Acta Oecologica 63 (2015) 36–46

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Patterns of fine-scale plant species richness in dry grasslands across the eastern Balkan Peninsula

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ARTICLE INFO

Article history:
Received 2 September 2014
Received in revised form
22 January 2015
Accepted 2 February 2015
Available online 14 February 2015

Keywords:
Alpha diversity
Bulgaria
Romania
Soil chemistry
Species pool
Steppe

ABSTRACT

Fine-scale plant species richness varies across habitats, climatic and biogeographic regions, but the large-scale context of this variation is insufficiently explored. The patterns at the borders between biomes harbouring rich but different floras are of special interest. Dry grasslands of the eastern Balkan Peninsula, situated in the Eurasian forest-steppe zone and developed under Mediterranean influence, are a specific case of such biome transition. However, there are no studies assessing the patterns of fine-scale species richness and their underlying factors across the eastern Balkans. To explore these patterns, we sampled dry and semi-dry grasslands (phytosociological class *Festuco-Brometea*) across Bulgaria and SE Romania. In total, 172 vegetation plots of 10 × 10 m^2 were sampled, in which all vascular plant species were recorded, soil depth was measured, and soil samples were collected and analysed in a laboratory for pH and plant-available nutrients. Geographic coordinates were used to extract selected climatic variables. Regression trees and linear regressions were used to quantify the relationships between species richness and environmental variables. Climatic factors were identified as the main drivers of species richness: (1) Species richness was strongly positively correlated with the mean temperature of the coldest month: sub-Mediterranean areas of S and E Bulgaria, characterized by warmer winters, were more species-rich. (2) Outside the sub-Mediterranean areas, species richness strongly increased with annual precipitation, which was primarily controlled by altitude. (3) Bedrock type and soil pH also significantly affected dry grassland richness outside the sub-Mediterranean areas. These results suggest that fine-scale species richness of dry grasslands over large areas is driven by processes at the regional level, especially by the difference in the species pools of large regions, in our case the Continental and Mediterranean biogeographic regions. Local environmental factors are of secondary importance over broad extents, but their effect on fine-scale species richness increases within climatically and biogeographically homogeneous regions.

1. Introduction

Eurasian temperate dry grasslands and steppes locally support the coexistence of a high number of vascular plant species (Kull and Zobel, 1991; Merunková et al., 2012; Wilson et al., 2012; Turtureanu et al., 2014). For several plot sizes smaller than 50 m^2, dry grasslands of Central and Eastern Europe hold the world records for richness of vascular plant species (Wilson et al., 2012). However, not all dry grasslands are so extremely species-rich: their richness varies considerably, and knowing the relationships of this variation to environmental factors can help to predict and eventually avoid biodiversity loss if combined with wise nature conservation management.

Several observational and experimental studies have been carried out in temperate grasslands to explore the relationships between vascular plant species richness (henceforth 'species richness') and environmental factors at the fine scale, i.e. the scale of vegetation plots (Grace, 1999). Still, there is a lack of a general

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http://dx.doi.org/10.1016/j.actao.2015.02.001
1146-609X/

agreement as to which set of factors and which underlying mechanisms are the most important controls of species richness in dry grasslands. Local environmental factors, such as site conditions (e.g. soil properties, water availability, productivity; Löbel et al., 2006; Chytrý et al., 2007; Merunková and Chytrý, 2012; Axmanová et al., 2013), biotic interactions (e.g. competition for light; Kull and Zobel, 1991; Löbel et al., 2006), and management (Bonanomi et al., 2013; Turtureanu et al., 2014), were found to be important controls of fine-scale species richness in different temperate and (hemi-)boreal grasslands. However, the species richness–environment relationship is also influenced by historical and evolutionary processes at the regional level (large-scale migration, extinction, and speciation), which determine the size and composition of the species pool (the set of species potentially able to occur within a given environment; Zobel, 1992). Therefore, patterns of fine-scale species richness can differ among biogeographic and climatic regions. The more common a habitat was throughout history, the more time there was for speciation and large-scale migration, leading to the evolution of a larger species pool ('species pool effect'; Taylor et al., 1990; Ewald, 2003). In many cases, even in the very species-rich dry grasslands where biotic interactions are supposed to set a limit to the number of coexisting species (Bengtsson et al., 1994), fine-scale species richness patterns seem to be influenced by species pools (Pärtel et al., 1996).

Many dry grasslands in the eastern Balkan Peninsula are considered to be natural remnants of the forest-steppe that has persisted in the Lower Danube Basin and the Upper Thracian Plain since the Pleistocene, serving as an important migration corridor for grassland species between the Pontic, Anatolian, and Pannonian steppes (Magyari et al., 2008; Tonkov et al., 2011). Because of their distinct evolutionary and migrational history, diversity patterns reported from dry grasslands in other regions of Europe cannot be directly transferred to the eastern Balkan Peninsula. However, fine-scale species richness patterns of these dry grasslands have never been explored. Several previous studies gathered valuable data on the dry grassland vegetation of this area, but all of them dealt with smaller regions and focused on vegetation classification (e.g. Tzonev et al., 2006; Pedashenko et al., 2013; Sopotlieva and Apostolova, 2014; see Doniţă et al., 2005 for references on the Romanian Dobrudzha) and the relationships between species composition (not richness) and the environment (Pedashenko et al., 2013).

