Research article

A test of the explanatory power of plant functional traits on the individual and population levels

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ARTICLE INFO

ABSTRACT

An important issue in plant ecology is the extent to which functional traits that explain patterns at one organizational level serve as explanatory variables at higher levels, while a related subject is the universality of relationships between traits and responses to environmental variables even at a given level. We addressed both questions experimentally by either mowing or abandoning plots within two meadows, one wet and one dry, and then measuring the performance of 42 species in terms of shoot growth and flowering (individual level) and species cover (population level), and relating these performance measures to traits assessed either directly on the individual level or indirectly (mostly using databases) on the species level. Of particular interest were traits thought to confer competitive advantages on individual shoots, to see if these traits were especially useful in predicting early population level responses to changed management. Our study found that (1) only one trait had predictive value for responses at both the individual and population level for the environmental alteration consisting of mowing vs. abandonment; (2) traits important to competitive ability were not particularly good predictors for responses to abandonment at the individual or population level; (3) the predictive value of particular traits was greater earlier than later after abandonment, with this relationship often site-specific; and (4) the number of significant results increased after phylogenetic correction. The limited ability of the predictive power of traits to transcend organizational level and ecological milieu suggests that trait function is highly context dependent, and implies the need for mechanistic examinations of interactions between traits and perturbation.

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Introduction

Plant functional ecology deals with traits on organizational levels ranging from single leaves to ecosystems (Lavorel and Garnier, 2002; Messier et al., 2010). One line of inquiry has been investigating the extent to which species traits can predict community level responses to environmental variables (Chapin et al., 1996; Chapin, 2003; McGill et al., 2006; Vile et al., 2006; Suding et al., 2008). However, the relationship between traits and community level responses differs among systems, so that, for example, unpalatable species avoided by grazers tend to dominate an overgrazed community in Israel (Noy-Meir et al., 1989), but not in Patagonia (Cingolani et al., 2005).

Over the last decade, the accumulation of tests of community level responses to grazing, in terms of plant traits (e.g. Hadar et al., 1999; Landsberg et al., 1999; Sternberg et al., 2000; Dupré and Diekmann, 2001; Vandvik and Birks, 2002; Dorrough et al., 2004; Kohler et al., 2004), has allowed meta-analyses across continents (Díaz et al., 2001, 2007; Vesk et al., 2004). These have shown that relationships between traits and community responses resist generalisation at this scale, with no universal, predictable relationship between management regimes and plant functional traits (Vesk et al., 2004; Díaz et al., 2007), and the importance of both historical context and environmental properties.

More generally, the ability to predict the consequences of a given trait at one organizational level based on its effects at a lower level could be limited by context dependence in multiple

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ways. Successful attempts to test whether a plant trait measured at one organizational level correlates with performance at a higher organizational level are still sparse. Among these studies, Niu et al. (2008) found that patterns in biomass allocation at the level of individual shoots explained changes in cover at the population level (and consequent community level changes) after fertilisation in an alpine meadow. This supported Grime's (1973) hypothesis which posits that soil fertility influences the importance of competition in structuring communities, and in turn, the importance of allocation traits that enable competitive ability. Gross et al. (2009) found that in the competitive environment of wet alpine meadows, the mean specific leaf area (SLA) on the community level corresponded to an SLA value that favoured growth on the individual level, whereas in dry alpine meadows the community level trait distribution of SLA reflected values promoting shoot survival, rather than growth and competitive ability.

Using parameterized simulations, Wildová et al. (2007) found that growth traits that determined biomass on the population level were consistent across the studied species of sedges (Cyperaceae). In contrast, traits concerning plant architecture and allocation to clonal reproduction were species-specific, with their effects contingent on other traits. Thus, one type of trait could be scaled up above the species level, whereas others showed context dependence on other traits. However, due to the scarcity of similar tests, additional data are needed before generalising widely from these findings (Goldberg et al., 2008).

In order to understand possible constraints on scaling up plant functional traits, we experimentally examined the predictive values of traits for plant responses to different management regimes at two levels – individual shoot and population – and then examined how the effects correlated with each other across the levels. In one field experiment, we compared two management regimens, and directly assessed two traits at the level of individual shoots: the occurrence of flowering and a growth measure. In a second experiment (run at the same field sites at a different time), we tested whether these two traits predicted population responses, in terms of cover, to these management regimes. In addition to the two focal traits assessed directly from individuals included in the experiment, we also included in our analysis assessments of other traits based on measurements of plants in the immediate vicinity of the experiment or on information available from the literature. By limiting our analysis to trait distributions immediately before and shortly after management changes, we were able to make comparisons within the same species without having to contend with changes in species composition over time.

We selected species-rich meadows as a model community due to the richness in growth forms and uniformity of disturbance. Traditionally, fodder for winter has been harvested and dried in summer from these European temperate meadows because they are situated in a climate where snow cover makes winter grazing by domestic animals impossible. This mowing typically occurs at the peak of biomass development, usually between mid June and July, when all the plant species have above-ground growth and most of them are flowering.

Traditionally managed meadows now remain on a very limited portion of their original range due to intensification of agriculture (Isselstein et al., 2005) and they are now protected, with their management sometimes government supported (Knop et al., 2006). In spite of this, abandonment still poses a major threat to species-rich meadows, because it is mowing that has suppressed dominant species, enabling coexistence (Klimešová et al., 2010).

In order to examine how traits, particularly of those related to shoot competitive ability, can shape both the shoot- and population-level responses to cessation of mowing "abandonment", we asked the following questions:

(1) What traits, if any, have predictive value for responses at both the individual and population level for the environmental alteration by "abandonment"?
(2) Are important traits for competitive ability particularly good predictors of responses to abandonment at the individual or population level or both, given that abandonment removes the disturbance that limits competitive exclusion?
(3) Does the predictive power of traits vary across time and space?
(4) How does phylogenetic correction affect detection of trait effects, given that many traits are shared by closely related species?

Material and methods

We studied 42 selected plant species in two meadows differing in water availability in two experiments at both localities, with some of the analyzed data collected over a 4-year period, and other data collected from 2 years to find out to what degree effects are site- or year-specific. In the first experiment (A), growth and flowering of individual plant shoots of selected species in response to mowing/abandonment were recorded, whereas in the second experiment (B), vegetation response to mowing/abandonment was assessed in terms of percentage cover of the species in the vegetation (diagram of the analyses is shown on Fig. 1).

