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Context-dependent assembly rules and the role of dominating grasses in semi-natural abandoned sub-Mediterranean grasslands

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ABSTRACT

We investigated fine-scale patterns of trait-based community assembly in calcareous grasslands of the Central Apennines, Italy. We used the habitat template of environmentally contrasting north-facing and south-facing slopes of a mountain valley to understand mechanisms that contribute to species coexistence (i.e. the persistence of diversity) after cessation of previous land use practices. Firstly, we tested late successional dominating grasses (*Sesleria nitida*, *Brachypodium rupestre* and *Bromopsis erectus*) for their ability to serve as biotic filtering effects on the diversity of subordinate species in plant communities. Secondly, we analyzed fine-scale trait-based (i.e. species-level traits related to competition, regeneration, establishment, dispersal, and flowering) community assembly of subordinate species in absence of dominant grass. We found that assembly rules for traits related to the same life-history process were mostly consistent within habitats. Further we established that within habitats the traits related to different life-history processes can show different assembly rules. For example, while generative regeneration traits (seed mass) may show convergence pattern, divergence was inferred for the vegetative (clonal) regeneration traits. Depending on traits, the assembly rules can be similar or contrasting in different habitats. We conclude that our finding of non-random assembly in the majority of investigated traits emphasizes the importance of hierarchical exclusion of strong biotic filters when searching for trait-based assembly rules in abandoned grasslands. Thus, for nature conservation purposes, disturbance appears to be the process that is most important in driving the survival of subordinate species by the exclusion of biotic filters. Subsequently, a multitude of trait-based mechanisms allow for coexistence of the subordinate species. These mechanisms depend on habitats and traits and thus may vary from community to community, indicating that heterogeneous landscapes might support multiple processes of coexistence.

1. Introduction

European grasslands represent a wealth of immense conservation value. Despite the prevailing secondary origin of this vegetation formation in Europe due to a long history of pastoralism and agrarian colonization, their primary nuclei represent the westernmost fragmented fringe of the Eurasian steppe and forest-steppe embedded within the temperate forest biomes (Walter and Straka, 1970; Ellenberg and Leuschner, 2010). These ecosystems support a rich flora and they may develop a very high small-scale species density, mirroring intricate coexistence mechanisms (Wilson et al., 2012). The sub-Mediterranean grasslands of the Apennines, which are included in habitat 6210 by the 92/43/EEC Directive as 'habitat of priority importance', characterize a typical pastoral landscape where grazing was the dominant land use type. Preserving these ecosystems is an urgent task to counteract possible negative effects of changes in land-use such as abandonment imposing threats on local biodiversity (Collins et al., 1998; Poschlod and WallisDeVries, 2002; Balmford et al., 2005; Catorci et al., 2011).

As a consequence of reduction of grazing pressure, some clonal tall grasses tend to prevail and dominate the grassland community through specific plant traits such as tall canopies, extensive lateral spread, litter deposition, and capacity to project shoots through litter and herbaceous cover (Campbell et al., 1992; Catorci et al., 2011). It was reported, for instance, that highly competitive, often late successional grass species of genera such as *Sesleria* and *Brachypodium*

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would negatively influence species diversity in grasslands of Southern and Western Europe (Crofts and Jefferson, 1994; Sebastià et al., 2008; Catorci et al., 2011, 2013).

Although much research has been conducted on the effects of grazing pressure and abandonment on vegetation patterns (e.g. Milchunas and Lauenroth, 1993; Biondini et al., 1998; Frank, 2005), the knowledge of the nature of the relationship between dominants the subordinate co-occurring species is scarce. Aiming to preserve species-rich grassland communities in times of abandonment of traditional land use we need to understand how the subordinate species, which represent most of the plant diversity, can sustain their existence under the new land-use conditions. New recent developments in the study of trait-based assembly rules focus on revealing the background of species coexistence and the strategy of species dealing with novel environmental challenges (Wilson, 1999; Grime, 2006; Shipley et al., 2006; Schamp et al., 2008, 2011; Götzenberger et al., 2012). Our study falls within this scope and aims to contribute to understanding the mechanisms of diversity maintenance in abandoned sub-Mediterranean grasslands. Taking into account the findings of previous studies on the community assembly (Watkins and Wilson, 1992; Wilson, 1999; Bartha et al., 2004), we establish that fine-scale spatial resolution offers the most appropriate scale of study of community assembly rules because of the fine scale of interactions between plants.

In this paper we explore the fine-scale species co-occurrence in calcareous dry grasslands of the *Festuco-Brometea* in a representative pastoral landscape of the Montagna di Torricchio Nature Reserve located in the Central Apennines, Italy, where the pastures have been abandoned over 30 years ago. We use the topographical habitat template of a typical V-shaped valley to compare two contrasting habitats–grasslands on north-facing *versus* south-facing slopes. These habitats differ in site disturbance history as well as in water and nutrient supply (Wellstein et al., 2013).

