Plant clonal traits, coexistence and turnover in East Ladakh, Trans-Himalaya

Koexistence a směna klonálních vlastnosti rostlin Východního Ladáku (Trans-Himálaj)

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To what extent does plant clonality contribute to the assemblage of species in communities? Two apparently contrasting, and largely untested, hypotheses envisage the potential role of plant clonal traits in community assembly: (i) environmental filters constrain coexisting species to have functionally similar traits (i.e. trait convergence); (ii) niche differentiation selects for functionally dissimilar species (i.e. trait divergence) allowing them to exploit different spatial and temporal niches. These hypotheses are assessed using a large dataset of 369 plots (100 m^2) covering altitudes between 4100 and 5800 m a.s.l. and including the major vegetation types found in Ladakh, NW Himalaya. Patterns of clonal traits, coexistence and turnover were assessed using a functional diversity partitioning framework in the context of different null models. Functional diversity was expressed both for morphologically delimited clonal growth forms (17 categorical growth forms) and for functionally delimited clonal characters (combining 16 different traits differentiating the 17 growth forms). PERMANOVA revealed that both α (within-plots) and β (between-plots) functional diversity varied across environmental conditions and vegetation types highlighting a filtering effect on clonal traits. Alpha diversity, however, was more stable across habitats than β diversity. Despite the significant turnover of clonal traits across habitats, most of the diversity of clonal traits was found within plots, with a higher trait divergence than expected by chance, which suggests that niche differences determine species coexistence. While both trait convergence and trait divergence were detected, convergence was stronger when using null models that shuffled all species in the regional pool across plots and functional diversity expressed in terms of different clonal growth forms. Divergence, in contrast, was detected mostly when using null models that shuffled species cover across species co-occurring in given plots and considering functional diversity in terms of clonal traits. By detecting both trait convergence and trait divergence this study supports both initial hypotheses and brings new evidence on the relevance of clonal traits as a function of species that both inhabit different environments and coexist.

K e y w o r d s: abiotic and biotic factors, functional traits, neutral theory, limiting similarity, Himalaya, trait divergence and convergence

Introduction

Species differ in their ecological functions and therefore are able to inhabit different environments and coexist (MacArthur & Levins 1967, Weiher & Keddy 1995, Grime 2006).

Such an ecological differentiation between species can be assessed in terms of their functional traits, which are characteristics of organisms with a demonstrable link to the organism's functions (Diaz et al. 1998, Mason et al. 2007, de Bello et al. 2010b). Among the different traits of plants, clonality (i.e. result of the vegetative growth of organs producing potentially independent vegetative offspring) remains largely unexplored as, rightly or wrongly, it is often considered by researchers as difficult or time-consuming to measure (Klimešová & de Bello 2009). Evidence is accumulating, however, that clonal traits might play a considerable role in the adaptations of species to environmental conditions (Grace 1993, Klimeš 2008, Sosnová et al. 2010) and for species coexistence (Wildová et al. 2007, Laanisto et al. 2008, Moora et al. 2009, Zobel et al. 2010, Doležal et al. 2011, Klimešová et al. 2011c).

Knowledge of the ecological importance of clonal traits is accumulating, especially thanks to the dedicated work of few specialists, among whom, Leoš Klimeš' contribution is outstanding (see e.g. http://clopla.butbn.cas.cz), especially for the largely unexplored Flora of Ladakh (http://www.butbn.cas.cz/ladakh/checklist.html). Among his seminal works, Leoš shows how basic broad categories of clonality (e.g. clonal vs non-clonal, splitters vs integrators) changes with altitude and other environmental gradients in the highly constraining conditions of the Himalayas (Klimeš 2003). Also, species from contrasting habitats have different clonal growth forms (with both habitat preference and clonal forms being phylogenetically conserved; Klimeš 2008). These findings indicate the importance of environmental factors as 'filters', i.e. selecting for or against species with given clonal traits (or, at least reducing the probability of species persisting in given environmental conditions). The underlying theory is that environmental filtering selects for functionally similar species in a given habitat (i.e. trait convergence), which results in a functional turnover among environments (Diaz et al. 1998, Cornwell et al. 2006, Grime 2006, de Bello et al. 2009).