In the present study, for the species that were followed in both experiments, the following data were analyzed: (1) the growth and flowering of individual plant shoots after 1 and 3 years of mowing/abandonment in Experiment A, were used as response variables in that experiment's test of individual shoot level responses, but as explanatory variables in assessment of population level response; (2) traits on a species level ("database" traits) taken from the literature or from plants in the vicinity of the experiment but not included in it, with these used as explanatory variables on both the individual shoot and population levels; and, (3) changes in the cover of species over the 3–4-year course of Experiment B, constituting the response variable used at the population level (Fig. 1).

Study sites

Both studied meadows are species-rich. The first (referred to as the "dry meadow") is located in the Bílé Karpaty Mts. (SE Moravia; 48°54′N, 17°25′E). The mean annual temperature there is 9.4 °C, and precipitation 464 mm (Meteorological Station Strážnice). This meadow is situated in Čertoryje Nature Reserve at an altitude of 440 m a.s.l. on a SW-facing slope with an inclination of 5–10°. The traditional management of this meadow is regular mowing in June, and it phytosociologically belongs to the *Bromion* alliance (Chytrý, 2007), hosting the following dominant species: *Bromus erectus*, *Carex montana*, *Molinia arundinacea*, *Festuca rupicola, Salvia pratensis*, *Potentilla alba*, and *Serratula tinctoria*. Some years prior to Experiment A, the mean number of vascular plant species recorded in 1.5 m × 1.5 m plots was 65 (Klimeš, 1999).

The second site is an oligotrophic meadow (referred to as the "wet meadow") located 10 km south-east of České Budějovice at an altitude of 510 m a.s.l. (South Bohemia; 48°57′N, 14°36′E). The mean annual temperature is 7.8 °C, and precipitation 620 mm (Meteorological Station České Budějovice). The meadow phytosociologically belongs to the *Molinion* alliance (Chytrý, 2007) and is dominated by grasses (about 15 species, e.g. *Molinia caerulea*, *Holcus lanatus*, *Nardus stricta*, *Festuca rubra*, *Anthoxanthum odoratum*) and other graminoids (*Juncus effusus*, about 10 species of *Carex*); common dicots are *Angelica sylvestris*, *Betonica officinalis*, *Galium boreale*, *Potentilla erecta*, *Ranunculus acris*, and *Lychnis floscuculi*. About 35–40 species were recorded per 0.5 m × 0.5 m plot
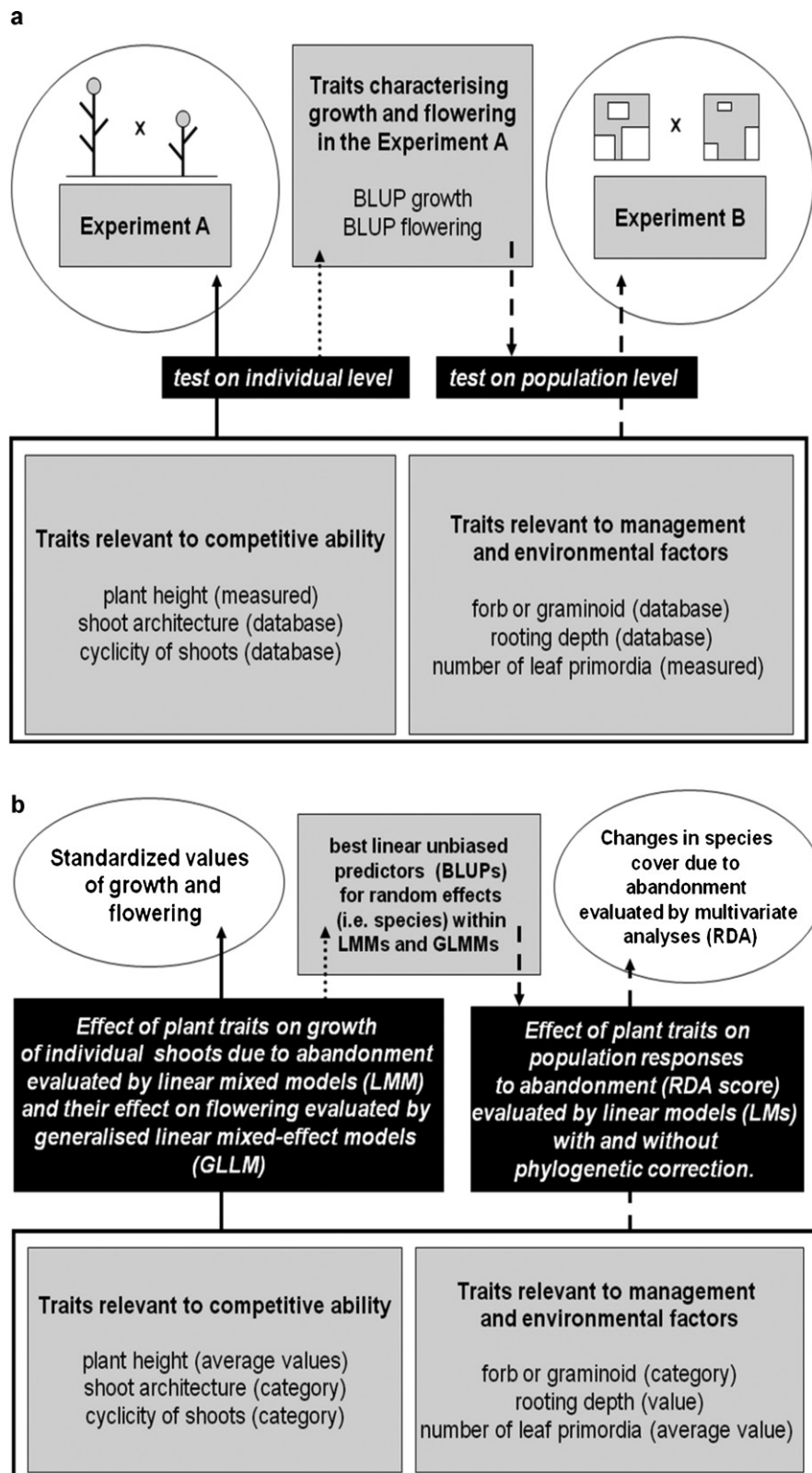
a

Traits characterising growth and flowering in the Experiment A

BLUP growth
BLUP flowering

Experiment A

Experiment B

test on individual level

test on population level

Traits relevant to competitive ability

plant height (measured)
shoot architecture (database)
cyclicity of shoots (database)

Traits relevant to management and environmental factors

forb or graminoid (database)
rooting depth (database)
number of leaf primordia (measured)

b

Standardized values of growth and flowering

best linear unbiased predictors (BLUPs) for random effects (i.e. species) within LMMs and GLMMs

Changes in species cover due to abandonment evaluated by multivariate analyses (RDA)

Effect of plant traits on growth of individual shoots due to abandonment evaluated by linear mixed models (LMM) and their effect on flowering evaluated by generalised linear mixed-effect models (GLLM)

Effect of plant traits on population responses to abandonment (RDA score) evaluated by linear models (LMs) with and without phylogenetic correction.

