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# Exposure-related forest-steppe: A diverse landscape type determined by topography and climate

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ABSTRACT

Topographic heterogeneity under dry continental climate can create a landscape mosaic called "exposure-related forest-steppe", characterized by a regular pattern of forest on the north- and steppe on the south-facing slopes. Here we identify the climatic and topographic determinants of this landscape type, using a model of the Altai Mountains in southern Siberia because they (1) contain large areas of forest-steppe together with forested and steppe landscapes, and (2) possess well-preserved natural land-cover. Based on the Landsat land-cover classification and digital elevation model we identified areas containing exposure-related forest-steppe and modeled their climatic and topographic thresholds using regression trees. The models showed that in the Altai exposure-related forest-steppe is most common in topographically heterogeneous areas with May–September precipitation of 226–377 mm and a mean July temperature of 13.8–15.6 °C. Its existence is jointly determined by hilly topography and a climate that is moist enough to support tree growth on north-facing slopes, but insufficiently so to support woodland development on south-facing slopes. This is consistent with the concept of effective topographic heterogeneity, suggesting that topographic heterogeneity on the landscape level is translated into high habitat diversity and species diversity only within a certain range of climatic conditions.



## 1. Introduction

Topographic landscape heterogeneity, promoting environmental heterogeneity, is one of the main factors that influence species diversity (Lundholm, 2009). While on the macroscale (areas of 10,000 km$^2$ and larger) the most important factor is climate (Field et al., 2009), topographic heterogeneity becomes prominent on the mesoscale (~0.01–10,000 km$^2$; Sarr et al., 2005). Heterogeneous landscapes tend to support high species diversity not only by providing different habitats for species with contrasting environmental requirements (Turner, 2004; Dufour et al., 2006; Kumar et al., 2006; Hofer et al., 2008), but also by providing a reliable system which enables species survival during environmental (especially climatic) changes. Heterogeneous landscapes often act as refugia by enabling species to move to more suitable sites (e.g. along the gradients of altitude, slope aspect, or humidity) in periods of large-scale environmental change, and to return to the original sites once the previous broad-scale environmental conditions are re-established (Ashcroft, 2010; Keppel et al., 2012).

Forest-steppe is a mosaic-like ecosystem in which topographic heterogeneity strongly influences the vegetation pattern and distribution of species diversity across landscapes. On the macroscale it usually represents a transitional zone between temperate grassland and temperate woodland biomes. The occurrence of this transitional zone is determined climatically, especially by the amount of precipitation and evapotranspiration. Forest-steppe mosaics can occur both on plains and in mountainous terrain. The Eurasian forest-steppe zone stretches from dry areas in central Europe such as the Pannonian Basin through an extensive zone north of the steppe zone in central Ukraine, southern Russia, northern Kazakhstan, northern Mongolia and northern China (Walter, 1974; Shahgedanova, 2002; Liu et al., 2015). Its analogues occur at the forest–prairie ecotone of North America (Loehle et al., 1996; Mast et al., 1997; Barbour and Billings, 2000; Frelich and Reich, 2010) and forest–steppe ecotone of southern South America (Anchorena and Cingolani, 2002).

A special type of forest-steppe can be found in semi-arid hilly landscapes where north-facing slopes support woodland while

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south-facing slopes are occupied by dry grassland (Figs. 1 and 2). In the Russian plant ecological and geographical literature, this type of landscape is usually called "ekspozitsionnaya lesostep'" (Ogureeva, 1980), which can be translated as "exposure-related forest-steppe", referring to the significant effect of exposure, i.e. slope aspect, on vegetation structure. Exposure-related forest-steppe is described especially from the mountainous landscapes of southern Siberia (Ogureeva, 1980; Makunina and Maltseva, 2008; Anenkhonov et al., 2015; Makunina, 2016), Kazakhstan (Rachkovskaya and Bragina, 2012), northern Mongolia (Hilbig and Knapp, 1983; Hilbig, 1995; Wallis de Vries et al., 1996; Dulamsuren et al., 2005b) and northern China (Liu et al., 2000, 2012), However, similar landscape types can be found in other regions of the world with a similar semi-arid continental climate such as the North American forest–prairie ecotone zone (Bailey, 1996).