The first studies by Leoš Klimeš were further complemented by a recent paper by Klimešová et al. (2011b) who, after a more detailed classification of clonal growth forms from Ladakh, show changes in clonal growth forms across different habitats. However, their study highlights another potential ecological role of clonal traits in plant communities. There is more of a turnover in the proportion of clonal traits across communities than in the range of traits (Klimešová et al. 2011a). These authors, therefore, hypothesize that almost the whole range and diversity of clonal organs will usually occur within communities, providing species richness is not very low. Taken together, these ideas actually advocate a role of clonal traits in allowing species to exploit different niches thus maintaining the coexistence of species (Wildová et al. 2007, Laanisto et al. 2008, Moora et al. 2009, Zobel et al. 2010). The underlying theory is that niche differentiation cause species to be functionally different in order to coexist (trait divergence; Stubbs & Wilson 2004, Mason et al. 2007, Gross et al. 2009, Mayfield & Levine 2010, Schamp et al. 2011).

In this study, using functional diversity partitioning (de Bello et al. 2009), the patterns of coexistence of clonal traits and turnover across extreme vegetation types in East Ladakh, in the Trans-Himalayan region, are elucidated. Little is known about how clonal traits influence species assembly and what is the response of clonal functional diversity (the dissimilarity in traits between species; referred to as 'FD' hereafter) to the environment, particularly in extreme habitats. First the hypothesis that almost the whole range and diversity of clonal traits can be often found in coexisting species was verified. The patterns

of observed FD were then assessed against those obtained by chance (i.e. from null models), in order to determine the main drivers of clonal trait assemblage. It was hypothesized that these analyses would reveal the extent to which the assembly of species based on clonal traits could be driven by contrasting ecological processes (environmental filtering vs niche differentiation). Finally, these hypotheses were tested both for morphologically delimited clonal growth forms (17 categorical growth forms) and functionally delimited clonal traits (combining 16 different characters differentiating these growth forms). Different clonal growth forms usually share some of these 16 traits (e.g. a given lateral spread might be achieved by morphologically different organs like rhizomes and roots with adventitious buds). Because clonal traits are directly related to space occupancy strategies, the expectation was that they will show higher divergence between coexisting species than in clonal growth forms, which might overlap in their ecological functions.

Methods

Study area

The study area was situated in the eastern part of Ladakh, Jammu and Kashmir State, India (32°41.5'–33°59.7'N, and 77°47.0'–78°33.4'E). It covers a total area of 6912 km^2 delimited by the Eastern Karakorum Range in the north and the Great Himalaya Range in the south, forming the south-westernmost extension of the Tibetan Plateau and including several large brackish lake basins without external drainage. The altitude ranges from 4180 m (bottom of the Indus River Valley) to 6670 m (Lungser Kangri Peak) with vascular plants occurring up to 6060 m a.s.l. (near snowline). Ladakh lies in the rain shadow of the Himalayas, which poses a barrier to seasonal monsoons. The climate is therefore generally arid with mean annual precipitation as low as 50–100 mm (Hartmann 1983, Wang 1988), although there is no official available climatic station located in this area. Evaporation exceeds precipitation at lower and middle altitudes. The few climatic data available for high altitudes in Eastern Ladakh suggest a mean annual temperature of around 0 °C. The mean monthly temperature rises above 0 °C only from June to August and winter temperatures can drop below –30 °C (Klimeš & Doležal 2010). The substrate ranges from siliceous rocks to calcareous and saline sediments.

Vegetation data

The field data were collected by nine expeditions each lasting four to seven weeks, from 1998 to 2003, and in 2005, 2008 and 2009. The time of sampling always corresponded with the peak of the vegetation season, which lasts from late July to mid-August in this area. Thus, it is likely that some early growing ephemeral plants were no longer visible. The 369 plots, each 100 m^2 in size, were selected to include all the physiognomically different vegetation types in the area, while avoiding places devoid of vascular plants (very unstable slopes, glaciers, lakes and extremely high altitudes). In each plot, species composition was recorded and species cover visually estimated using different classes (< 5%, 15%, 30%, 60% and 80%). TWINSPAN analysis (Hill & Šmilauer 2005) was used to classify the floristic composition of plots into different vegetation groups. The resulting vegetation groups were: (i) alpine meadows; (ii) vegetation on screes; (iii) steppes; (iv)

subnival vegetation; (v) animal resting places; (vi) shrubby vegetation; (vii) salt marshes and (viii) vegetation near water bodies. The vegetation cover ranges from around 10% (steppes dominated by several *Artemisia* and *Stipa* species) to 100% (alpine meadows dominated by *Kobresia* and *Carex* species). For more details of these vegetation types see Dvorský et al. (2011) and Electronic Appendix 1. Each plot was characterized by different environmental variables: altitude (measured using an altimeter); slope (three categories); soil moisture (three categories); soil salinity (three categories); soil stability (three categories) and percentage of rock, sand, loam and silt, which were estimated to an accuracy 10%. PCA, with centring by mean of each environmental variable, was used to characterize the main axes of environmental differentiation between plots. Two axes were retained (see Electronic Appendix 2; with eigenvalues 1.94 and 1.59 respectively)