Traits relevant to competitive ability

plant height (average values)
shoot architecture (category)
cyclicity of shoots (category)

Traits relevant to management and environmental factors

forb or graminoid (category)
rooting depth (value)
number of leaf primordia (average value)

Fig. 1. (a) Diagram of the two-level testing of predictive power of plant functional traits. Both the traits relevant to competitive ability and the traits relevant to management and environmental factors were used to test individual level responses in Experiment A. The above mentioned traits, together with the traits characterising growth and flowering in Experiment A, were used to test population level responses in Experiment B. (b) Overview of methods used in the two-level testing from (a).

(Lepš, 1999). The traditional management is regular mowing once or twice a year.

Experiments

Experiment A: The experiment in which responses of individual plant shoots to mowing/abandonment were measured was set up in a randomised block design on regularly mown meadow. In June 2005, six blocks were designated in the dry meadow and five in the wet meadow. Each block contained 9 permanent plots (3 rows of 3) in which either the abandonment treatment (i.e. cessation of mowing) was applied beginning in 2005, or mowing was continued. In both meadows, for the plots selected for the mowing treatment, this was carried out in the second half of June in 2005, 2006, and 2007. The mowing treatment was applied only to plots located in the corners of blocks, therefore resulting in four mown and five unmown plots per block. In each block, two plots with contrasting management were used for data collection in 2006, the first year of data collection, and two other plots were used in 2008. In 2006, the central, unmown plots were not used for data collection, whereas in 2008, for each of the blocks used, data were collected from the central, unmown plot in addition to one of the outer unmown plot. Only those species occurring in all the selected plots in a given meadow in June 2006 were selected for data collection, resulting in 24 species for the dry meadow and 18 species for the wet meadow. The species were neither very rare nor extremely common at these localities, with this degree of representation considered satisfactory for evaluation of vegetation change in response to environmental alteration (Pakeman and Quested, 2007)

For each species, in each plot from which data were collected, one individual shoot ("IS") was marked with a white plastic label on a metal needle placed next to the plant individual (shoot). This yielded 12 ISs per species × treatment combination in the dry meadow and 10, in the wet meadow. In the case of erosulate shoots, if a parental shoot were lost due to mowing, the nearest offspring shoot would then be measured. Some labels were damaged by browsing animals or were lost. Nearly all of the selected species are clonal, and therefore we marked as ISs ramets that had no obvious aboveground connection (stolon) between them. However, we were not able to identify rhizomes or other belowground connections. In 2008, a new set of 5–12 individuals per species × treatment combination was marked. The number of marked individuals varied because some species had started to disappear from the abandoned plots. The total dataset was thus based on 872 and 582 ISs measured, in the growing seasons of 2006 and 2008, respectively, and belonging to 42 species.

The marked plants were measured five times each in 2006 and 2008: before peak meadow biomass in June (i.e. before the meadows were mown) and then in monthly intervals (in July, August, September and October). We measured two plant shoot characteristic at each IS in each month (in what we henceforth refer to as the "time census"). The first characteristic, here designated as "growth", was, for semirosettes and rosettes, the length of the longest leaf (when fully extended), or for erosulates (except *J. effusus*, which forms only leaves), the height of the stretched shoot. The second characteristic was flowering status, i.e. whether a marked IS was flowering.

Experiment B: In the dry meadow, a medium-term experiment on effects of altered management was conducted from 1997 to 2000, with 9 randomised blocks located in stands dominated by either *Calamagrostis epigejos*, *M. arundinacea*, or *B. erectus*. For the purposes of the present study, data on species cover from mown (representing a continuation of traditional management)

and abandoned plots (unmown in 1997, 1998, and 1999), were collected annually in the first half of June, before mowing was done to the plots receiving that treatment, with the last assessment in 2000.

In the wet meadow, the experiment was established in 1994 and is still running (Lepš, 1999; Lepš, unpublished). The design included three pairs of alternative treatments (mowing vs. abandonment, dominant removed vs. dominant present, fertilisation vs. no fertilisation) applied once per year in a factorial design, yielding eight possible combinations, each having three replicates. For the present study, data from the first 4 years were used (treatments were applied in 1994, 1995, 1996, last assessment in 1997). As in the case of the dry meadow, data were collected each year in the second half of June, before mowing was applied to the plots receiving that treatment.

Plant functional traits

We selected 10 functional traits characterising plants at species level, (1) some of them likely directly relevant to competitive ability of the shoot (shoot height, shoot cyclicity, shoot architecture), (2) some reflecting different plant characteristics likely relevant to meadow management or water availability (forb or graminoid, rooting depth, number of leaf primordia), and (3) others describing growth and flowering of plants in the first and third years of Experiment A. Values for the traits (except for those obtained from Experiment A) of the studied species are listed in Table S1. In the case of continuous traits, we used average values for the species. The quantitative traits were partly correlated with each other (Supplementary Table S2). However, these correlations disappeared after phylogenetic correction, which is in agreement with other studies (e.g. Silvertown and Dodd, 1996; Bolmgren and Cowan, 2008). Therefore, since they carry different biological information, we used all of these traits in our analyses.

(1) Traits relevant to competitive ability:

Height of flowering shoot is the trait most often used to assess species response to grazing (Díaz et al., 2007). Tall plants have greater competitive ability but lose more biomass than small plants through mowing. Moreover, small plants compensate more successfully to lost biomass than tall plants (Klimešová et al., 2010). This competitive ability – disturbance avoidance trade-off is considered to be a factor enabling species coexistence in mown meadows (Klimešová et al., 2008). In our study, plant height was measured on 5–12 individuals per studied species in the areas immediately surrounding the experimental plots from May to June 2007 in both meadows.

