Agriculture, Ecosystems and Environment 182 (2014) 96–105

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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

Changes in trait divergence and convergence along a productivity gradient in wet meadows

Marta Carboni[a,b,*], Francesco de Bello[a], Štepán Janeček[a], Jirí Doležal[a], Jan Horník[a], Jan Lepš[c], Triin Reitalu[d], Jitka Klimešová[a]

[a] Institute of Botany, Academy of Sciences of the Czech Republic, Section of Functional Ecology, Dukelská 135, 37982 Třeboň, Czech Republic
[b] Laboratoire d'Ecologie Alpine, Université Joseph Fourier/CNRS Grenoble, BP 53, 2233 Rue de la Piscine, 38041 Grenoble Cedex 9, France
[c] Department of Botany, Faculty of Science, University of South Bohemia, Na Zlaté stoce 1, 37005 České Budějovice, Czech Republic
[d] Institute of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086 Tallinn, Estonia

ARTICLE INFO

Article history:
Received 18 August 2013
Received in revised form 6 December 2013
Accepted 9 December 2013
Available online 30 December 2013

Keywords:
Competition
Clonal traits
Limiting similarity
Niche differentiation
Species coexistence
Environmental filtering

ABSTRACT

Ecological theory predicts that species coexisting locally may either be functionally more dissimilar than expected by chance due to niche differentiation ('trait divergence'), or rather be functionally similar given that species bearing traits associated with low competitive ability are likely to be excluded ('trait convergence'). How the importance of trait divergence and convergence varies with productivity and depending on different plant traits still remains controversial. However assessing the effect of site productivity on meadow species assembly can help defining proper management practice for these ecosystems. We sought evidences for trait convergence and divergence across a productivity gradient over 21 wet meadows in Železné hory Mts. (Czech Republic), considering 13 plant traits. In each meadow, we recorded species composition in four 1 m^2 plots divided into 100 subplots, and different environmental parameters and site characteristics linked to productivity (standing biomass, soil water table and soil nutrients content). Species spatial aggregation within plots (calculated by the *V*-score metric on the 100 subplots per plot averaged across all plots in each meadow) was correlated with trait dissimilarity between species in a rather limited number of cases. Significant divergence was observed when traits were considered in combination or when using phylogeny as a proxy of functional similarity. Moreover, plot level patterns of trait divergence and convergence depended on local environmental characteristics. Specifically, for several of the traits studied (e.g. lifespan, combined traits) there was evidence that functional divergence of species decreased with increasing productivity. Overall from these results at fine scale we cannot rule out neutrality, but, where significant, patterns suggest stronger effects of niche differentiation between coexisting species (trait divergence) rather than convergence of functionally similar species. Nevertheless our results also support the view that increased productivity, coupled with intense competition for resources (mainly for light), can lead to the coexistence of more functionally similar species. This is relevant because biodiversity enhancement is generally achieved by maintaining low productivity in these meadows. In general our study gives insights on how species coexistence is related to life history traits and environmental variation, which is also relevant for the conservation and management of species-rich meadows.

1. Introduction

Semi-natural grasslands of temperate Europe are very species rich ecosystems (Wilson et al., 2012). In particular, wet meadows are considered threatened biodiversity hotspots (Lepš, 1999). These systems have historically been managed by humans through regular and frequent grazing or mowing. The traditional management regime, together with other ecological factors, has contributed to the coexistence of a high number of species. However large areas of meadows are nowadays being abandoned or heavily fertilized, because the traditional extensive management is no longer cost-effective (de Bello et al., 2010; Doležal et al., 2011). Both these practices generally lead to a loss in biodiversity and altered species interactions (Poptcheva et al., 2009; Klimešovà et al., 2011). Hence, the management of semi-natural meadows for the preservation of

* Corresponding author at: Institute of Botany, Academy of Sciences of the Czech Republic, Section of Functional Ecology, Dukelská 135, 37982 Třeboň, Czech Republic.

E-mail addresses: marta.carboni@gmx.net, marta.carboni@uniroma3.it (M. Carboni).

0167-8809/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.agee.2013.12.014

biodiversity in Central Europe depends on a better understanding of the mechanisms determining species coexistence.

The question of why so many species can coexist in small areas has long been at the center of ecological research inspiring many theories of plant community assembly (Weiher and Keddy, 1995; Zobel, 1997; Chesson, 2000; Ackerly, 2003; Gotzenberger et al., 2012; Wilson and Stubbs, 2012). Specifically, community assembly is thought to be regulated by the degree to which species share or do not share adaptations (Pavoine and Bonsall, 2011). This can be measured with the help of functional traits that have predictive value for plant strategies. Increased knowledge of functional ecology and availability of data on species functional traits through large databases has advanced this field of research (Kleyer et al., 2008; Klimešová and de Bello, 2009). Hence, functional trait composition is increasingly used to infer processes underlying community assembly, in an attempt to find predictive rules governing community structure and regulating biodiversity in the face of global change (Cornwell and Ackerly, 2009; Mason et al., 2011; Wilson and Stubbs, 2012).

