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Small-scale plant species richness and evenness in semi-natural grasslands respond differently to habitat fragmentation

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ABSTRACT

The study explores whether small-scale species diversity, species evenness and species richness in semi-natural grassland communities are similarly associated with present management regime and/or present and historical landscape context (percentage of different land-cover types in the surroundings). Species diversity, evenness and richness were recorded within 441 50 × 50 cm grassland plots in a 4.5 × 4.5 km agricultural landscape on Öland, Sweden. Recent and historical land-cover maps (years 2004, 1959, 1938, 1835, and 1800) were used to characterize the present and past landscape context of the sampled vegetation plots. Partial regression and simultaneous autoregressive models were used to explore the relationships between species diversity measures (Shannon diversity, richness and evenness) and different explanatory variables while accounting for spatial autocorrelation in the data. The results indicated that species richness was relatively sensitive to grassland isolation, while the response of species evenness to isolation was characterized by a degree of inertia. Because the richness and evenness components of species diversity may respond differently to habitat fragmentation, we suggest that monitoring projects and empirical studies that focus on changes in biodiversity in semi-natural grasslands should include the assessment of species evenness – as a complement to the assessment of species richness. In addition, our results indicated that the development and persistence of a species-rich and even grassland vegetation was favoured in areas that have historically (in the 19th century) been surrounded by grasslands. Information on landscape history should, whenever possible, be incorporated into the planning of strategies for grassland conservation.

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1. Introduction

Species diversity can be divided into two main components: "richness", which represents the number of species in a given area, and "evenness", which represents the variability in species abundances (Magurran, 2004). While some theoretical studies have suggested that there will always be a direct positive relationship between species evenness and species

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richness (e.g., Hill, 1973; Alatalo, 1981), recent empirical studies reveal that the relationship between species richness and evenness is not always positive (Stirling and Wilsey, 2001; Manier and Hobbs, 2006). Species evenness and richness also differ in their responses to local habitat factors (Lundholm and Larson, 2003; Ma, 2005; Wilsey and Stirling, 2007), suggesting that the two diversity components may vary independently and be influenced by different ecological processes. For example, Wilsey and Stirling (2007) showed that, while the richness component of plant species diversity in prairie microcosm communities was sensitive to migration rates, the evenness component was more sensitive to changes in the intensity of competition. Additionally they showed that while species richness may be influenced by the availability of seed sources in the surroundings, species evenness is more likely to be affected by the abiotic and biotic properties of local habitats. Several other studies have concluded that species evenness may show a stronger association (than species richness) with ecosystem stability and function (e.g., Wilsey and Potvin, 2000; Mattingly et al., 2007).

Base-rich and neutral semi-natural (unimproved, extensively managed by grazing or mowing) grasslands are among the most diverse plant communities in Europe and are important habitats for a large number of rare plants and animals (Söderström et al., 2001; Pärtel et al., 2005). Grassland habitats are a priority area for biodiversity conservation (Söderström et al., 2001; Billeter et al., 2008). The abandonment of traditional management practices during the last century has led to the rapid loss of semi-natural grassland habitats, and the increasing fragmentation of remaining habitats represents a major threat to biodiversity (Pärtel et al., 2005; Billeter et al., 2008). Species diversity is regarded as one of the most central criteria in biodiversity assessments and in decisions about management priorities for fragmented semi-natural grasslands (e.g., Söderström et al., 2001). However, the majority of studies on the impact of landscape and environmental variables on plant species diversity in semi-natural grasslands have focussed on the assessment of species richness (e.g., Bruun, 2000; Söderström et al., 2001; Lindborg and Eriksson, 2004; Helm et al., 2006; Cousins et al., 2007; Gustavsson et al., 2007; Öster et al., 2007; Johansson et al., 2008) and species evenness is less often considered in such studies (e.g., Fischer and Wipf, 2002; Foster and Tilman, 2003; de Bello et al., 2006; Aavik et al., 2008).

Plant species richness in fragmented semi-natural grasslands has been shown to be associated with present and past habitat area (Helm et al., 2006; Öster et al., 2007), with present and past habitat connectivity (Bruun, 2000; Helm et al., 2006), with the type and intensity of current management (de Bello et al., 2006; Gustavsson et al., 2007) and with habitat continuity and previous land-use (Gustavsson et al., 2007; Johansson et al., 2008). Species evenness in semi-natural grasslands has been shown to be influenced by management intensity (de Bello et al., 2006), by management continuity over a 40-year period (Aavik et al., 2008), and by changes in management regime (Fischer and Wipf, 2002). It is, however, unclear how species evenness responds to differences in habitat fragmentation because there are few studies that explore these responses in semi-natural grasslands.

Ma (2008) showed in a study of field-edge vegetation that species evenness within 50 m^2 sampling sites was associated with the density of field-edges in the nearby farmland (within the surrounding 36 ha). Species richness, on the other hand, was associated with the pattern of arable land-use at larger scales (within the surrounding 196 ha). In a study of forest communities Vellend (2004) demonstrated that, while habitat continuity and habitat area had a positive influence on both species richness and species evenness, only species richness was negatively related to habitat isolation. Species evenness and richness in semi-natural grasslands may also be expected to differ in their response to landscape properties during the process of habitat fragmentation. If this is the case, both monitoring projects that evaluate the success of restoration projects and empirical studies that focus on changes in biodiversity in semi-natural grasslands should include the assessment of species evenness – as a complement to the assessment of species richness.

In the present study, we investigated the relationships between the small-scale (within 50×50 cm plots) diversity of vascular plant species in semi-natural grassland communities and variables related to the habitat fragmentation (present and past landscape context described in terms of percentages of different land-cover types in the surroundings of the sampled vegetation plots). The objective of the study was to examine whether species diversity, species richness and species evenness in semi-natural grasslands respond similarly to differences in (i) the present management regime and (ii) the present and historical landscape context. If the different components of species diversity do respond independently to variation in management intensity and/or changes in habitat availability and landscape context, there is a risk that restoration and monitoring projects that focus solely on species richness may be providing a biased assessment of grassland diversity and habitat status.

2. Methods

2.1. *Study area*

The 4.5×4.5 km study area (centred on 56°40′49″N, 16°33′58″E) includes the village of Jordtorp and four adjacent villages on the Baltic Island of Öland (Sweden). The bedrock of the area consists of Cambro-Silurian limestone and the overall topography is relatively flat, with a number of low ridges and deposits of glaciofluvial material (Forslund, 2001). The mean annual temperature is 7 °C (July mean = 16 °C, January mean = −1 °C) and the mean annual precipitation is 468 mm (Forslund, 2001).

At the beginning of the 19th century, the landscape in the Jordtorp area was dominated by grasslands (80% of the study area), with arable land surrounding the villages (Fig. 1). The grassland area decreased dramatically during the next two centuries, and the present-day landscape consists of a mosaic of arable fields, deciduous forests and semi-natural grasslands. Semi-natural grasslands represent 8.7% of the present-day landscape in the study area (Johansson et al., 2008) and these grasslands belong to the Natura 2000 habitat type

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