Dry grasslands in the eastern Balkan Peninsula have developed under a unique combination of the Mediterranean and continental climatic influences. Therefore, they are a suitable model for assessing the relative effects of these two climate types on fine-scale species richness. Few previous studies have reported climate as a control of fine-scale species richness patterns in temperate grasslands (e.g. Adler and Levine, 2007; Chytrý et al., 2007; Reitalu et al., 2014; Turtureanu et al., 2014), possibly because most other research projects have not encompassed large climatic gradients or biogeographic transitions. In general, factors operating over broad scales such as macroclimate are considered to be poor predictors of fine-scale species richness (Pausas and Austin, 2001). Nevertheless, we hypothesize that, if filtering by local environmental factors is not too strong and the climatic gradient is large, climate may explain more variation in fine-scale species richness than local factors (as in Adler and Levine, 2007; Chytrý et al., 2007). Further, we hypothesize that climate should have a contrasting effect on the richness of different life forms, because Mediterranean and temperate grasslands considerably differ in the participation of different life forms (Cain, 1950).

Besides contrasting climates, the Balkan Peninsula is characterized by a very rich flora, especially in its Mediterranean and sub-Mediterranean areas (Barthlott et al., 2005), with many endemics occurring mainly on calcareous substrates, and calcicole species that immigrated from diversity hotspots (such as Anatolia; Médail and Quézel, 1997) where calcareous soils prevail (Mücher et al., 2009). Thus, based on the species pool hypothesis (Taylor et al., 1990), we expect soil pH to be a strong correlate of fine-scale species richness in dry grasslands in the eastern Balkan Peninsula. Positive relationships with soil pH, explained by the prevalence of calcicole species in the existing species pools (Ewald, 2003), were found under continental, oceanic, and Mediterranean conditions across Eurasia (Pärtel, 2002; Schuster and Diekmann, 2003; Chytrý et al., 2003, 2007, 2010). However, the relationship between species richness and soil pH could be modified by the interaction with other factors such as climate (Löbel et al., 2006; Chytrý et al., 2007). The decrease in species richness on soils with very high pH might be due to the lower number of species adapted to the drought stress (low precipitation) associated with very basic substrates (Chytrý et al., 2007). Thus, we consider dry grasslands in the eastern Balkan Peninsula, occurring on different bedrock types and distributed over a large precipitation gradient, to be a good model for evaluating the species richness–soil pH relationship in different biogeographic contexts.

To explore fine-scale species richness patterns in dry grasslands in the eastern Balkan Peninsula, we sampled vegetation plots along a broad spatial extent and long climatic and altitudinal gradients, and assessed the relative importance of these and other measured variables on species richness. Our main questions were:

1. Is there a geographical pattern in fine-scale species richness in the eastern Balkan Peninsula coinciding with the transition between the subcontinental and the sub-Mediterranean biogeographic regions?
2. Which factors are the most important drivers of the variation in fine-scale species richness of dry grasslands across the eastern Balkan Peninsula: soil properties, climate, or management?
3. Do species of specific life forms or biogeographic histories (e.g. sub-Mediterranean vs. subcontinental) contribute differently to species richness patterns?

2. Materials and methods

2.1. Study area

The study area is located in the eastern Balkan Peninsula (41.87°–45.15° N, 22.59°–29.08° E), and includes two major lowlands separated by the Stara planina (Balkan) mountain range: the Dobrudzha (Dobrogea) plateau and the Lower Danube basin in the north, and the Upper Thracian plain in the south. Dry grasslands were sampled from the Black Sea coast up to the mid-altitudes, including the karstic low mountains in western Bulgaria, the Stara planina, and the Strandzha-Sakar massif (14–1211 m a.s.l., Fig. 1). Limestones and other calcareous rocks of different ages and origins prevail in the study area. An exception is the Upper Thracian plain, with predominating Quaternary alluvial-diluvial sediments and Neogene continental deposits, and the Strandzha-Sakar massif, with predominating volcanic, metamorphic, and granitoid rocks. But even so, dry grasslands in the latter regions are mainly associated with outcrops of carbonate bedrocks, such as crystalline limestone. In the northern Dobrudzha and the Lower Danube basin, Quaternary loess deposits form a 20–60 km broad band parallel to the river (Kopralev, 2002).

The climate is temperate-continental (henceforth 'subcontinental') to the north of the Stara planina and in western Bulgaria, continental-Mediterranean (henceforth 'sub-Mediterranean') in