



## Micro-topographic heterogeneity increases plant diversity in old stages of restored grasslands

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### Abstract

It is a truism in ecology that environmental heterogeneity increases diversity. Supporting field studies are mostly concerned with a large-scale topographic heterogeneity, ranging from a couple of metres to landscape-scale gradients. To test the role of fine-scale micro-topography on plant diversity, we studied the initial vegetation of recently filled (1-year-old), and established vegetation on old (7-year-old) soil-filled channels in an alkali landscape, East-Hungary. We hypothesised that (i) recently filled channels are characterised by a high cover of ruderal species and high species diversity and (ii) high micro-topographic heterogeneity increases the diversity of species and plant strategy types (mixed C–S–R categories) in early stages but later on this effect diminishes. We found that diversity of species and plant strategy types was higher in recently filled channels compared to old filled channels. Micro-topographic heterogeneity had no effect on the studied vegetation parameters in recently filled channels. Conversely, in old filled channels higher micro-topographic heterogeneity resulted in higher diversity and lower cover of the dominant grass *Festuca pseudovina*. Higher micro-topographic heterogeneity resulted in increased ruderality and decreased stress-tolerance, but it did not increase the diversity of plant strategy types. In contrast with former studies, we found that a couple of centimetres of micro-topographic heterogeneity had no effect on vegetation in recently filled channels, but supported a high diversity in old filled channels. An important practical implication of our study is that in grassland restoration projects, micro-topographic heterogeneity has a crucial role in sustaining biodiversity.

### Zusammenfassung

Es ist eine einfache ökologische Wahrheit, dass eine heterogene Umwelt die Diversität steigert. Freilandstudien, die dies unterstützen, betrachten meist großskalige topographische Heterogenität von einigen Metern bis hin zu Landschaftsgradienten. Um die Bedeutung feinskaliger Mikro-Topographie auf die Pflanzendiversität zu überprüfen, untersuchten wir, die anfängliche Vegetation von kürzlich (1 Jahr) verfüllten Entwässerungskanälen und die etablierte Vegetation von alten (7 Jahre) verfüllten Kanälen in einer Alkalilandschaft (Ost-Ungarn). Wir postulierten, dass (i) kürzlich verfüllte Kanäle durch eine hohe Bedeckung von Ruderalpflanzen und hohe Artendiversität charakterisiert sein sollten, dass (ii) hohe mikro-topographische Heterogenität die Artendiversität und die Diversität der Pflanzenstrategietypen (C–S–R-Kategorien) in frühen Stadien steigern sollte,

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während dieser Effekt später geringer wird. Wir fanden, dass die Diversität der Pflanzenarten und Strategietypen bei kürzlich verfüllten Kanälen höher war als bei alten Kanälen. Die mikro-topographische Heterogenität hatte bei kürzlich verfüllten Kanälen keinen Effekt auf die untersuchten Vegetationsparameter. Dagegen resultierte bei alten verfüllten Kanälen eine höhere mikro-topographische Heterogenität in höherer Diversität und geringerer Bedeckung durch das dominante Gras *Festuca pseudovina*. Höhere mikro-topographische Heterogenität bewirkte vermehrte Ruderalität und verminderte Stresstoleranz, aber sie erhöhte nicht die Diversität der Pflanzenstrategietypen. Im Gegensatz zu früheren Studien fanden wir, dass mikro-topographische Heterogenität von ein paar Zentimetern bei kürzlich verfüllten Kanälen keinen Einfluss auf die Vegetation hatte, dass aber eine hohe Diversität in alten verfüllten Kanälen unterstützt wurde. Eine wichtige praktische Schlussfolgerung aus unserer Studie ist, dass die mikro-topographische Heterogenität eine entscheidende Rolle für den Erhalt der Biodiversität in Grasland-Restaurationsprojekten spielt.