Shoot architecture: Shoot architecture, expressed as the location of leaves on a stem, reflects biomass distribution along the vertical axis of the plant, with leaves either regularly distributed along the stem (erosulate), partly concentrated at the plant base (semirosette), or all near the ground, at the shoot base, with the middle and upper cauline leaves missing (rosette). Tall, erosulate shoots are particularly competitive (Lepik et al., 2004), but they are especially negatively affected by mowing, with the loss not only of large proportions of biomass but also of apical meristems which the plant needs to regenerate from bud banks after mowing (Klimešová et al., 2008). On the other hand, basal leaf rosette minimizes biomass loss in grazed or mown communities (Díaz et al., 2007). For our study, shoot architecture data were extracted from the CLO-PLA database (Klimešová and Klimeš, 2006)

Cyclicity of shoots refers to the life-span of a shoot over several years, starting with the sprouting of a bud, followed by vegetative growth, flowering and fruiting, until shoot death. In a mown meadow, plants with monocyclic (annual) shoots are penalised when they flower at the time of mowing as they lost their investments into generative regeneration and are not able to flower after mowing (Klimešová et al., 2008). On the other hand, plants with dicyclic shoots are favoured in meadow as the mowing fits to life-history of their shoots (Klimešová et al., 2008). Shoot cyclicity data were extracted from the CLO-PLA database (Klimešová and Klimeš, 2006).

Plant height, shoot architecture and cyclicity of shoots tend to covary. For example, in the studied dry meadow the plants mostly have tall, semirosette and dicyclic shoots, and less often, intermediate, erosulate, monocyclic shoots (Klimešová et al., 2008).

(2) Traits relevant to management and environmental factors:

Designation as a forb or graminoid: This taxonomic distinction has proved to be useful in delimiting the main functional groups of meadow plants (Lepik et al., 2004), although the functional explanation of this delimitation remains largely untested. The graminoids are characterised by lower carbohydrate storage (Janeček et al., 2011), lower investment into height growth (Klimešová et al., 2010) and more effective space occupancy when extra illumination is provided (Lepik et al., 2004) than forbs.

Rooting depth: Because the dry meadow was limited by water availability in summer, we believed rooting depth would be an important plant functional trait. Data on rooting depth were extracted from a root atlas (Kutschera et al., 1982; Kutschera and Lichtenegger, 1992). For 9 species, however, such data were not available, and, for them, observations at the localities during sampling of roots for carbohydrate assessment (see Janeček et al., 2011) were used.

Number of leaf primordia (*bud preformation*): The number of leaf primordia present in axillary buds before the vegetation season expresses the degree to which a plant shoot is developed before spring regrowth. Plants with preformed leaves develop faster in spring but are more conservative in regrowth following disturbance during the vegetation season (Diggle, 1997). Axillary buds, usually located at the soil surface, were sampled in January 2007 from plants in the vicinity of the experimental plots. Buds were fixed in formalin–acetic acid–alcohol (FAA) and transferred to a laboratory for further examination. Only those buds likely to actually yield shoots in the following season were counted. For the purposes of our study, we used data only on leaf primordia, because preformed generative structures, i.e. inflorescences or flowers, (Geber et al., 1997) were developed only in a few species (*Geranium sanguineum*, *P. alba*, *Primula veris*, and *Valeriana dioica*). In assessing the average number of primordia per bud for each species, we aimed to count the leaf primordia in at least 10 buds for each species (using one bud per individual plant), but due to the fact that some buds were already transformed to generative meristems, and some were dead, the final number was 6–12 buds for each species.

(3) Traits measured during Experiment A:

Plant growth and flowering: Growth and flowering values in the first and third year of Experiment A were, for each species, extracted from mixed models as a BLUP (Best Linear Unbiased Predictors). The BLUP denotes the 'standardized' mean value for the species based on the structure of the final model. It is analogous to the extraction of an RDA score for a species in response to mowing (see below).

Data analyses

Plant response to mowing/abandonment at the level of individual plant shoots

For a diagram of the analyses and data used, see Fig. 1. Prior to the analyses, the growth data were related to the maximum value for each IS over all individuals and species (range 0–1) recorded during the 2006 or 2008 seasons (values were divided by the maximum value of an IS measured during the season). This procedure enabled us to compare the growth of three groups differing in shoot architecture, in which either the length of the longest leaf (in rosettes and semirosettes), or stem height (in erosulates) were measured. Thereafter, the data were arc-sin ($\sqrt{x}$) transformed to avoid heteroscedasticity.

The hierarchical structure of the growth data allowed us to identify differences among ISs, using linear mixed models (LMM) with the growth data as a dependent variable, and with treatment (abandonment and mowing), time (continuous; number of days), plant traits (Table S1), treatment × time and treatment × trait interactions as fixed effects, and species and IS nested within species as random effects.

These two random-effect predictors were included to account for the fact that our data were nested in two different ways: (i) dependency of observations due to repeated measuring of the same individual, and (ii) dependency of observations due to the use of the same species. Use of these predictors ensures that an appropriate number of degrees of freedom is used in parameter estimation, and allowed us to avoid pseudoreplication.

We fitted a suite of models, starting with the most complex but still biologically reasonable model (henceforth called the "initial" model), as well as all simpler combinations of the initial model. Thereafter, their Akaike information criterion (AIC) values were compared. LMMs were fitted using maximum likelihood estimation. Such models of different fixed-effect structure can be compared with the AIC criterion, which is not the case for models using restricted maximum likelihood estimation (Pinheiro and Bates, 2000). The model with the lowest AIC value is considered to be the most parsimonious model, i.e. using the fewest necessary parameters as possible to explain observed variation. The flowering data were evaluated using generalised linear mixed-effect models (GLMM), providing estimates both for random and fixed effects. We used treatment, time census, plant traits (Table S1), and the interactions treatment × time and treatment × trait interactions as fixed explanatory variables, with species, and IS nested within it, as random effects. We used a stepwise backward elimination model selection on the GLMM (comparing AIC values). GLMMs were calculated using the lmer function in the R library lme4, assuming a binomial distribution of the data (IS flowering vs. not flowering; with logit link) and by maximising penalised quasi-likelihood (glmmPQL) using the "Laplace" approximation. We computed Bayesian highest probability density (HPD) intervals using Markov chain Monte Carlo simulations, as this is favoured over normal confidence limits for GLMMs. The random effect block (a measure of environmental condition) was not included in the models for simplicity since its effect was non-significant in preliminary analyses (*P*-values for the block were always higher than 0.55).