Trait diversity

The Rao quadratic entropy index of diversity, expressed in terms of equivalent numbers of species (Ricotta & Szeidl 2009, de Bello et al. 2010a), was used for partitioning functional diversity into α-, β- and γ-diversity components (i.e. within-plots, between-plots and overall diversity, respectively). This index expresses the sum of dissimilarities between pairs of species, weighted by species relative abundances (see Ricotta & Szeidl 2009 and de Bello et al. 2010a for details). The Rao index of diversity (Rao 1982, Lepš et al. 2006) for α (i.e. within-plots) FD can be expressed as:

$$FD_{Rao} = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} \cdot p_i \cdot p_j$$

with S being the number of species in a plot and p_i expressing the relative species abundance in a plot (if all species are equally abundant $p_i = 1/S$). The parameter d_{ij} expresses the dissimilarity between each pair of species i and j and varies from 0 (two species have exactly the same traits) to 1 (two species have completely different traits). It should be noted that this index is a generalization of the Simpson index of species diversity, so that if all species in a plot are functionally different (i.e. if $d_{ij} = 1$ for all pairs of species, which is unlikely) then functional diversity is equivalent to species diversity. At the same time the FD_{Rao} is not trivially correlated with species diversity so that their correlation can be assessed across different species assemblages (Lepš et al. 2006).

The partitioning of FD into α, β and γ diversity was computed according to Ricotta & Szeidl (2009) and de Bello et al. (2009, 2010a). In this way, the FD was computed for each plot (α) and for the whole region (γ). Beta diversity (i.e. between-plots diversity) was then calculated as β = (γ–α) × 100/γ (Ricotta 2008, de Bello et al. 2010a). According to this formula, β diversity summarizes the proportion of between-plot FD with respect to the total FD. This partitioning was computed for the whole region and for each pair of plots. The β diversity for each pair of plots was used to determine the effect of habitat conditions on trait turnover using PERMANOVA (see below). To obtain an accurate partitioning of α and β diversity, a correction was applied based on equivalent numbers (Jost 2007), which can be used also in the context of the Rao index (Ricotta & Szeidl 2009, de Bello et al. 2010a). This involves transforming α and γ as $1/(1–FD_{Rao})$.

Two general approaches were used for calculating d_{ij} in FD: (i) that based on clonal growth forms of species ('GF', species are grouped into functionally similar units) and (ii) by using various clonal traits (Electronic Appendix 1). Both approaches were applied using both species presence/absence only and species relative abundances. The GF approach was applied using the growth forms identified by Klimešová et al. (2011b) for the flora of Ladakh. Among the 20 groups defined by Klimešová et al. (2011b), 17 were represented in this dataset. With the GF approach the number of groups in a community (GF richness, i.e. 'GFrich') and the diversity of GF in a community ('GFdiv') were calculated, with GFdiv that corresponds to calculating the Simpson index where each group is considered as a species with its abundance determined by total the cover of all species belonging to that group.

The second approach ('traits') involved calculating the dissimilarity between each pair of species in the dataset, using 16 clonal traits. These traits were selected as those that underlie the differentiation between the GF selected (so that a dendrogram based on these traits would largely produce the different groups considered). In this way, all species within a given GF have exactly the same trait information while species among groups differ in at least one trait. The 16 traits therefore could be used to differentiate the different GFs, as illustrated by the classification tree presented in Klimešová et al. (2011b). For each species, every trait was binary coded as zero or one, depending on whether the species had or did not have a given trait. To compute the dissimilarity based on these 16 traits the Euclidean distance based on the whole set of traits was used; the resulting distance was then standardized between zero and one. The FD 'traits' computed with the Rao index did not produce markedly different values when including, or not, species relative abundance (with the exception of the results presented in Table 1). Therefore, in this study only the results obtained for species cover data are shown.