The occurrence of exposure-related forest-steppe depends on regional climate, which is sufficiently humid to enable forest growth on north-facing slopes, and at the same time too dry to support tree encroachment on south-facing slopes. This simultaneous requirement is met within a relatively narrow range of regional climatic conditions, which, in combination with hilly terrain, enable a highly heterogeneous landscape mosaic of contrasting habitat types to develop. Such a mosaic can be very important as a refugium of forest species in periods of drier climate or a refugium of steppe species in periods of wetter climate. Because exposure-related forest-steppe enables the simultaneous occurrence of species with contrasting environmental requirements, it can also support the development of species-rich communities due to the spatial mass effect (Shmida and Ellner, 1984; Zelený et al., 2010). For example, Chytrý et al. (2012) reported that the birch-pine forests of the exposure-related forest-steppe zone in the northern Altai Mountains of southern Siberia are the most species-rich extratropical forests of Eurasia known so far.

The high biological diversity of the exposure-related forest-steppe landscape, depending on the interaction between topography and climate, is an example of the concept of effective (biologically meaningful) landscape heterogeneity. Assuming constant topographic heterogeneity, effective landscape heterogeneity can be high under semi-arid climatic conditions, but low under arid, under which the whole landscape becomes treeless, and also low under humid, under which the landscape becomes continuously forested (Sarr et al., 2005).

Given the high relevance of mesoscale landscape heterogeneity regarding biodiversity, it is important to understand the climatic and topographic determinants of the exposure-related forest-steppe mosaic. Therefore the aim of this study is to identify the climatic and topographic determinants of the exposure-related forest-steppe in southern Siberia. We selected the Altai Republic in southern Russia as an appropriate model area because (1) its landscape contains large areas of forest-steppe, but also forested landscapes and predominantly treeless steppe landscapes, and (2) it has a sparse human population, and, therefore the landscape pattern of forest vs. open areas is less influenced by human activity than in many other forest-steppe areas of Eurasia.

## 2. Methods

### 2.1. Study area

The study area is the Altai Republic (92,600 km$^2$), a part of the Russian Federation located in southern Siberia, bordering Kazakhstan, China, and Mongolia. Its population density is only 2.2 people/km$^2$, and the population is strongly concentrated near its northern and north-western borders. Consequently, industrial and agricultural activities are limited, and most of the area is covered by natural vegetation. However, livestock grazing, mainly by cattle and horses, can locally extend treeless areas to potential forest sites. The area encompasses a broad range of natural conditions within an altitudinal range of 258–4506 m a.s.l. (mean altitude 1676 m). The northern part is humid and relatively warm, with annual precipitation in the foothills being higher than 800 mm, a mean July temperature of about 18 °C and a mean January temperature of about −16 °C. The climate becomes progressively drier and cooler when moving to the high-mountain areas in the south. The

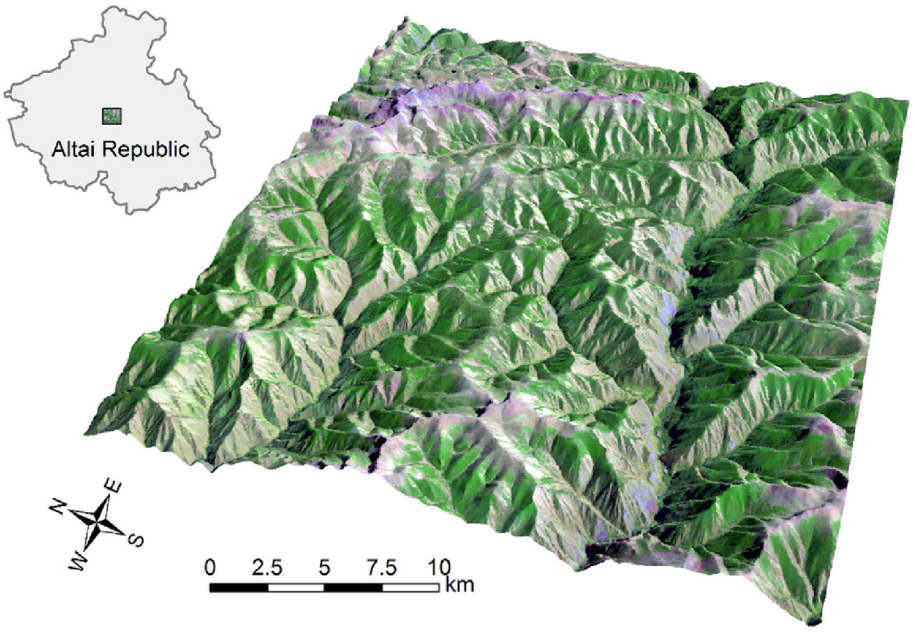


**Fig. 1.** A typical example of exposure-related forest-steppe in the area around the Kadrin river valley in the central Altai Republic (ca. 30–70 km E of Onguday town) based on a pseudocoloured Landsat 543 composition. Forest (green color) covers mainly the north-facing slopes, while steppe (grey color) occurs mostly on the south-facing slopes. Areas above the timberline are violet. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)