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Where forests meet grasslands: Forest-steppes in Eurasia

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Abstract: Despite the ecological, economic and conservation importance of forest-steppes, a continental scale synthesis of this complex ecosystem has been lacking. In a recent review, we compiled scattered knowledge about Eurasian forest-steppes in a new synthesis, proposed a new forest-steppe definition, reviewed how the biogeographic position of this ecosystem is perceived by different authors from different regions, delineated the main regions based on criteria of flora, physiognomy (i.e., vegetation structure), relief, and climate, and explored the conservation importance of forest-steppes. Here we complement some of the key findings of the review and illustrate some topics with further specific examples.

Keywords: complexity; forest-steppe; heterogeneity; meadow steppe; vegetation mosaic; wooded-steppe.

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Introduction

Forest-steppes are among the most complex ecosystems in the temperate zone, and have outstanding ecological, economic and conservation importance (Erdős et al. 2018a). At the same time, forest-steppes belong to the most threatened ecosystems due to habitat loss and insufficient protection (Chibilyov 2002; Hoekstra et al. 2005). While reviews and syntheses on forest-steppes have been available at national (e.g. Molnár et al. 2012) and regional scales (e.g. Berg 1958), overviews over broad areas have been lacking. To fill this gap, a recent synthesis (Erdős et al. 2018a) has collected scattered knowledge about the entire area covered by forest-steppes in Eurasia, gave an up-to-date definition of forest-steppes, examined the different views on this ecosystem, described major biogeographic patterns, identified the main forest-steppe regions, and explored the conservation importance of forest-steppes. In this paper we complement some of the key findings of Erdős et al. (2018a) with important additional information and add specific examples to the main topics.

A definition of forest-steppes

The first task in our review was to provide a forest-steppe definition. We evaluated criteria that have often been used in defining forest-steppes, and concluded that an up-to-date definition should be based on physiognomic features (a mosaic of arboreal and herbaceous components) and the underlying factors (the most important of which is climate). Thus, we define forest-steppes as 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 co-existence of forest and grassland is enabled primarily by the semi-humid to semi-arid climate, complemented by complex interactions of biotic (e.g. grazing, land use) and abiotic (e.g. soil, topography) factors operating at multiple scales (Erdős et al. 2018a). 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%.

In the temperate zone, humid environments generally support forests, whereas grasslands have developed in arid environments (Dengler et al. 2014). In areas with a transitional (i.e. semi-humid to semi-arid) climate neither forests nor grasslands have a decisive advantage over the other. Thus, both have a more or less equal chance to develop, and local factors (e.g. microclimate, soil properties, grazing) determine competition outcomes (Walter & Breckle 1989; Lavrenko & Karamysheva 1993; Borhidi 2002).

Forest-steppe autonomy

The recognition of forest-steppes as a separate biome or zone in its own right continues to be a subject of scientific controversy. Forest-steppes are perceived differently by researchers, depending on the scale of the investigation, the exact study question, and the main interest of the researcher. Textbooks that describe global vegetation patterns and provide only a brief introduction to main vegetation zones may not mention forest-steppes at all (e.g. Lomolino et al. 2010). Most global and continental (or quasi-continental) scale descriptions of vegetation zones regard forest-steppes as the northern part of the steppe zone (e.g. Müller 1981; Lavrenko & Karamysheva 1993; Archibold 1995; Schultz 2005; Smelansky & Tishkov 2012; Pfadenhauer & Klötzli 2014; Wesche et al. 2016). In the well known and widely used global classification system of Walter (1979), forest-steppe is considered a zonoecotone, i.e. a transitional area between the forests and the steppes. The above categorizations have two important consequences. First, the main emphasis is usually on the grassland component, with the importance of forest patches being underestimated. Second, forest-steppe is typically considered a mere transitional zone rather than a separate zone (or biome) in its own right.