Correlations among quantitative traits used as fixed effects in the models (i.e. plant height, rooting depth and number of leaf primordia) were tested using Pearson's product moment correlation analyses (Table S2). To correct for possible phylogenetic dependence of individual species, phylogenetically independent contrasts (PIC) were used. We used PICs in the regressions since they have a much lower type-I error than simple cross-species anal-

yses (Silvertown and Dodd, 1996). The phylogenetic tree (Fig S1) was constructed according to the phylogenetic code for each species published in the BiolFlor database (Klotz et al., 2002, pp. 75–91), using the NEXUS format (Huson and Bryant, 2006).

We extracted the best linear unbiased predictors (BLUPs) for random effects (i.e. species) within LMMs and GLMMs as estimates of growth and flowering modes of the species, which were used in further analyses. The BLUP is an estimate derived from repeated measures on ISs. It describes the rate of growth and flowering of each species, and is calculated as an additional parameter (standardized to a mean of zero) to the predictions of the fixed effects selected in the most parsimonious model. BLUPs have the advantage of being less sensitive to extreme values within the data and providing more appropriate estimates of the growth profile of a species than the mean of all measures for that species (Pinheiro and Bates, 2000). To determine temporal consistency in growth and flowering, we calculated the correlation (using Pearson's product moment correlation) between the 2006 and 2008 data.

Plant response to mowing/abandonment at the population level

For a diagram of the analyses and data used, see Fig. 1. Responses to abandonment at the population level (Table S1) were obtained from the experimental data sets using the CANOCO 4.5 program (ter Braak and Šmilauer, 2002). This was done using redundancy analysis (RDA) with the Monte Carlo permutation test because species composition in the plots was homogenous. We used a model that took account of the repeated measures structure and split-plot design for the dry and the wet meadow data on plant species cover in the permanent plots.

The species score on the constrained first RDA axis was taken as a response to abandonment. The values of the first RDA axis were obtained from an analysis (499 permutations), in which the interaction between management type (abandonment vs. mowing) and time was the only explanatory variable ("environmental" in CANOCO terminology) and the interactions with other experimental treatments (i.e., dominant removal vs. dominant present and, in the wet meadow, fertilisation vs. no fertilisation) and vegetation type characterised by dominant species (for the dry meadow) were used as covariates. This procedure is analogous to that described by Lepš and Šmilauer (2003), p. 222. In our case, the interaction between management type and time is of greatest interest because it corresponds to the effect of the experimental manipulation. Within the RDA framework, after the effect of covariates is eliminated, the residual variation is then related to the explanatory variable.

In the next step, we analyzed population responses using linear models (LMs) with and without PICs. The plant traits (listed in Table S1) including growth and flowering (responses to management at the level of individual plant shoot, i.e. BLUPs) in the 2006 and 2008 were used as fixed effects in LMs for the dry and the wet meadow.

Additionally, we wanted to visualize the relationships between responses to cessation of mowing on the level of individual plant shoot and population level responses. To do this, we calculated the growth responses of individual plant shoots in selected moths (in June and October) expressed as the growth if abandoned minus growth if mown in 2006 and 2008 (for this purpose means of measured values not related to year maximum were used) and the responses of individual plant shoots in flowering (expressed as flowering frequency summed for whole year if abandoned minus flowering frequency if mown in 2006 and 2008) and then used LMs with and without PICs to estimate the effects of these responses on plant population responses to abandonment in cover. Within each

LM analysis, species were always considered as replicates, enabling us to study relationships between traits.

All statistical analyses except RDAs were performed using R (R Development Core Team, 2008).

Results

Plant response to mowing/abandonment at the individual shoot level

Growth of individual shoots (Fig. 2) differed depending on the studied locality and year. In the first year after abandonment (2006), in the dry meadow, the only direct effects found were those of time and shoot cyclicity; the effect of management was significant only when considering time (Tables 1 and S3). On the other hand, in the wet meadow, the effects of management, time, shoot cyclicity, designation as graminoid vs. forb, number of leaf primordia, and plant height each significantly affected plant growth (Tables 1 and S4). The traits which were revealed by the analysis as important predictors of responses to different treatments (Abandoned vs. Mown × Trait interaction in Tables S3 and S4) differed between the meadows as well. In the dry meadow, plants with erosulate shoot architecture and monocyclic shoots, a high number of leaf primordia, and shallow rooting depth benefited from abandonment. However, in the wet meadow, tall plants with a low number of leaf primordia and/or shallow rooting depth benefited from abandonment.

In the third year after abandonment (2008), the number of significant traits decreased, and the variance in data explained by species increased from 9.79% to 14.44% in the dry meadow and from 0.44% to 14.34% in the wet meadow. The overall growth of the plants in that year was modulated by shoot architecture and rooting depth in the dry meadow and shoot cyclicity and plant height in the wet meadow. In the dry meadow, only shoot architecture was found to be a significant trait affecting plant growth differently in the mown and the unmown plots (plant with erosulate shoots benefited from the abandonment), whereas in the wet meadow shoot cyclicity was only marginally significant (Tables 1, S3 and S4).

Flowering of individual plant shoots (Fig. 3) was partly affected by other traits than was plant growth (Tables 1, S5 and S6). In 2006, flowering in the dry meadow was affected by designation as graminoid vs. forb and by rooting depth, whereas in the wet meadow, plant architecture, designation as graminoid vs. forb, number of leaf primordia, and plant height were important traits. The traits which were revealed by the analysis as important predictors of plant growth in the differently treated plots (interaction Abandoned vs. Mown × Trait in Tables S5 and S6) differed partly from those important for plant growth and also those that differed significantly in value between the meadows. Whereas plants with erosulate shoots flowered more in the abandoned plots of the dry meadow, they flowered more in the mown plots of the wet meadow. In both types of meadows, plants with a higher stature flowered more in the abandoned plots. Moreover, in 2006, flowered was greater among shallowly rooting plants in the dry meadow, and forbs in the wet meadow.

