



# Invasibility of grassland and heath communities exposed to extreme weather events – additive effects of diversity resistance and fluctuating physical environment

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Understanding the resistance of plant communities to invasion is urgent in times of changes in the physical environment due to climate change and changes in the resident communities due to biodiversity loss. Here, we test the interaction between repeated drought or heavy rainfall events and functional diversity of grassland and heath communities on invasibility, measured as the number of plant individuals invading from the matrix vegetation. Invasibility of experimental plant communities was influenced by extreme weather events, although no change in above-ground productivity of the resident communities was observed. Drought decreased invasibility while heavy rainfall increased invasibility, a pattern that is consistent with the fluctuating resource hypothesis. Higher community diversity generally decreased invasibility, which can be explained by a combination of the fluctuating resource hypothesis and niche theory. The effects of the physical environment (extreme weather events) and diversity resistance (community composition) were additive, as they were independent from each other. Differences in the composition of invading species sets were found, and Indicator Species Analysis revealed several invading species with significant affinity to one particular extreme weather event or community composition. This finding supports niche theory and contradicts neutral species assembly. Our data supports theories which predict decreased resistance of plant communities due to both increased climate variability and biodiversity loss. The effects of these two factors, however, appear to be independent from each other.

Invasibility is an emergent property of ecological units such as plant communities and it is the outcome of three basic factors; (1) the physical environment, (2) the resident community, and (3) the traits of the invaders (Lonsdale 1999, Schoolmaster and Snyder 2007). For all three factors, a rich body of empirical data and theoretical considerations was generated within the last few years. Contradicting chains of reasoning nevertheless still prevail and general solutions integrating all aspects are not at hand (Fridley et al. 2007).

Invasion theory applies equally well to both native and exotic invaders (Aarssen et al. 2003), and insights from community ecology are obviously relevant for invasion ecology and vice versa (Shea and Chesson 2002, Davis et al. 2005). Consequently, we call any species that enters a habitat in which it has not recently occurred an ‘invader’, whether or not it is a member of the regional flora.

## The physical environment – drought and heavy rainfall

The fluctuating resource theory (Davis et al. 2000) states that fluctuations in resource availability is the key factor

controlling invasibility. Unused resources can arise through a decrease in resource use in the resident community (e.g. due to disturbance) or through an increase in total resource abundance without immediate use by the residents (e.g. rainfall). To act as a facilitator for invasion, resource release should occur only intermittently and, to result in invasion at all, must coincide with availability of invading propagules (Davis and Pelsor 2001). Recently, this theory has been broadened by the environmental heterogeneity theory, stating that spatial and invader-driven heterogeneity besides temporal heterogeneity increase invasion success (Melbourne et al. 2007).

Climate is one of the most important determinants of species distribution. Consequently, climate change is considered to be an important driver of community dynamics and invasibility. Climatic forcing, for example, has been identified as one of the major contributing factors for the increasing capability of exotic species to establish (Dukes and Mooney 1999). Especially extreme weather events can have strong implications for community composition, as they create physical disturbance (Buckland et al. 2001) or alter the relative competitive balance between the resident species (Fay et al. 2003). Gap creation by

disturbance is generally known to increase invasibility (reviewed by Hughes et al. 2007). However, consequences of extreme weather events for community resistance have yet hardly been addressed experimentally (Jentsch et al. 2007). Since weather extremes of unprecedented magnitudes and increased frequency are identified as one important aspect of current climate change (IPCC 2007), their consequences for invasibility of communities need to be considered.

### **The resident community – community composition and diversity**

The diversity resistance hypothesis states that the diversity of a resident community acts as a barrier against invasion (Elton 1958). Within this framework, resistance is thought to be due to a more competitive environment with increasing species richness. At fine spatial scales (the level at which all occurring plant individuals interact), more diverse communities generally decrease invasibility (reviewed by Fridley et al. 2007). Theoretically, this pattern can be explained by niche filling (Tilman 2004) or even by neutral processes (Herben et al. 2004). It is, however, highly controversial which facet of diversity (species richness, functional group richness, key species with special importance of dominants) is responsible for this decreasing invasibility with increasing diversity (reviewed by Hooper et al. 2005).

In stochastic niche models, low invasibility is predicted to result from uniformly low levels of resources or open niches, not from diversity (Tilman 2004). This view supports the general theory of fluctuating resources as a trigger of invasion (above). More diverse systems, however, generally fulfill the conditions of generating low levels of unused *per se* resources better than less diverse systems (see reviews and meta-analysis by Balvanera et al. 2006, Cardinale et al. 2006).