There is general agreement that habitat filtering in heterogeneous landscapes (e.g. along an environmental gradient) will lead to spatial aggregation of functionally similar species ('trait convergence') because of shared ecological preferences for an environmental condition (Cornwell et al., 2006; Willis et al., 2010). However, in locally homogenous sites (i.e. with little within-site environmental variability) where all coexisting species can tolerate the specific environment in the absence of neighbors, further spatial aggregation patterns should be mainly driven by biotic interactions such as competition and facilitation. Classical *niche theory* predicts that species coexisting locally should be functionally dissimilar to promote niche differentiation ('trait divergence') (Weiher and Keddy, 1995; Kraft et al., 2008). However the opposing *weaker competitor theory* postulates the coexistence of functionally similar species given that those species bearing traits associated with low competitive ability are likely to be excluded (resulting in a pattern of 'trait convergence') (Grime, 2006; Mayfield and Levine, 2010). Past empirical studies have found evidence for both mechanisms depending on the community type, the studied traits, the spatial scale and/or the methods used, leading to an on-going lively debate (Kraft et al., 2008; Cornwell and Ackerly, 2009; Freschet et al., 2011; Mason et al., 2011; Bernard-Verdier et al., 2012; Spasojevic and Suding, 2012).

The ability to detect trait divergence or convergence may strongly depend on the specific trait or trait combination under consideration, given that contrasting assembly processes may occur for different niche axes (Cavender-Bares et al., 2004). In fact, different selective pressures may operate for different traits. Mayfield and Levine (2010) argued that convergence can be expected for traits linked to competitive ability such as height, whereas traits linked exclusively to resource exploitation such as soil preference are more likely to drive divergence. Conversely, Grime (2006) noted that different patterns of trait variation should be expected depending on whether we consider regenerative (e.g. seed mass) or productivity-related traits (e.g. SLA), hypothesizing that divergence is to be expected especially for the former. Coexistence of species is, therefore, the result of a balance between traits limiting similarity and those promoting it, which still requires further clarification.

In this context, the discussion on whether to focus on single traits or on trait combinations to measure similarity is particularly relevant (Swenson and Enquist, 2009; Kraft and Ackerly, 2010). Multivariate combinations of traits hold promise of a better quantification of functional similarity among coexisting species. Under the assumption of trait conservatism (i.e. that closely related species share similar traits), phylogenetic relatedness is often used as a multivariate proxy of functional similarity (Blomberg and Garland, 2002). This approach also overcomes the uncertainty linked with selecting the traits which are most influential to determine species' responses to the environment. Hence the literature regarding the phylogenetic structure of communities is rapidly accumulating, albeit often with controversial results found in different studies (Webb, 2000; Cavender-Bares et al., 2006; Kraft et al., 2007; Vamosi et al., 2009; Reitalu et al., 2013). Studies applying both functional and phylogenetic approaches alongside are increasing (Cadotte et al., 2009; Swenson and Enquist, 2009; Kraft and Ackerly, 2010; Bernard-Verdier et al., 2013; Mason and Pavoine, 2013). In fact, when applied in combination, these two approaches can give far more insight into the processes that determine community assembly.

Selective pressure for niche differentiation can vary with many factors, including local competitive intensity linked to productivity and natural disturbance. Traditional *niche differentiation theory* leads to assume that trait convergence should be expected in regions of strong abiotic stress, whereas trait divergence should be promoted in regions characterized by strong competitive pressure (Weiher and Keddy, 1995). For example Mason et al. (2011) found that greater standing biomass was associated to less niche overlap of coexisting species (more niche differentiation with competitive intensity). In contrast, Grime (2006) suggested that more favorable and productive conditions should lead to the assembly of more functionally convergent communities (Pakeman, 2011), more in line with the *weaker competitor theory*. According to Grime (2006) divergence should rather be a consequence of disturbances such as grazing or mowing (Klimešovà et al., 2010). Overall, there is still on-going controversy on how the importance of trait divergence and convergence varies across productivity gradients and how it depends on different vegetative and regenerative traits.

In synthesis, while there is general agreement that habitat filtering will lead to the coexistence of species bearing similar traits, the debate is not yet settled on whether biotic filters imposed by competitive and facilitative interactions will result, locally, in patterns of trait divergence or convergence. Here we identify four reasons that contribute to this unresolved controversy: (1) the amount of environmental heterogeneity providing for habitat filtering depends on spatial scale; (2) contrasting assembly processes can occur for different niche axes so that results may vary depending on traits considered; (3) using single traits, trait combinations or phylogeny as proxies for species similarity can lead to different conclusions; (4) the importance of niche differentiation processes may vary with environmental conditions, productivity and species richness. Consequently in this work we take all four these aspects into account by seeking evidence for convergence and divergence of traits across a productivity gradient spanning 21 wet meadows in the Czech Republic.

Specifically, we address the following questions:

(1) Does the choice of *spatial scale* influence the degree of trait convergence or divergence of coexisting species?
(2) Does the detected convergence and divergence in the community depend on the *traits* and on the *trait-combinations* considered?
(3) Is the functional divergence within the community related to *productivity and to species richness gradients*?

By addressing these questions we can explore implications for community structure and functioning and draw conclusions on favorable conditions for the preservation and enhancement of biodiversity in wet meadows.