Plant traits shown by the analysis to significantly affect flowering in 2008 differed between the meadows, and also partly differed from those traits important for plant growth in the 2006 (Table 1). The rooting depth in the dry meadow was an important predictor of both plant growth and flowering, whereas, in the wet meadow, plant height was an important predictor of growth and designation as graminoid vs. forb was an important predictor of flowering.
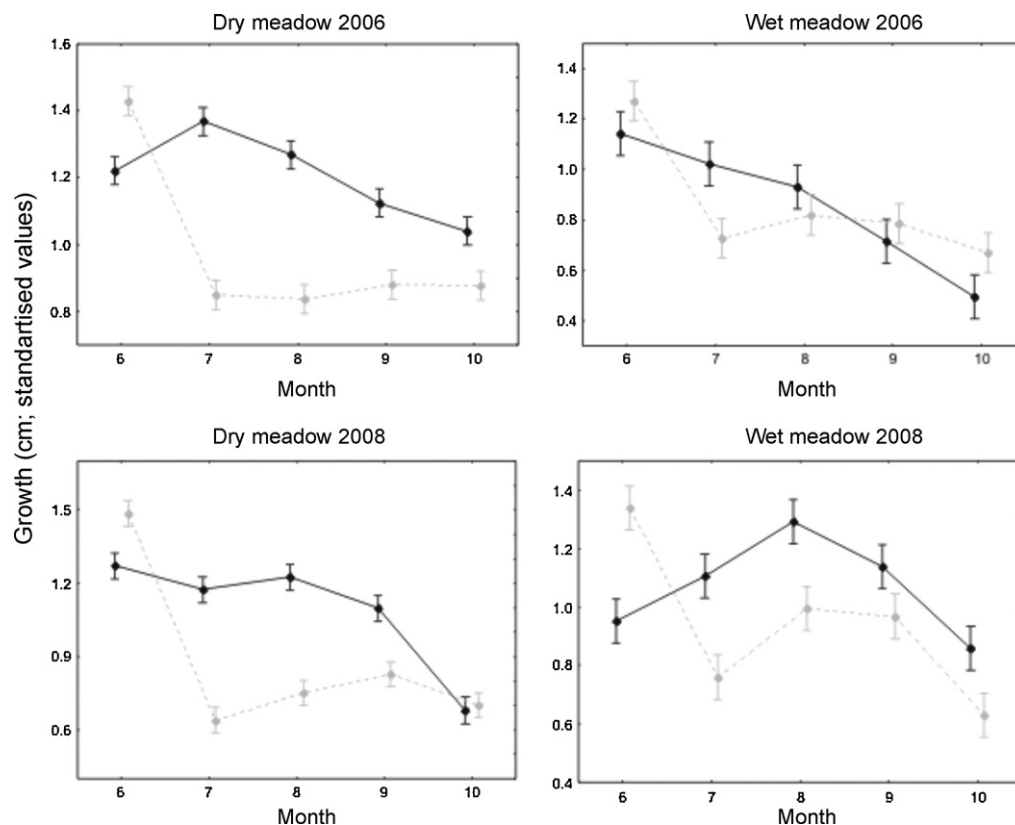
Fig. 2. Mean plant growth by month (07–10; June–October) in the dry and the wet meadows in 2006 and 2008. Although the Treatment × Year interaction was significant only in 2006 in the dry meadow, it was significant in both years in the wet meadow. Whiskers denote 0.95 confidence interval. The decreasing growth pattern reflects the seasonal trend from summer (peak growth) to early autumn. Grey symbols denote the growth in mown plots; black symbols denote the growth in abandoned plots.

In the dry meadow, flowering was enhanced by abandonment in plants with a high number of leaf primordia and in the graminoids, while, in the wet meadow, it was increased in plants with erosulate shoots, deep rooting, small stature and a high number of leaf primordia in buds (Tables 1, S5 and S6).

The random factor "species" was significant in both 2006 and 2008 on the dry meadow, but only in 2006 on the wet meadow (Tables S5 and S6). In the dry meadow, there were non-significant relationships between growth in 2006 and 2008 (adj. $R^2 = 0.08$, df = 22, $P = 0.169$) and between flowering in 2006 and 2008 (adj. $R^2 = 0.11$, df = 22, $P = 0.11$). In the wet meadow, there was also non-significant relationships between growth in 2006 and 2008 (adj. $R^2 = 0.13$, df = 16, $P = 0.165$) and between flowering in 2006 and 2008 (adj. $R^2 = 0.16$, df = 16, $P = 0.101$).

Population level responses to mowing/abandonment

When considering plant species as independent from each other, we had only one significant result for RDA scores in linear models (Table S7), with the number of leaf primordia related to cover changes of the species after abandonment. However, taking phylogenetic relationships among species into account, different characteristics, depending on the locality, predicted species-specific responses to mowing (Tables 1 and S7). In the dry meadow, growth in 2006, flowering in 2008, and the number of leaf primordia were each positively related to species' responses to abandonment. In the wet meadow, the only trait related to the response to abandonment was the number of leaf primordia (negative response; Table 1).

Table 1
Summary table of explanatory variables for plant responses to abandonment. Dry: dry meadow, Wet: wet meadow, 1/3 yrs: 1 and 3 years after abandonment, +: significant positive effect, −: significant negative effect, ·: no effect, in parentheses: marginally significant. For itemized results, see Table S7 included in the supplementary material. Traits in bold are likely relevant to shoot competitive ability, *: the trait taken from a database.

