36	28 – 43	25 – 40	37 – 44	36 – 72	40 – 70	0.5 – 34	10 – 70	47 – 76
Remaining forest-steppe area	+	+	+	++	+++	++	+	++	+++
Land-use of near-natural forest-steppes									
grazing	++	+++	++	++	++	+++	+++	+++	+++
mowing	+	+	+	++	+	++	+	+	-
burning	+	+	-	+	++	++	-	-	-
traditional crop cultivation	-	-	-	-	-	-	++	-	-
abandoned	+++	+	++	++	+	+	+	-	+