Perspectives in Plant Ecology, Evolution and Systematics 17 (2015) 44–53

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

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

Research article

Different effects of elevation, habitat fragmentation and grazing management on the functional, phylogenetic and taxonomic structure of mountain grasslands

Matteo Dainese[a,*], Jan Lepš[b,c], Francesco de Bello[b,d]

[a] Department of Land, Environment, Agriculture and Forestry, University of Padova, Viale dell'Università 16, I-35020 Legnaro, Padova, Italy
[b] Department of Botany, University of South Bohemia, Na Zlate stoce 1, CZ-370 05 České Budějovice, Czech Republic
[c] Institute of Entomology, Biology Centre of Czech Academy of Sciences, CZ-370 05 České Budějovice, Czech Republic
[d] Institute of Botany, Biology Centre of Czech Academy of Sciences, Dukelská 135, CZ-379 82 Trebon, Czech Republic

ARTICLE INFO

Article history:
Received 31 January 2014
Received in revised form
10 September 2014
Accepted 10 September 2014
Available online 19 September 2014

Keywords:
Biodiversity components
Community weighted mean (CWM)
Environmental filtering
Mountain pastures
Plant traits
Rao quadratic entropy index

ABSTRACT

Ecological theory suggests that several nested environmental filters, acting at different spatial scales, shape the assemblages of local plant species. However, it is unclear whether different biodiversity components, that is, taxonomy, function and phylogenetic, respond similarly to these filters. The integration of these different components into coherent and comprehensive analytical frameworks also remains unclear. In this study, we developed an approach to test the relative effects of elevation, habitat fragmentation and grazing management on the functional, phylogenetic, and taxonomic structures of mountain pastures. Thirty summer farms, distributed along an elevational gradient were surveyed in the Italian Alps. Within these farms (around 100 ha), we identified all areas as one of two types of management (intensive or extensive), and we sampled three plots for each area, a total of 180 plots. Using the same mathematical framework, we quantified the functional (FD), phylogenetic (PD) and taxonomic (TD) diversity of each plot. We tested the influences of three environmental filters (elevation, habitat fragmentation and grazing management), using a series of partial regression analyses within a univariate and multivariate framework, as well as specific permutation schemes that accounted for our nested design. We found that elevation, habitat fragmentation, and grazing management affected the community structure, but in different ways. This finding confirmed that these filters operate at different scales and, despite some similarities, have different effects on various biodiversity components. Interestingly, FD was the only component that responded to all three types of predictors. Regarding functional aspects, elevation, as a broad-scale environmental gradient, showed a greater influence on dominant trait values, whereas at finer scales, grazing management had a primary effect on both dominant trait values and diversity measures. Habitat fragmentation showed a primary influence on TD, probably because the effect on dispersal limitations concerned mostly species availability. The hierarchical, multi-faceted approach adopted in this study yielded insights into the factors influencing biodiversity and community assembly processes in mountain pastures, thereby highlighting the importance of considering multiple facets of diversity in assessing the role of environmental filtering in vegetation structure.

Introduction

Biodiversity is a complex, multi-faceted concept that includes not only species diversity but also functional diversity (i.e., the extent of trait differences between species) and phylogenetic diversity (i.e., the extent of diversity in terms of species lineages) (Pavoine and Bonsall, 2011). Therefore, the study of these often complementary components of biodiversity is crucial for the understanding of the structure, composition and dynamics of natural communities (Pavoine and Bonsall, 2011; Webb et al., 2002). For instance, functional and phylogenetic diversity may help us comprehend the response to environmental changes because they capture not only different aspects of a species' resource use and habitat requirements (Cadotte et al., 2009; Suding et al., 2008), but also the accumulated evolutionary history of a community, which could be related to its capacity to adapt to those changes

* Corresponding author. Tel.: +39 0498272674; fax: +39 0498272686.
E-mail address: matteo.dainese@unipd.it (M. Dainese).

http://dx.doi.org/10.1016/j.ppees.2014.09.002
1433-8319/

(Forest et al., 2007; Mace et al., 2003). Moreover, functional and phylogenetic diversity have been suggested as relevant for nature conservation targets because they might ensure the maintenance of ecosystem functions (Devictor et al., 2010), the provision of ecosystem services (Díaz et al., 2007a) and the preservation of the Tree of Life (Mace et al., 2003).

A common idea in the study of ecology is that taxonomic, functional and phylogenetic diversity are positively correlated, that is, accounting for one of these components also accounts for the others. However, recent studies (Cadotte et al., 2013; Pavoine and Bonsall, 2011; Pavoine et al., 2013) suggested that these components might also represent independent aspects of community structure. Indeed, there is an increasing interest in quantifying several facets of diversity within species assemblages (Carmona et al., 2012; de Bello et al., 2006; Devictor et al., 2010) although the degree to which these components of diversity are redundant or complementary is still unclear. In particular, the extent to which taxonomic, functional and phylogenetic components will respond similarly to common environmental filters remains to be clarified. Ecological theory suggests that in addition to stochastic processes (Hubbell, 2001), deterministic factors, such as environmental filtering, shape the assemblages of local species by progressively filtering out maladapted species from the regional species pool to local communities (de Bello et al., 2013; Weiher and Keddy, 1999). Elevational gradients (de Bello et al., 2013; Swenson et al., 2011) and land use (Carmona et al., 2012; Pakeman, 2011; Vandewalle et al., 2014), for example, have repeatedly been identified as filters of community assemblies. Environmental filters should apply mainly to species traits, but such effects are also observed on species diversity and, when traits are phylogenetically conserved, on phylogenetic diversity (Cadotte et al., 2013).

