Agriculture, Ecosystems and Environment 182 (2014) 59–68

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Determinants of fine-scale plant diversity in dry calcareous grasslands within the Baltic Sea region

Triin Reitalu[a,*], Aveliina Helm[b], Meelis Pärtel[b], Karin Bengtsson[c], Pille Gerhold[b,d], Ejvind Rosén[e], Krista Takkis[b], Sergey Znamenskiy[f], Honor C. Prentice[g]

[a] Institute of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia
[b] Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, 51005 Tartu, Estonia
[c] School of Culture, Energy and Environment, Gotland University, 62167 Visby, Sweden
[d] Department of Experimental Plant Ecology, Institute for Water and Wetland Research, Radboud University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands
[e] Department of Ecology and Genetics, EBC, Uppsala University, Norbyvägen 18D, 75236 Uppsala, Sweden
[f] Institute of Biology, Karelian Research Centre RAS, Pushkinskaya 11, 185910 Petrozavodsk, Karelia, Russian Federation
[g] Department of Biology, Lund University, Ecology Building, 22362 Lund, Sweden

A R T I C L E I N F O

Article history:
Received 4 July 2012
Received in revised form 12 October 2012
Accepted 12 November 2012
Available online 16 January 2013

Keywords:
Alvar
Biogeographic
Habitat history
Immigration histories
Phylogenetic clustering
Species density
Standardized effect size

A B S T R A C T

We used an extensive dataset (1220 vegetation plots of 1 m^2) to study vegetation gradients and fine-scale plant diversity in dry calcareous grasslands (including alvar grasslands) in the Baltic Sea region. The study area covers the entire European distributional range of alvar habitats: Sweden (Öland, Gotland, Götaland), Estonia (Saaremaa, Hiiumaa, north Estonia, west Estonia), and western Russia (Izhora, Izborsk). Fine-scale plant diversity was characterized by species richness and standardized phylogenetic diversity (comparing the observed mean pairwise phylogenetic distance (MPD) with MPD values from random communities). Ordination techniques (DCA) were used to characterize the main vegetation gradient. Variables describing local environment, climate, the biogeographic composition of the plant communities, and geographic location were related to fine-scale species richness and phylogenetic diversity using variation partitioning techniques and linear mixed models.

The main vegetation gradient in the dry calcareous grasslands in the Baltic Sea region had a strong geographic component, was associated with soil depth, species' stress- and disturbance-tolerance and the age of the grassland habitat.

Fine-scale phylogenetic diversity and species richness were negatively associated suggesting that these two diversity components are influenced by different sets of environmental and historical parameters. Fine-scale species richness was unimodally associated with the main vegetation gradient, and the highest levels of species richness were found under intermediate environmental (disturbance, light conditions and temperature) conditions where there was a mixture of species from different biogeographic regions. In contrast to species richness, fine-scale phylogenetic diversity was negatively associated with the main vegetation gradient. The highest phylogenetic diversity was found in the extremely thin-soiled alvar grasslands in Götaland and on the Baltic islands (especially on Öland) where the high phylogenetic diversity is likely to be a reflection of a long history of continuous openness that has allowed time for the "collection" of phylogenetically different species within these unique habitats.

1. Introduction

In Europe, the climax community for most of the boreo-nemoral region is forest. The majority of European grasslands have an anthropogenic origin and require at least a moderate level of management (grazing or mowing) for their long-term persistence. Naturally open habitats only persist where conditions are unfavourable for trees; for example, on floodplains, in saline coastal areas and on thin soils overlying bedrock (Laasimer, 1965). Primary open habitats with sparse vegetation also characterize regions that have relatively recently emerged from the sea as a result of neotectonic land uplift (Zobel and Kont, 1992).

Within the Baltic Sea region, dry calcareous grasslands occupy a range of habitats: from those where the vegetation is more-or-less naturally open (for example, in sites on limestone outcrops), to those on deeper soils and calcareous moraines where the grassland vegetation has a clearly secondary origin. Calcareous grasslands that occur on thin soils (generally <20 cm) on Ordovician or Silurian limestone are referred to as "alvars" (Laasimer, 1965; Ekstam and Forshed, 2002). The word "alvar" originates from

* Corresponding author. Tel.: +372 530321; fax: +372 6203011.
E-mail address: triin.reitalu@mail.ee (T. Reitalu).

0167-8809/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.agee.2012.11.005

Swedish, where it applies in a broader sense to “unproductive ground” (Pärtel et al., 1999a). In Europe, alvars are found within an area that stretches from southeastern Sweden, through Estonia and into north-western Russia (Laasimer, 1965; Ekstam and Forshed, 2002) and the vegetation composition and environmental conditions of European alvar habitats show considerable variation (Dengler and Löbel, 2006; Znamenskiy et al., 2006; Helm et al., 2007). Similar plant communities on thin calcareous bedrock have also been described in southeastern Canada (Belcher et al., 1992; Schaefer and Larson, 1997).

Dry calcareous grasslands have a substantial nature conservation value because they contain a high diversity of specialized species belonging to a range of different taxonomic groups of organisms (plants, insects, lichens, birds) (Schaefer and Larson, 1997; Veen et al., 2009). European grasslands also represent an important historical and cultural heritage. The history of human influence on the alvar grasslands in the Baltic Sea region dates back to the Neolithic (7000–4000 years ago) (Königsson, 1968; Poska et al., 2004).