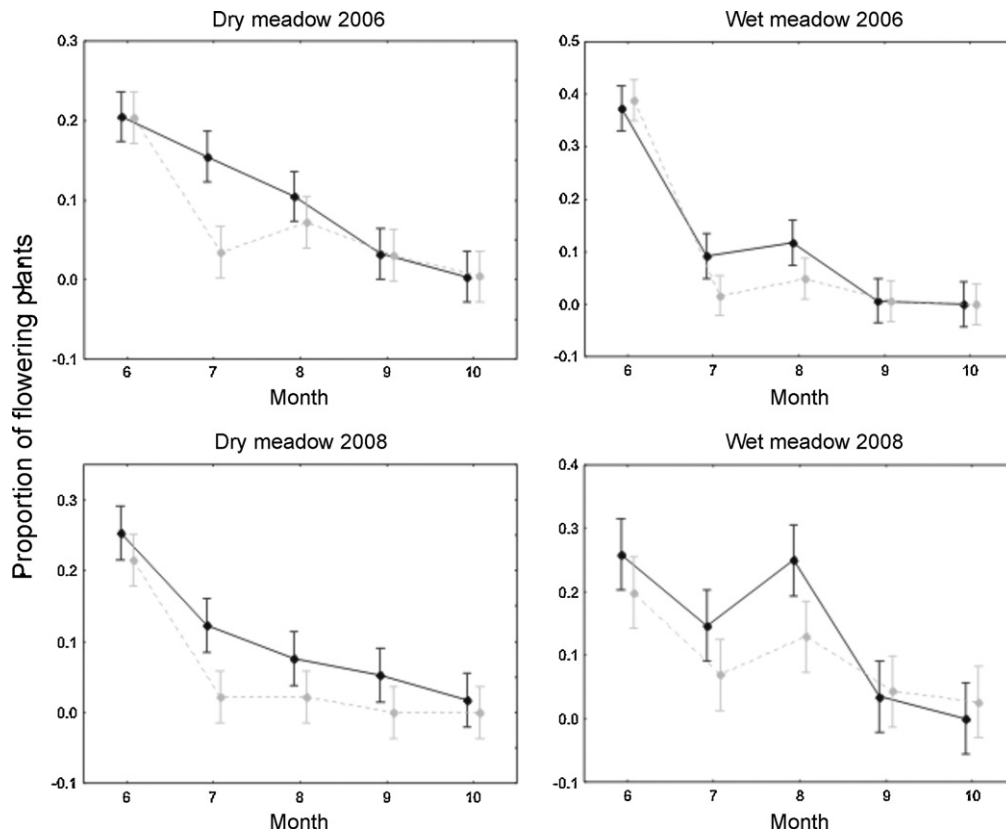| Level and trait (parameter)	Individual and growth		Individual and flowering		Population and cover	
Meadow	Dry 1/3 yrs	Wet 1/3 yrs	Dry 1/3 yrs	Wet 1/3 yrs	Dry 3 yrs	Wet 3 yrs
Architecture (erosulate)*	+/+	·	+/·	−/+	·	·
Cyclicity (monocyclic)*	+/·	·/+	·	·	·	·
Shoot height	·/·	+/·	+/·	+/−	·	·
Rooting depth*	−/·	−/·	−/·	·/+	(+)	·
Graminoid*	·	·	·/(+)	−/·	·	(−)
Preformation	+/·	−/·	·/+	·/+	+	−
Growth 06					+	(+)
Growth 08					·	·
Flowering 06					·	·
Flowering 08					+	·

Fig. 3. Proportion of flowering plants per treatment, year, month (07–10; June–October), and site. The Treatment × Year interaction was significant only in 2008 in the dry meadow and in 2006 in the wet meadow. Whiskers denote 0.95 confidence interval. Grey symbols denote the flowering in mown plots; black symbols denote the flowering in abandoned plots.

Comparison of the individual shoot level and the population level

To visualize results (Fig. 4), we selected data for shoot growth and flowering from June (peak of season) and October (end of season) – see Figs. 2 and 3 – to show relationships between population- and shoot-level responses to abandonment. We found the following significant relationships, which differed slightly from those in the preceding analysis based on the whole dataset: (1) in the dry meadow, positive relationships between population cover and shoot growth (size of shoot in abandoned minus mown plots) in October 2006 ($t = 3.44$, df = 22, $P = 0.002$; without phylogenetic correction: $t = 3.97$, $P = 0.002$) and in October 2008 ($t = 2.42$, df = 22, $P = 0.024$; without phylogenetic correction: $t = 2.65$, $P = 0.015$) and between population cover and flowering (frequency in abandoned minus frequency in mown plots) in 2008 ($t = 2.45$, df = 22, $P = 0.023$; without phylogenetic correction: $t = 0.84$, $P = 0.412$); (2) in the wet meadow, the only significant relationship detected was a positive one between population cover and shoot growth in June 2008 ($t = 3.27$, df = 16, $P = 0.005$; without phylogenetic correction: $t = -0.52$, $P = 0.613$) (Fig. 4).

Discussion

Whereas our analysis revealed some significant results, the most important finding was the lack of consistent relationships among the variables studied. Instead, relationships were contingent on numerous factors, including site, length of time after abandonment,

source of trait data, phylogenetic relatedness, and depended largely on the particular trait in question. Thus,

(1) only one trait, bud preformation, had predictive value for responses at both the individual and population level for the environmental alteration consisting of mowing vs. abandonment. However, the trends for this relationship were opposite each other for the two studied meadows, indicating context-dependency, although we have yet to discern the mechanisms that enable these disparate outcomes;

(2) traits important to competitive ability were not particularly good predictors for response to abandonment at the individual or population level. Out of the five traits likely relevant to competitive ability, only the growth of individual shoots in the first year after abandonment correlated (and for the wet meadow the result was only marginally significant) with the population level response. Thus, although traits related to competitive ability of shoot measured in situ could be reliable explanatory variables of population cover in a community (Goldberg et al., 2008), they do not necessarily predict responses to perturbation;