Null models

Different null models were used to compare the recorded values of clonal trait diversity with those expected by chance. First the relative abundance of each trait within each vegetation type was determined (Electronic Appendix 1). A randomly simulated trait abundance was computed by shuffling the total cover of species in all plots within a given vegetation type (999 randomizations per trait and vegetation type). This analysis shows if, for a given vegetation type, the relative abundance of traits differs by chance, that such traits are an adaptation to the environmental conditions prevailing in that vegetation type.

For the second and third null models, for each plot (here an assemblage of coexisting species) 999 simulated species assemblages expected by chance were generated. For the second approach, these simulated assemblages had the same number of species and total cover as in the observed plots, while the species identity was randomly selected among the whole pool of species in the dataset (this roughly corresponds to null model no. 3 discussed in Gotelli 2000). With this null model the case that each species in the region could be found in all plots, while assuming different carrying capacities across plots (de Bello et al. 2009), were simulated. Comparing observed vs simulated FD patterns with this null model is expected to maximize the importance of environmental filtering in determining clonal trait diversity.

Table 1. – PERMANOVA results showing the effect of vegetation type (TWINSPAN groups) and multiple environmental conditions (first two axes of the PCA in Electronic Appendix 1) on α and β functional diversity components. In the PERMANOVA permutations of α and β diversity values were used to test the significance of the explanatory variables. Environmental conditions were nested within vegetation type, which already accounts for differences in habitats between plots. The results give, for each model, the variance explained by each factor and the corresponding P-value. Different PERMANOVAs were run for the different facets of functional diversity considered (α and β diversities), expressing functional diversity in terms of clonal growth forms vs traits and considering, or not, species relative abundance.

	Clonal growth-form richness		Clonal growth-form diversity		Clonal traits – only presence/absence		Clonal traits – with species abundances	
	R^2	P	R^2	P	R^2	P	R^2	P
Beta diversity:								
Vegetation type	0.0738	0.012	0.0530	0.014	0.0640	0.022	0.0363	0.012
PCA axis1	0.0236	0.013	0.0181	0.015	0.0177	0.025	0.0262	0.011
PCA axis2	0.0076	0.072	0.0047	0.182	0.0039	0.165	0.0052	0.116
Total explained	10.5%		7.6%		8.5%		6.7%	
Alpha diversity:								
Vegetation type	0.0250	0.893	0.0196	0.713	0.0335	0.502	0.0501	0.032
PCA axis1	0.0001	0.732	0.0009	0.617	0.0031	0.245	0.0150	0.021
PCA axis2	0.0002	0.724	0.0015	0.568	0.0003	0.890	0.0020	0.324
Total explained	2.5%		2.2%		3.7%		6.7%	

For the third approach, null plots were simulated by randomizing species covers within each sampled plot. In this way not only the number of species in a plot and the total cover (as in the second randomization) were kept constant, but also the identity of co-occurring species. The expectation is that all the species present in a plot are adapted to the within-plot environmental conditions but their abundance ranking will be dependent on the niche partitioning existing at the plot level (Mason et al. 2011) and more specifically it will reveal those biotic ecological processes governing niche differentiation (Mayfield & Levine 2010).

To evaluate the results of the second and third null models a standardized effect size (SES; Gotelli & McCabe 2002): SES = (observed FD – mean of expected FD)/standard deviation of expected FD, was computed. SES > 0 suggests the prevalence of trait divergence and SES < 0 suggests trait convergence in both approaches. The SES was calculated for each plot based on the whole data set (where the mean of observed FD values was for all plots). The statistical significance of the assembly patterns was based on the number of times the observed FDcomm values were lower or higher than the expected FD values. SES > 1.55 and SES < 1.55 generally indicate significant departure from non-random patterns in a one tailed p-test, where the observed FD values were higher, or lower, than the 5% of null communities.

Finally permutational multivariate analysis of variance using distance matrices (PERMANOVA; Anderson 2001) was used to assess the effect of habitat conditions on FD components. In particular, tests were designed to assess the effect of vegetation type (TWINSPAN groups) and multiple environmental conditions (first two axes of the PCA in Electronic Appendix 2) on α and β diversities. In the PERMANOVA randomizations of α- and β-diversity values (with the second expressed as pair wise plot diversity; see the Trait diversity section above) were run to test the significance of the explanatory variables.

This test assessed whether, despite random noise, α and β diversities differed significantly between vegetation types and, within each vegetation type, according to major environmental conditions. Environmental conditions were nested within vegetation type, which accounts for differences in habitats between plots. The function "adonis" in the package "vegan" in R (R Development Core Team 2009) was used to compute PERMANOVAs.