On the other hand, there are some overviews on global (Pielou 1979), continental (Berg 1958; Tishkov 2002), or national scales (Rachkovskaya & Bragina 2012) that treat forest-steppes as forming a separate zone of their own. As biome definitions rest on climate and vegetation physiognomy (e.g. Lomolino et al. 2010; Cox et al. 2016), it follows that forest-steppes satisfy the criteria to be considered a biome (see our definition above and in Erdős et al. 2018a).

Forest-steppe biogeography and main regions

In our review (Erdős et al. 2018a), based on criteria of flora, physiognomy, relief, and climate, we delineated the following eight main forest-steppe regions (Fig. 1): (1) Southeast Europe, (2) East Europe, (3) North Caucasus and Crimea, (4) West Siberia and north Kazakhstan, (5) Inner Asia, (6) Far East, (7) Middle East, and (8) Central Asia and southwestern Inner Asia. In addition, we provisionally treated parts of the Eastern Tibetan Plateau as a forest-steppe region, where the main driver behind the forest and the steppe vegetation is probably a combination of low temperature and low precipitation.

Boundaries between the regions were sometimes hard to locate as they are gradual and rather blurred. The classification of the transitional areas to one or the other region may be debated in some cases. Also, it has to be emphasized that we tried to integrate the views of several authors, which was extremely difficult, given that we could not find two publications with the same delineation of the forest-steppe zone and its main regions. Thus our delineations should by no means be considered a final scheme, and may need further clarifications.

During our work, we encountered several areas the inclusion of which among the forest-steppes is intensively debated. For example, the Carpathian Basin is regarded as lying on the border of the closed-canopy deciduous forests and the forest-steppes (e.g. Walter & Breckle 1989). However, recent evidence shows that most of the lowlands of the Basin were covered by forest-steppes prior to intensive anthropogenic impacts (Magyari et al. 2010).

The existence of forest-steppes in Mongolia is sometimes attributed to human activity (Hilbig 2000; Fujita et al. 2013), but there is strong evidence suggesting that the forest-steppes are natural in this region (Dulamsuren et al. 2005; Hais et al. 2016)

The existence of forest-steppes in the Russian Far East is sometimes attributed to human deforestation. The debate has not yet settled, but there is some evidence on the natural origin of forest-grassland mosaics in this area (Berg 1958; Skripnikova & Uspenskaya 2006; Martynenko 2007).

Forest-steppes of northern Eurasia, extending from the Carpathian Basin to the Chinese and Russian Far East are relatively well-known. However, there is also a less known southern belt of forest-steppes, extending from Turkey and Iran to the Qilian Mountains and the Chinese Loess Plateau. Granted, these southern forest-grassland mosaics are usually known under names such as “open woodland” or “sparse arid woodland”. In addition, their structure is somewhat different: instead of the meadow-steppes of the northern belt, the grassland component in the southern belt is usually semidesert-like. According to Walter (1956), this difference is due to the different effects of grazing: while the meadow-steppes of the northern belt can better tolerate grazing, the steppes of the Middle East are more sensitive and, when grazed, these southern steppes turn into a semidesert-like state (see alo Fırıncıoğlu et al. 2009). Despite some obvious differences, however, these forest-grassland mosaics of the southern parts of Eurasia undoubtedly satisfy the criteria of forest-steppes, as they have formed under semi-arid to semi-humid conditions, and have alternating woody and herbaceous components