Few studies have explored the relative role of environmental filters in simultaneously shaping all three facets of diversity (taxonomic, functional and phylogenetic). To our knowledge, no study has investigated threatened mountain pastures in the European Alps. These semi-natural grasslands are among the most species-diverse ecosystems in Europe, and they are currently threatened by anthropogenic habitat changes (Dainese et al., 2012). In this context, mountain grasslands are under a dual process of land-use intensification in productive and accessible areas and abandonment in remote areas (Dainese et al., 2012; Spiegelberger et al., 2006), with the consequent fragmentation associated with habitat loss and isolation (Lindborg et al., 2012; Vandewalle et al., 2014). To predict the biodiversity response of these communities to global change, it therefore is important to consider a multi-faceted framework of taxonomical, functional and phylogenetic diversity.

In this study, we developed an approach to test the relative effects of (i) elevation, as a proxy variable of climate filtering, (ii) habitat fragmentation, and (iii) grazing management on the functional, phylogenetic, and taxonomic structures of mountain pastures. These environmental filters are expected to exert a major effect on the community structure of these ecosystems. For instance, elevation (Dainese et al., 2012; de Bello et al., 2013), habitat structure (Schmucki et al., 2012), and land-use management (Wesuls et al., 2012) were previously identified as important drivers of community structure within plant communities. These filters are also expected to act at different spatial scales and, based on the available literature, we expect that despite some similarities, they influence various biodiversity components differently (Carmona et al., 2012; de Bello et al., 2006; Devictor et al., 2010; Vandewalle et al., 2014). Specifically, broad-scale environmental factors, such as elevation, act similarly on the components of taxonomic, functional and phylogenetic diversity. In fact, we expect that a smaller pool of species is evolutionarily adapted to constrained conditions at higher elevation compared to lower elevation. For this reason, we presume a decrease in taxonomic, functional and phylogenetic diversity with increased elevation. We then expect that elevation also strongly acts on the functional structure of communities, in particular shifting the mean trait value of the dominant species ('community weighted mean' [CWM]; Garnier et al., 2004) in local communities across the environmental gradient (de Bello et al., 2013; Weiher and Keddy, 1999), with the selection of a greater number stress-tolerant species under the colder conditions at higher elevations.

When species have been filtered from the regional species pool by broad-scale environmental factors, such as elevation, we expect the increasing influence of local environmental filters, such as grazing management (Adler et al., 2001) and habitat connectivity (Fahrig, 2003). These two sets of filters could affect the biodiversity components differently (Carmona et al., 2012; de Bello et al., 2006; Mayfield et al., 2010; Vandewalle et al., 2014). Recent studies (Carmona et al., 2012; Pakeman, 2011) found a reduction in the functional diversity of species in grasslands caused by the intensification of land use, possibly in response to disturbances, such as grazing. In addition, the effect of such disturbances should be the selection of the assemblages of closely related species (i.e., phylogenetic similarity; Helmus et al., 2010). While these components of diversity could decrease, species diversity has often been found to increase with a moderate increase in disturbance (Grime, 1973). In interpreting the local environmental filters, however, the contingency of grazing management and soil fertility in mountain regions should be considered; that is, extensive pastures are usually located on less productive and less fertile sites (Dainese et al., 2012). Therefore, grazing could create a stronger filter effect that acts similarly on different components of diversity. For instance, the disturbance and resource availability gradients could influence trait differentiation among dominant species, thus favouring the coexistence of species differing in their traits of dispersal and nutrient economy in extensive pastures (Garnier et al., 2007). We also expect a mediation between elevation and grazing management (i.e., lower grazing pressure in high-elevation farms; Dainese et al., 2012) regarding biodiversity components. This could cause the combined effects of elevation and grazing on the assemblage of community structure components. Local factors could even cause further adjustments in the mean of trait values related to resource availability, with increased disturbance selecting for species that have ruderal growing strategies (Grime, 1979).

The effect of homogenization caused by habitat loss and isolation is expected to be the most evident in the taxonomic component (Carlson et al., 2014). Large habitat connectivity is supposed to be associated with a large regional species pool, so focal patches may receive a higher diversity of potential colonists by dispersal (Lindborg et al., 2012; Marini et al., 2012). Trait-based analyses may provide complementary insights into analyses of species diversity, especially plant traits related to either species persistence or dispersal. The ongoing abandonment of less productive and remote grasslands and the consequent fragmentation associated with habitat loss and isolation, acts as filters of species assemblages, based on their ability to persist and their capacity to disperse (Lindborg et al., 2012).

Materials and methods

Study site and sampling

The study area is situated in the Province of Trento (~6200 km^2; NE Italy; WGS84: N 45°43.8′–46°28.3′, E 10°31.9′–11°53.4′) on the southern border of the European Alps. The annual mean temperature is 8.2 °C (7.7–8.5 °C) in the low-elevation grasslands (elevation