Results

The proportion of given functional clonal trait in the flora was relatively constant across vegetation types (Electronic Appendix 1). For example, the proportion of non-clonal species with a perennial main root (first line in Electronic Appendix 1) ranged from 27 to 42% across the different types of vegetations. Nonetheless the abundance of traits was often higher or lower than expected by chance, indicating non-random assemblages of species in terms of their traits across different vegetation types.

Functional diversity of clonality tended to increase with species richness (number of species per sample; Fig. 1). This increase was more marked in terms of number of clonal growth forms ($r = 0.77$) and their relative dominance ($r = 0.57$) than FD based on different clonal traits ($r = 0.41$). All these relationships tended to reach a certain level of saturation, with the highest values of FD recorded in plots with low numbers of species.

The partitioning of FD into α-, β- and γ components (Fig. 2) revealed that α diversity made up a relatively high proportion of the total diversity, especially when FD was based on different clonal traits. This pattern was detected in spite of a strong species turnover between plots (taxonomical β diversity was around 80% of γ; not shown) and support the hypothesis that a large proportion of the existing trait diversity in a region can be found at the scale of coexisting species. A lower proportion of α diversity was detected when FD was based on growth forms instead of species' clonal traits and especially when based on the relative abundance of each group.

Of the components of FD, β diversity varied more markedly than α diversity (Table 1) across vegetation types and along different environmental factors (see summary in Fig. 2). Results of the PERMANOVA indicated that β diversity between pairs of plots was partially explained (up to around 10% of total variability) by vegetation types and different environmental factors (first two PCA axes in Electronic Appendix 2), which indicates a significant functional turnover between vegetation types and, within each vegetation type, according to different environmental factors. The turnover was more marked, and better explained by growth form based FD than turnover of trait FD (Fig. 2 for a summary and Table 1 for details). Differences in α diversity between plots were little affected by vegetation type and environmental factors (Fig. 2 and Table 1), indicating a relatively stable α diversity in different habitats. When based on FD in terms of traits, the response was generally more marked, with higher α diversity in scree vegetation (not shown).

The patterns in species assembly based on clonal traits (Fig. 3) show the importance of non-random processes in species assemblages. Both trait convergence and trait divergence had an effect. Interestingly, convergence was mainly detected in the diversity of clonal growth forms (especially at low levels of species diversity) and when using null models based on all the species in the regional pool. Divergence, in contrast, was detected mostly when FD based on different traits was used and null models that shuffled species cover between species coexisting within a given plot.
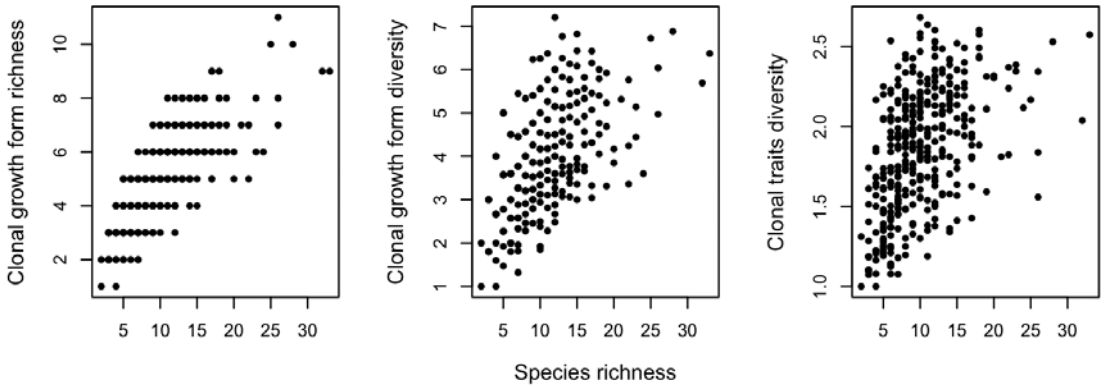
Fig. 1. – The number of species (species richness) in a community and its increase with α functional diversity in terms of clonal traits and clonal growth forms. From left to right the panels refer to (i) richness of clonal growth forms, i.e. number of growth forms after Klimešová et al. (2011a) (ii) diversity of clonal growth forms, in which the diversity is expressed in terms of the evenness (1 over Simpson dominance) of growth forms and (iii) diversity of traits based on 16 traits (i.e. those in Electronic Appendix 1).
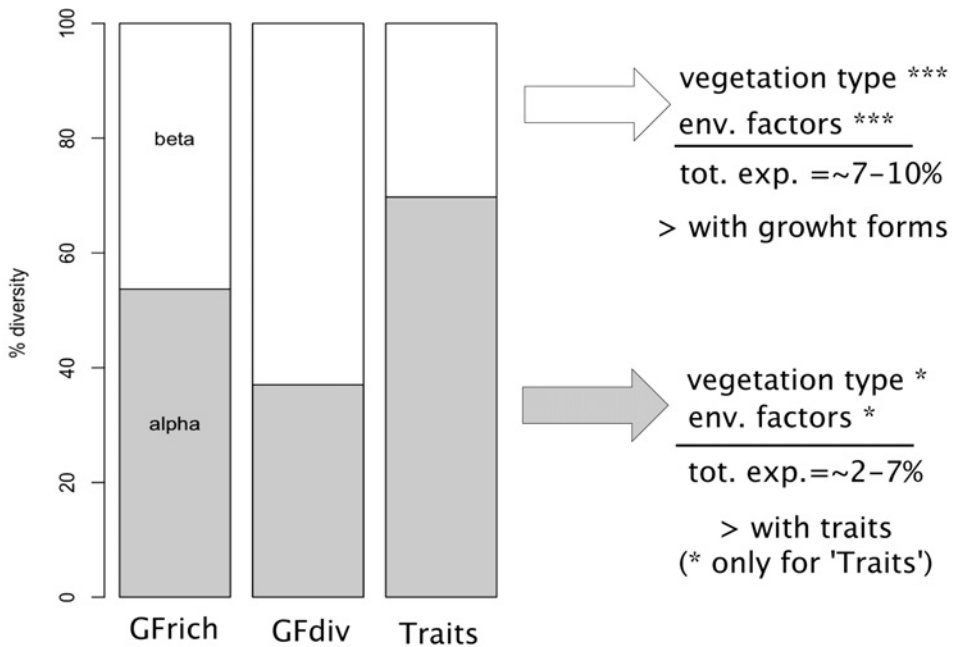