(3) the studied traits had better predictive value earlier than later after abandonment and often were site specific. The number of traits with significant relationships to management at the individual shoot level decreased with time, suggestive of changing indirect effects and feedback loops, discussed below, that could make other traits, not considered here, became more important. Moreover, our study, like others (Niu et al., 2008; Gross et al., 2009), only evaluated short term (2–3 year) plant
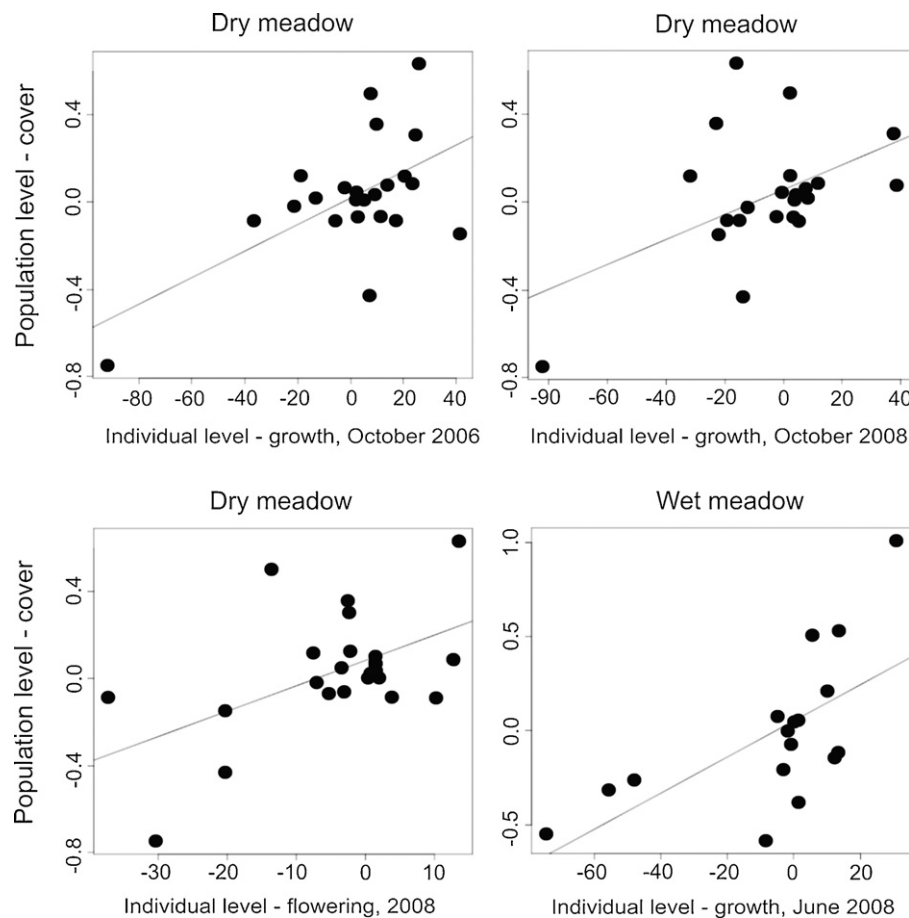
Fig. 4. Relationships between changes in plant cover after abandonment (population level RDA score) and individual responses to abandonment (growth or frequency of flowering in abandoned minus mown plots) in the dry and wet meadows. Only significant results with regression lines based on analyses with phylogenetic corrections are shown. Note that the same positive relationships are obtained when the outlier values located in the bottom left corner of the upper two panels are removed.

responses, with its inferences relevant to this temporal scale. Therefore, over an even longer time scale, the predictive value of the traits we studied could diminish even further, if for example, those related to clonal multiplication or seed production and dispersal become more important (see for example Ozinga et al., 2007).

In addition to our study showing the predictive power of traits changing over time, it shows stark differences in their explanatory ability over space, as many relationships were site-specific. This was manifested in the opposite trends, for bud preformation, discussed above, in each of the meadows, in terms of the relationship between individual and population level responses to abandonment. Site-specific relationships were also found, for example, in flowering early after abandonment, which was enhanced by contrasting shoot architectures in the different meadows, and growth early after abandonment, which was promoted by contrasting levels of bud preformation at the two locations.

(4) the increased number of significant results found after taking phylogenetic relatedness into account imply that overall variability among taxa can hinder detection of trends.

In general, the fact that we failed to detect a universal trait which explained responses to abandonment on both the individual and the population levels suggests the great importance of context-specific effects at both levels (including environmental factors varying over space and time). Moreover, this further indicates that the ability to use plant traits as predictors for vegetation

changes after meadow abandonment is limited (Díaz et al., 2007; Klimešová et al., 2008). Even using specific functional groups of taxa, which has been suggested to be more appropriate for such studies than traits taken separately (Körner, 1995; Lavorel et al., 1997, 1998) would have the same limitation of context specificity.

Although our study was based on data from 42 species (about 20 per locality), both meadows harbour much higher number of species, and omitting rare ones could have affected the outcome of our study as rare species tend to possess unique traits and to respond the first responses changes in management (Thompson et al., 2010; Klimeš et al., in preparation).

Unlike preceding studies (Wildová et al., 2007; Niu et al., 2008), ours found very little correlation between advantageous traits on the individual level and those on the population level. This might have been due to the fact that we used not only the traits that we directly measured at both levels, but we also incorporated species level ("database") traits. Moreover, in contrast to the field study by Niu et al. (2008) and the simulation of Wildová et al. (2007) we used two sites and two experiments at each site running at different times, thus presenting us with higher variability than in these studies.

Our findings imply that the understanding of functionality of plant traits is still rudimentary and that we should employ more detailed, comparative studies on relating species traits to their responses to biotic and abiotic perturbations, and examining trait combinations within species as well as the co-occurrence of traits within communities. We should especially investigate whether changes in trait distributions within target species following per-

turbation are direct responses to the perturbation itself or to changes in trait distributions of co-occurring species, including changes in the co-occurring species composition. Furthermore, we should not overlook the possibility of random changes in trait distributions.

In our case, the release from a management regime in which taller plants had been penalised in terms of larger loss of above-ground biomass and lower regrowth after mowing (Klimešová et al., 2010) is probably the reason that the growth of individual shoots was the best explanatory trait and is a better predictor than final height. Even though the plants most hindered in growth by mowing are typically those with tall, erosulate monocyclic shoots (see description of traits in *Methods*), in our species set, plants with erosulate monocyclic shoots (and with high numbers of leaf primordia in buds – see table in Supplementary data), were not the tallest on the wet meadow and were likely suppressed by increasing competition after abandonment. On the dry meadow, on the other hand, the plants with erosulate monocyclic shoots were among the tallest plants, and their response to abandonment contrasted with that in the wet meadow.

For a better understanding of trait functionality in relation to early and late response to perturbation of a community, it would be useful to distinguish between traits not only as "growth" or "architectural," as proposed by Goldberg et al. (2008), but also on the basis of the pathway of their response to the perturbation. Thus, traits could be recognized as being directly and immediately affected by the perturbation, or reflecting consequent changes in competitive hierarchies or, finally, responding even later and more indirectly to feedback loops initiated by the perturbation. For example, such a feedback loop might be caused by higher availability of nutrients due to decomposition of biomass when mulch is applied on a nutrient- poor mountain meadow (Doležal et al., 2011). Although it has been abundantly documented that a perturbation can have long term consequences on species and functional composition of a community (e.g. Fynn et al., 2005; Chytrý et al., 2009; Kahmen and Poschlod, 2004), records of succession in trait characteristics are still scarce (Kuiters et al., 2009; Pakeman and Marriott, 2010; Doležal et al., 2011). Such data could provide valuable insights into trait functionality and interactions, and help explain the context dependency found in our study.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2011.05.003.

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