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## Introduction

Understanding processes shaping the spatial pattern of vegetation has been in the focus of vegetation science for decades (Newman 1982). In this respect the relationship between environmental heterogeneity and diversity is of crucial importance (Sebastiá 2006; Tamme, Hiiesalu, Laanisto, Szava-Kovats & Pärtel 2010). Heterogeneity of abiotic environment generally supports high species diversity at multiple scales (Lundholm 2009; Stein, Gerstner & Krefl 2014). The niche theory suggests that species with different resource preferences can co-exist in a heterogeneous environment due to niche differentiation (Newman 1982; Tamme et al. 2010; Richardson, MacDougall & Larson 2012). Small-scale environmental heterogeneity is often represented by micro-topographic heterogeneity (Rose & Malanson 2012). Micro-topographic heterogeneity enables diverse germination and establishment conditions for a wide range of species providing safe sites in various quality and quantity (Tilman 1994). Micro-topographic heterogeneity has also several indirect effects on diversity by affecting other environmental variables like soil moisture (Vivian-Smith 1997; Moeslund, Arge, Bøcher, Dalgaard, Ejrnæs et al. 2013), light availability and solar radiation (Hough-Snee, Long, Jeroue & Ewing 2011), soil salt-content (Valkó, Tóthmérész, Kelemen, Simon, Migléc et al. 2014) or nutrient availability (Loiseau, Louault, Le Roux, & Bardy 2005). By creating various micro-sites, micro-topographic heterogeneity is considered to increase plant diversity both in natural (Moeslund, Arge, Bøcher, Nygaard & Svenning 2011) and experimental ecosystems (Vivian-Smith 1997; Biederman & Whisenant 2011).

Although the link between environmental heterogeneity and diversity is a hot topic in community ecology, opinion and review papers have pointed out that most of the published literature focused on the beneficial effects of large-scale (sampling unit bigger than 200 m<sup>2</sup>) environmental heterogeneity on diversity (Stein et al. 2014; Lundholm 2009). There are some fine-scale field studies testing this

relationship (Moeslund, Arge, Bøcher, Dalgaard, Ejrnæs et al. 2013; Moeslund, Arge, Bøcher, Dalgaard, Odgaard et al. 2013), but most of these studies focus on wetlands. Recent reviews found only one experimental and four field studies on fine-scale micro-topography – plant diversity relationships (sampling unit smaller than 200 m<sup>2</sup>; Lundholm 2009). Most of these studies are either experimental ones or focus on restored ecosystems, likely because these systems are more dynamic compared to permanent plant communities. In most cases the effects of micro-topographic heterogeneity were studied only for a short time, thus temporal effects could not be considered. Although in the few cases when temporal patterns were considered, it was found that micro-topographic heterogeneity supports diversity only in the short run in the first few years after disturbance; however, later its effect diminishes (Ewing 2002; Biederman & Whisenant 2011).

There is a growing consensus that trait-based analyses contribute to a better understanding of community assembly processes (Lavorel & Garnier 2002). The competitor–stress–ruderal (C–S–R) classification of plant strategy types (Grime 2002) is frequently used to explore the functional composition of vegetation, reflecting environmental conditions and biotic interactions in plant communities (Hunt, Hodgson, Thompson, Bungener, Dunnett et al. 2004; Cerabolini, Brusa, Ceriani, De Andreis, Luzzaro et al. 2010). Grime (2002) classified species into three main functional groups based on their tolerance to disturbance and stress, i.e. competitors (C), stress-tolerators (S) and ruderals (R). Competitors are generally perennial, large-sized plants with dense canopy structure and high ability of rapid lateral spread. Stress-tolerators are often slow-growing species with a high root-shoot ratio. Ruderals are generally short-lived small-sized herbs with limited lateral spread, characterised by sparse canopy structure and increased rate of seed production (Grime 2002; Kelemen, Török, Valkó, Migléc et al. 2013).

Micro-topography can be a crucial driver of local patterns in soil moisture in habitats located within a few metres

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