Fig. 2. – Amount of functional diversity (FD) contained (on average) within-plots (α) over the diversity recorded for the whole region (as a percentage over γ). According to this formulation, the β FD summarizes the proportion of between-plots FD with respect to the whole regional FD. FD was computed, as in Fig. 1, for number of clonal growth forms (GFrich) and for the diversity of growth forms (GFdiv) based on 16 clonal traits (Traits). The text on the right summarizes the results presented in Table 1 on the effect of habitat conditions on α (after the grey arrow) and β diversities (after the white arrow). It indicates whether vegetation type and different environmental factors (PCA axes from Electronic Appendix 2) influence the response of α and β diversity (number of asterisks denotes significance levels; the total explained variability is also approximated; see Table 1 for specific values). It also indicates whether the response was more marked in terms of FD based on growth forms or on clonal traits.
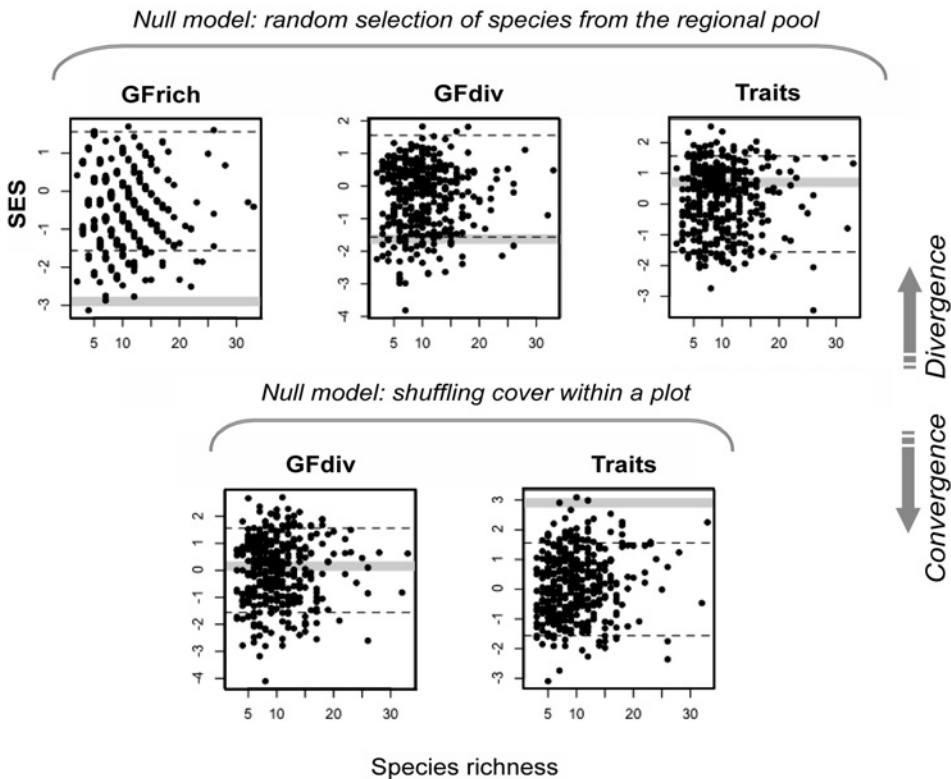
Fig. 3. – For each plot an observed and expected α functional diversity (FD) value was calculated. A standardized effect size, i.e. SES was used to detect deviation of a community from expected. SES > 1.5 indicates significant functional divergence, SES < 1.5 indicates significant functional convergence. Two groups of null models were run: (i) sorting species randomly from the total pool of species in the region, and (ii) randomizing only species cover among the already coexisting species. As for previous figures, FD was then calculated based on clonal growth forms (richness and diversity) and 16 traits (those in Electronic Appendix 1). SES values are given for each plot (points) and the whole dataset (grey line).