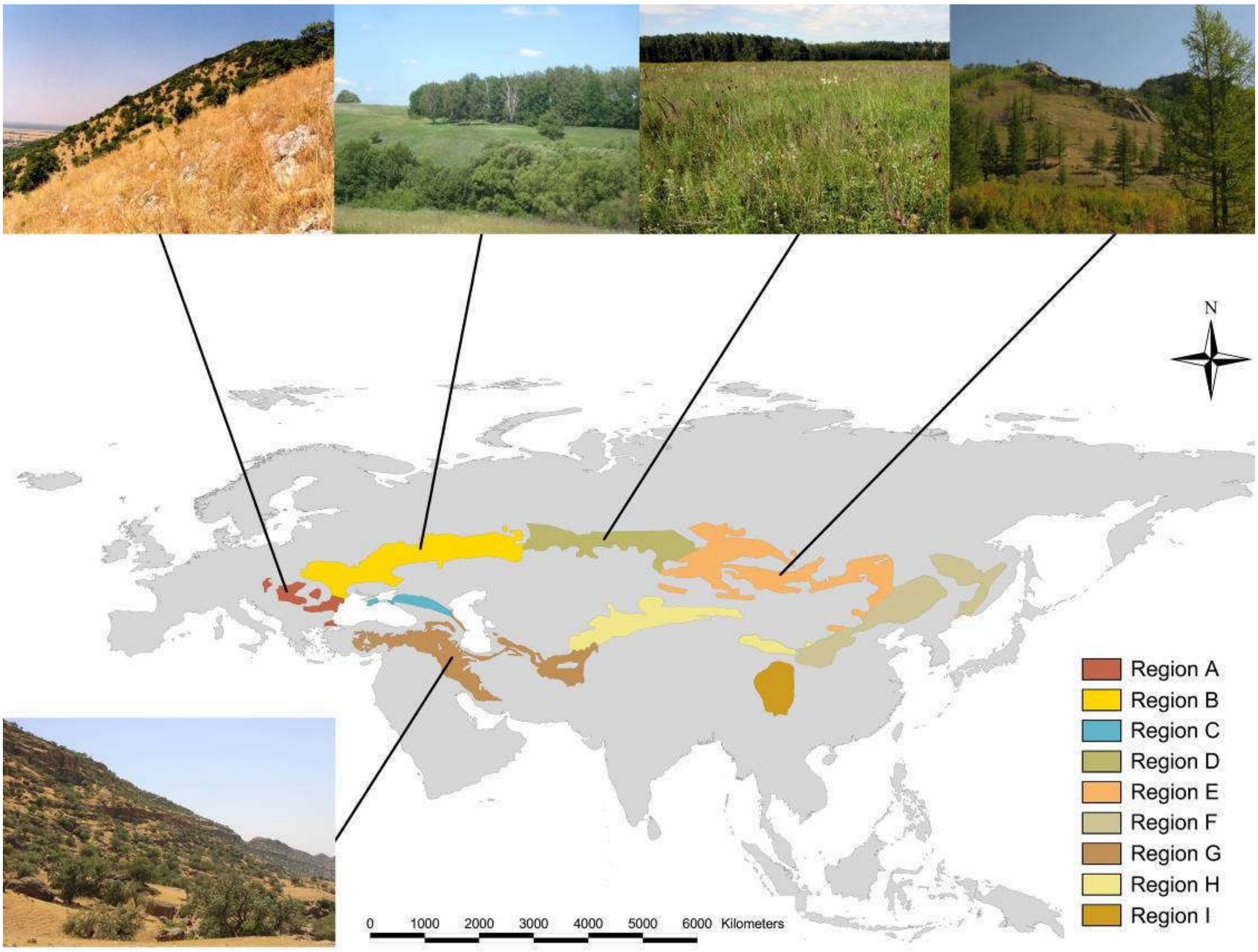

Fig. 1. The main forest-steppe regions of Eurasia: Southeast Europe (Region A), East Europe (Region B), North Caucasus and Crimea (Region C), West Siberia and north Kazakhstan (Region D), Inner Asia (Region E), Far East (Region F), Middle East (Region G), Central Asia and southwestern Inner Asia (Region H), and Eastern Tibetan Plateau (Region I). Photo credits: upper line: László Erdős, Yury A. Semenishchenkov, Zoltán Bátori, Zsolt Molnár; bottom left: Alireza Naqinezhad.

(Wesche et al. 2016). If both the northern and the southern forest-steppes are shown on a map, it turns out that forest-steppe regions form an elongated shape surrounding the most arid central parts of Eurasia (Erdős et al. 2018a).