Alvars have interested biologists since 1741 when Carl von Linné visited Öland and Gotland (Linnaeus, 1745). The largest area of alvar is found on the Baltic island of Öland where the Great Alvar, with its 255 km^2 of grassland habitat, has become the main centre of alvar research in Europe. Research on the Great Alvar has focused on wide range of different topics – from habitat management and restoration (e.g. Rosén, 1982; Bakker et al., 2007) to vegetation patterns (e.g. Bengtsson et al., 1988; Rusch and Fernández-Palacios, 1995), determinants of species diversity (e.g. van der Maarel and Sykes, 1993; Löbel and Dengler, 2007) and genetic diversity (e.g. Prentice et al., 1995; Lönn and Prentice, 2002). Estonian alvar grasslands have also been the subject of a number of plant ecological studies focusing on community classification (Pärtel et al., 1999a), environmental conditions (Pärtel and Helm, 2007), and plant diversity patterns (e.g. Pärtel and Zobel, 1999; Zobel et al., 2000; Helm et al., 2006, 2009; Pärtel et al., 2007). In addition, a few studies have compared the vegetation in different alvar regions (Znamenskiy et al., 2006; Helm et al., 2007) or examined relationships between the vegetation composition of alvar grasslands and other calcareous grasslands in Europe (Dengler and Löbel, 2006). Even though alvars and associated dry calcareous grasslands have been the subject of a large number of plant ecological and phytosociological studies, there are no vegetation studies that have covered the whole distributional range of European alvar grasslands.

Environmental conditions in the most extreme, thin-soiled alvar sites are characteristically harsh: the soils typically dry out completely during the summer but are also often waterlogged during the spring or autumn. Frost heaving may cause severe physical disturbance during the winter months (Rosén, 1982; Pärtel et al., 1999a). Extremely thin-soiled alvar areas, such as those that are characteristic of the southeastern part of the Great Alvar on Öland, are thought to have remained more-or-less open during most of the Holocene (Königsson, 1968). Some of the taxa that are presently common in the alvar areas are known to have been present in the open habitats around the margins of the retreating ice-sheet during the Late Glacial (e.g. *Gypsophila*, *Helianthemum*, *Artemisia*, *Saxifraga*) (Berglund, 1966; Königsson, 1968; Veski et al., 2012) and it is likely that the populations of these light-demanding alvar species have been able to persist throughout the Holocene in fragments of open habitat in the otherwise forested landscape (Königsson, 1968; Bengtsson et al., 1988). Many of the characteristic alvar species, especially on the Great Alvar on Öland, are on the limits of their geographic ranges or represent disjunct occurrences outside their typical distributional ranges (Bengtsson et al., 1988). These species belong to a range of phytogeographical groups, for example, *Artemisia rupestris* and *Astragalus danicus* have their main distributional areas in steppe regions in southern Siberia and southeastern Europe, *Poa alpina* and *Draba incana* in northern European mountain areas and *Sedum album* and *Gypsophila fastigiata* in southern and central Europe (Hultén and Fries, 1986).

Fine-scale plant species richness in semi-natural grasslands within local landscapes has been shown to depend on a range of local variables: present-day management and disturbance regime (Rosén, 1982; Schnoor and Olsson, 2010), management history (Pärtel et al., 1999b; Reitalu et al., 2010), nutrient status (Diekmann et al., 2004; Löbel et al., 2006), and environmental and microclimatic heterogeneity (Rosén, 1982; Pärtel and Helm, 2007). Extending the extent of a study area from a local (within an individual landscape) to a regional (extending over several thousands of square kilometres) scale is expected to increase the importance of large-scale factors, such as climatic variation and species' immigration histories, as determinants of fine-scale species richness (Pärtel and Zobel, 1999; Harrison and Cornell, 2008).

Both patterns of immigration from different geographic areas and species' bioclimatic tolerance limits are expected to have a strong influence on the composition of a particular regional species pool – which, in its turn, will influence levels of local and fine-scale species richness within plant communities (cf. Pärtel et al., 1996). We can, therefore, predict that levels of fine-scale species richness are likely to be enhanced in regions where species have a wide range of geographic origins, and that the highest levels of fine-scale species richness will be found in communities that have diverse biogeographic composition.

Biodiversity is most commonly characterized by measures of taxonomic diversity, such as species richness. Biodiversity can also be characterized using measures of phylogenetic diversity, based on the variety of different evolutionary lineages (Faith, 1992). Phylogenetic diversity has a high conservation value because it reflects both the evolutionary history of a community and its potential to persist in a changing environment (Sechrest et al., 2002; Forest et al., 2007). Local phylogenetic diversity depends on large-scale and long-term processes such as speciation and immigration (Procheş et al., 2006). For example, Gerhold et al. (2008) showed that in northern Europe, phylogenetic diversity in local communities is associated with the size of the regional species pools that have been built up by species' immigration since the last glaciation.

The aim of the present study is to characterize the fine-scale taxonomic and phylogenetic diversity in alvar grasslands (and associated dry calcareous grasslands) over the entire European distribution of alvar habitats (Sweden, Estonia, northwestern Russia). We have assembled a large set (1220 vegetation plots) of fine-scale (1 m^2) vegetation data and we ask the following questions:

(1) How is the vegetation of dry calcareous grasslands related to large scale environmental and geographic gradients across the Baltic Sea region?
(2) What is the relationship between fine-scale species richness and phylogenetic diversity in dry calcareous grasslands in the Baltic Sea region?
(3) What are the main environmental and climatic factors associated with fine-scale grassland species richness and phylogenetic diversity?
(4) How is the biogeographic composition of the grassland vegetation related to fine-scale species richness and phylogenetic diversity?

2. Materials and methods

2.1. Study area

The study area covers a ca. 200 000 km^2 region (13–30°E, 56–60°N) (Fig. 1) that can be divided into nine distinct grassland regions in Sweden (Öland, Gotland, Götaland), Estonia (Saaremaa,