Discussion

By finding support for both initial hypotheses, this study brings new evidence on the relevance of clonal traits as a function of species that both inhabit different environments and coexist together. In particular it is shown that clonal traits are important ecological attributes that drive species assemblage in response to both environmental filtering (resulting in trait convergence) and niche differentiation (resulting in trait divergence).

An increasing number of studies (Cornwell et al. 2006, Grime 2006, Mason et al. 2007, de Bello et al. 2009, Thompson et al. 2010) demonstrate how coexisting species tend to converge in their functional traits (i.e. to be more similar than expected by chance), reflecting shared ecological tolerances to the prevailing environmental conditions at a site. These patterns were observed in the present study, especially in terms of clonal growth forms and

low species diversity in a plot. As a consequence of such habitat filtering, a significant functional turnover between different vegetation types was observed, albeit low. Altogether these patterns advocate unequivocally that clonal traits have a role as adaptations to environmental conditions, which is certainly not novel but often neglected (but see Grace 1993, Klimeš 2003, 2008, Sosnová et al. 2010, Klimešová et al. 2011a).

In addition to the expected response to abiotic filters, it is firstly shown that the clonal traits can have a considerable role in maintaining the diversity of species within plant assemblages. Of the diversity of clonal traits in a region a considerable portion can be found in coexisting species in a plot. This implies that although environmental filters reduce trait diversity at a site it does not constrain it completely (Jónsdóttir 2011). Rather, as hypothesized by Klimešová et al. (2011a) environmental filters seem to act more by modifying the proportion of existing clonal traits than their range. This also implies that the effect of environmental conditions on trait diversity might be more detectable at the β-diversity than the α-diversity scale. In fact, if the convergence between species traits in a community is counterbalanced by such a divergence between species, α diversity could be rather unresponsive across different environmental conditions.

An important result of this study is that the clonal trait diversity between coexisting species can be often higher than expected by chance. There is little evidence for such a trait divergence in the literature. The open question, still largely debated in many recent studies (Westoby et al. 2002, Stubbs & Wilson 2004, Corwell et al. 2006, Grime 2006, de Bello 2011, Schamp et al. 2011), is what are the drivers of high trait divergence between species. Two main ecological processes could be involved: one largely abiotic and the other related to species interactions, both suggesting the operation of niche differentiation between species. In both cases the diversity of clonal traits enhances a process by which different species coexist (Wildová et al. 2007, Zobel et al. 2010). First, the high trait diversity within a community could be caused by environmental heterogeneity at the local scale (abiotic effect; Tamme et al. 2010, Willis et al. 2010). That is, the patchiness in resource availability could cause an α-niche differentiation between coexisting species (Ackerly & Cornwell 2007) leading to trait divergence. Indeed, for many of the vegetation types in East Ladakh, the low soil moisture combined with stony substrate could create the heterogeneous matrix favouring the coexistence of different traits. As a second ecological process underlying trait divergence there are biotic processes such as competition and facilitation, which could result in a community composition with species functionally more dissimilar than expected by chance (Petchey et al. 2007, Mayfield & Levine 2010). One of the most discussed hypothesis regarding these biotic effects is the so-called principle of limiting similarity (MacArthur & Levins 1967), i.e. species must be functionally different to coexist (Mason et al. 2007, 2011, Gross et al. 2009). Different clonal traits, in this sense, could play a crucial role in allowing species to share the space and hence the resources available in a community more complementarily (Zobel et al. 2010) and so reduce competition between them. Such mechanisms should be less important in highly competitive conditions because in such conditions, species bearing traits associated with low competitive ability may be even excluded, causing biotic trait convergence (Grime 2006, Farrer et al. 2010, Mayfield & Levine 2010). However, such biotic convergence is not expected in harsh environments where plant growth is constrained by multiple stresses, as in East Ladakh. As such, the trait divergence patterns are more likely to be manifested in the system studied as in similar arctic conditions (Jónsdóttir 2011).