In our study we target two aims. (1) Firstly, we are asking whether there is spatially explicit dependence between the three late successional, potentially dominating grasses (*Sesleria nitida*, *Brachypodium rupestre* and *Bromopsis erectus*) and the subordinated species in the respective studied grasslands. (2) Secondly, we are seeking assembly rules at fine spatial scales for subordinate species coexisting in grassland communities under exclusion of the dominating grasses.

Ecological theory of assembly rules and evidence from recent field studies show two contradictory streams of reasoning regarding competition-related traits. On one hand, the increase in competition for light, which usually occurs under favorable conditions, could promote divergence in competition-related traits such as specific leaf area (SLA) or plant height and hence demonstrate a mechanism of limiting similarity (e.g. Spasojevic and Suding, 2011). On the other hand, following Keddy (1990), Grime (2006), and supported by recent studies by Violle et al. (2009) and Bernard-Verdier et al. (2012), more favorable conditions (implying enhanced availability of resources) can lead to an assembly of functionally similar species with respect to traits related to the life-history processes of competition and establishment. This phenomenon was also described as trait convergence through mechanisms of equalizing fitness (Chesson, 2000). In comparison, the absence of competitive filters in unfavorable habitats would then allow for trait divergence (see Stubbs and Wilson, 2004). However, one could also argue that functional divergence under such circumstances would be due to other reasons such as facilitation (e.g. Spasojevic and Suding, 2011) or habitat heterogeneity. Some recent studies, however, suggest that both convergence and divergence may be detected for competition- and establishment-related traits associated with a single aspect of life history (e.g. Stubbs and Wilson, 2004; Mason et al., 2011; Gross et al., 2013). Based on these findings and the controversial evidence on the role of traits in grassland assembly, we *predict random pattern (i.e. neither divergence nor convergence) in the competition- and establishment-related traits in either of the investigated habitats* (H1).

As the regeneration traits are more important in environments with frequent disturbance (Klimešová and Klimeš, 2007) we predict *convergence in regeneration traits on the south-facing slope characterized by higher erosion rates* as a consequence of the open grassland canopy and increased evaporation enhancing the localized drought stress (H2). Following Wright and Westoby (1999) and Pakeman et al. (2008) larger seed mass offers an advantage or is more common under drier environmental conditions owing to its reserve effect under drought stress. We therefore expect the constraints on the regeneration niche to be larger on the drought prone south-facing slope and consequently predict that the *seed mass would show trait convergence* (H3).

Further, because of general lack of evidence of the role of regeneration-related belowground traits as well as of flowering phenology in grassland assembly, we shall ask if there are ecologically meaningful patterns for these traits.

2. Materials and methods

2.1. Study area and site selection

Our field sampling was carried out in the Montagna di Torricchio Nature Reserve near Camerino (Province of Macerata, Marche Region, Italy) in the Central Apennines, Italy (Fig. 1) – an area of 317 ha which has been under strict protection since 1970. Previously, the grasslands were managed as pastures. Mean annual precipitation reaches 1250 mm and mean annual temperature is around 11 °C (Halassy et al., 2005). Jurassic-Cretaceous limestone (Ital. 'scaglia rosata') prevails in the area. For this study, we selected two sites with an area of about eight (north-facing slope) and five (south-facing slope) hectare representing the contrasting environmental conditions of the north- and south-facing slopes (Fig. 2 and Table 1). The north-facing slope is covered with a dense, late-successional dry grassland community assigned to the *Seslerio nitidae–Brometum erecti* (Venanzoni and Kwiatkowski, 1995). This association has its core area in the upper montane belt of the Central Apennines. This secondary grassland replaces beech forests which used to cover the north-facing mesic slopes. The dense grassland canopy is interrupted by a mosaic of gaps created by solifluction and presence of rocky outcrops. The south-facing slope hosts open pioneer dry grassland with a scanty cover assigned to the *Asperulo purpureae–Brometum erecti* (Venanzoni and Kwiatkowski, 1995). This association has its core area in the lower montane belt of the Central Apennines; and it is rich in species showing sub-Mediterranean and Apennine distribution ranges. Due to higher erosion rates the soils are poorly developed, shallow and skeletal (Kwiatkowski and Venanzoni, 1994). As indicated by the constituent species, the south-facing slopes could be seen as relatively stable habitat where populations of steppe flora found suitable conditions during glacial periods of the Quaternary and a regional refugium during the forest spread in the Holocene. Finally, the environmental conditions characteristic of the north-facing slope (with favorable conditions of water and nutrient supply) as opposed to south-facing slope (with stressful conditions of water shortage and erosion), provide a well-defined contrasting habitat template to study context-dependent trait-based assembly rules.

2.2. Data collection

In both grassland communities, presence of plant species was recorded along 52 m long topologically circular belt transect of 1040 units of 0.05 m × 0.05 m contiguous sampling units