The importance of habitat heterogeneity for diversity and conservation

Numerous types of forest, scrub and grassland habitats with different environmental, structural and compositional features occur in forest-steppes (Erdős et al. 2018a). Despite this fact, the conservation implications of habitat heterogeneity have received surprisingly little attention in many forest-steppe areas. For example, in the Carpathian Basin, conservation actions usually focus on the grassland component, which may have serious conservation consequences in forest-steppes. For example, a recent study has shown that different components of forest-steppes contribute differently to the overall conservation value of the total landscape in sandy forest-steppes (Erdős et al. 2018b): grasslands contain the largest number of protected, endemic and rare species, north-facing forest edges have the highest species richness, south-facing forest edges are the main areas for tree recruitment, while forest patch interiors are important for structural reasons (shrubs and large trees). Kelemen et al. (2017) reported that the presence of small shrubs improves the flowering success of plants in grazed forest-steppe habitats. Forest edges and forest interiors (primarily in openings) can support species that are not able to survive under the harsh conditions of the grasslands (Erdős et al. 2014). Forest patches may support some grassland species during unusually severe drought events and may thus contribute to grassland regeneration in more humid years (Bartha et al. 2008, 2011). Similarly, forests and their edges may serve as refuges for steppe species during habitat destruction or degradation (Molnár et al. 2008). In addition, forest patches can lessen the effects of increasing aridity from ongoing climate change, thus having a primary role in forest-steppe resistance against climate change (Bartha et al. 2008; Biró et al. 2008; Erdős et al. 2015). A study from the Vienna Basin also showed that the mosaic-like configuration of forest and grassland patches is the most desirable from a conservation perspective (Erdős et al. 2017).

The above examples show that conservation measures should take the mosaic character of forest-steppes into account. For example, the recruitment of native trees should be of high priority in areas that have been overgrazed. During forest-steppe restoration, both woody and non-woody habitats should be reconstructed, as was done in a recent project (Török et al. 2017).

Cultural significance of forest-steppes

Some of the forest-steppes in Southwest Asia (present-day Turkey, Iraq, Iran) are located in a region that is usually considered the cradle of Western civilization (Poschlod 2015; Wesche et al. 2016). In northern Eurasia, forest-steppes (together with steppes) served as conduits for cultural inventions and as major migration routes for several peoples during history (Anthony 2007; Bone et al. 2015). The distribution pattern of forest-steppes even influenced settling patterns, as certain tribes and nations probably preferred park-like landscapes and tended to avoid closed forests (Borhidi 2002; Sümegi et al. 2012).

Herders of the forest-steppe belt 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). While "modern" cultures eliminated natural vegetation in vast areas for arable cultivation and confined billions of animals into factory farms, herders' lifestyle seems to be much more compatible with forest-steppe survival and animal welfare. It seems clear that traditional ecological knowledge can contribute to a better, ecologically and culturally more site-specific nature conservation management (Molnár 2013; Molnár et al. 2016).

The human species and its ancestors have spent much of the last couple of million years of their evolution in forest-grassland mosaics (tropical or temperate), which probably contributes to the fact that humans (well beyond the circle of ecologists) usually seem to prefer park-like habitats, as shown by several analyses (e.g. Orians 1980; Balling & Falk 1982). This is in line with the biophilia hypothesis of Wilson (1984), which presumes that humans might be genetically determined to enjoy forest-steppes and other ecosystems with similar patterns. Whether our aesthetic preference for woody-herbaceous mosaics has a genetic background remains to be explored. What seems evident is that losing Eurasian forest-steppes would not only mean a huge loss in terms of diversity at several levels, but also the vanishing of some of our history and culture as well.

Author contributions

L.E. planned the study, L.E. and P.T. led the writing, D.A., O.A.A., D.C., L.E., M.K., H.L., M.M., A.N. and Y.A.S. did the delineation of the main regions, Z.B., L.E., G.K-D., Z.M., C.T. and P.T. contributed to the parts about heterogeneity and conservation, L.E. and Z.M. wrote about the cultural significance, and all authors critically revised the manuscript.

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