It is particularly interesting to note that trait divergence was detected only when using null models randomizing species cover of coexisting species (as opposed to randomizing species composition across plots; Fig. 3) and especially when considered in terms of clonal traits rather than growth forms. These observations have two key implications. First, randomizing species from different habitats makes it more likely that trait convergence will be detected because the null communities will systematically show higher FD (i.e. by including species from very different habitats and thus different traits; de Bello 2011). This effect is reduced when only species that actually coexist together are included in the null models (Mason et al. 2011) thus increasing the chances of detecting trait divergence. Second, even if some clonal growth forms dominate a community, the space occupancy strategies within these groups (as underlined by the 16 traits considered) might differ leading to a higher trait divergence between coexisting species, even within a given group.

In conclusion, this study tested two contrasting hypotheses regarding the nature of clonal traits as functions of a species ability to inhabit different environments vs their role in species coexistence. The detection of both trait convergence and divergence implies that both mechanisms are involved.

See http://www.preslia.cz for Electronic Appendix 1, 2

Souhrn

Do jaké míry klonální růst rostlin přispívá ke schopnosti druhů koexistovat ve společenstvu? Existují pro to dvě kontrastní, dosud málo testované hypotézy: (1) selekční tlak prostředí způsobuje, že koexistující druhy mají funkčně podobné vlastnosti (tj. dochází k jejich konvergenci); (2) diferenciace nik koexistujících druhů vede ke společnému výskytu funkčně nepodobných vlastností (tj. k jejich divergenci), které umožňují dokonalejší využití prostorových a časových nik. Testovali jsme tyto dvě hypotézy na velkém datovém souboru, pocházejícím z 369 ploch (100 m^2), nacházejících se v nadmořských výškách mezi 4100 a 5800 m n.m. a charakterizujících základní vegetační typy Ladáku v severozápadním Himáláji. Podobnost klonálních vlastností koexistujících druhů byla zkoumána s využitím parametrů funkční diverzity (FD) a testována oproti různým nulovým modelům. FD byla zkoumána pro 17 morfologicky charakterizovaných klonálních růstových forem a pro 16 funkčně charakterizovaných klonálních vlastností. Jak funkční diverzita α (uvnitř plochy), tak β (mezi plochami) byly ovlivněny podmínkami prostředí a typem vegetace, což značí, že selekční tlak prostředí má vliv na zkoumané klonální vlastnosti. Obzvláště β diverzita mezi plochami závisela na vegetaci a prostředí, zatímco α diverzita byla stabilnější. Nehledě na zmíněnou selekci prostředí pro určité klonální vlastnosti, většina FD byla nalezena už na úrovni plochy a navíc byla zaznamenána divergence vlastností na této úrovni. I když byla zaznamenána jak konvergence (mezi plochami), tak divergence (uvnitř plochy) pro zkoumané klonální vlastnosti a klonální růstové formy, konvergence byla detekována, zvláště když se jako nulový model použilo společenstvo náhodně vybrané z lokálního zásobníku druhů (všech druhů zaznamenaných na zkoumaných plochách) a funkční diverzita byla počítána pro klonální růstové formy. Naproti tomu divergence byla detekována, bylo-li jako nulový model použito společenstvo, kde druhům vyskytujícím se na ploše byly přiřazeny náhodně pokryvnosti a funkční diverzita byla stanovena pro funkční klonální vlastnosti. Tím, že studie podpořila jak hypotézu o konvergenci, tak o divergenci vlastností, přinesla nové důkazy o významu klonálního růstu rostlin pro osidlování různých prostředí a schopnost koexistence ve společenstvu.

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