### **Interaction between the physical environment and the resident community**

The absence of disturbance – or more generally of spatio-temporal heterogeneity – from many experimental studies on the relationship between diversity and invasibility has been criticized recently as being unrealistic and might even explain part of the invasion paradox (a negative relation between invasion and diversity at fine scales and the opposite pattern at large scales; Fridley et al. 2007). Spatial and temporal heterogeneity is even seen as a major driver of invasibility (Melbourne et al. 2007), and should therefore not be excluded in experiments (Richardson and Pysek 2006).

Based on the insurance hypothesis (Yachi and Loreau 1999), which states that more diverse systems are expected to be more resilient against perturbations, we expect that effects of extreme weather events and diversity resistance are non-additive. Viewed from the perspective of the fluctuating resource hypothesis, the increased 'predictability' (McGrady-Steed et al. 1997) or 'reliability' (Naeem 1998) of more diverse communities would imply that less unused resources would occur even in times of strong

environmental perturbations due to complementarity in disturbance response traits. Since any situation in which residents do not keep resources at uniformly low levels is a potential colonization opportunity (Shea and Chesson 2002), the insurance hypothesis predicts less invasion opportunities in more diverse systems in face of disturbance.

Consistent with this, Tilman et al. (2006) demonstrated a linear relationship between species diversity and the recovery of grassland after severe drought. But mixed results are also reported. A stabilizing effect of plant diversity during a manipulated extreme drought was found for below-ground biomass, but not for above-ground biomass in a semi-natural central European grassland (Kahmen et al. 2005). Despite these studies, no experiment so far provides data for both controlled weather manipulations and controlled diversity levels. The reported results rely either on naturally occurring weather events without comparisons with controlled weather conditions, or on naturally occurring species diversity, which might also go along with differences in substrate and stand history. In aquatic microcosms, however, evidence suggests that community level resilience (Steiner et al. 2006) and stability (McGrady-Steed et al. 1997) increases with increasing diversity within and between trophic levels.

### **The traits of the invaders**

Neutral or random assembly have been demonstrated to effectively predict observed processes in community invasibility (Herben et al. 2004). The validity of the neutral theory in this context, however, is questioned by the notion that resident species inhibit the establishment and growth of species similar to them more strongly than they inhibit species with less similar functional traits (Fargione et al. 2003, Strauss et al. 2006, Mwangi et al. 2007), thereby supporting Darwin's naturalization hypothesis, which assumes intense competition between congeners, leading to easier invasion by non-allied genera. Modern analogues to this hypothesis are stochastic niche models (Tilman 2004). The above cited empirical studies evaluated the invasion success of species in relation to their functional and/ or phylogenetic similarity to resident species.

Here, we consider the three basic factors which determine invasibility (the physical environment, the resident community, and the traits of the invaders) simultaneously by testing the following hypotheses. (1) Extreme weather events alter invasibility, with drought limiting water availability and invasibility; and heavy rainfall increasing water availability and invasibility according to the fluctuating resource hypothesis. (2) Increased diversity in terms of species richness and functional composition reduces invasibility according to expectations from the diversity resistance hypothesis. (3) Furthermore, increased diversity buffers effects of extreme weather events on invasibility according to the insurance hypothesis, with diversity and disturbance being non-additive in their effects on community invasibility. (4) Community assembly is not neutral, but depends on the identity of invaders.

## Methods

### Experimental design

The EVENT-experiment (Jentsch et al. 2007) is located in the Ecological Botanical Garden of the Univ. of Bayreuth, Germany (49°55'19''N, 11°34'55''E, 365 m a.s.l.). Mean annual temperature is 8.2°C. Mean annual precipitation reaches 724 mm. Precipitation is distributed bi-modally with a major peak in June/July and second peak in December/January (data: German Weather Service). The experiment was carried out with three fully crossed factors. The factors were (1) extreme weather events (drought, heavy rain and control), (2) community diversity (two species of one functional group, four species of two functional groups, and four species of three functional groups), and (3) two different vegetation types (grassland and heath). The setup consisted of five replicates of each factorial combination, with a total of 90 2 × 2 m plots. The factors were applied in a split-plot design with the vegetation types and diversity levels blocked and randomly assigned within each of the five replications of the weather manipulations (Jentsch et al. 2007). The soil of the experimental site consisted of homogenized substrate from a nearby sand quarry (about 80 cm in depth) underlain by drainage facilities to avoid soil related singularities. The topsoil from this quarry was used to build an upper horizon of 20 cm depth containing higher amounts of organic material (2% total carbon against 0.2% in the lower horizon). The texture of the soil body was loamy sand (82% sand, 13% silt, 5% clay) with pH = 4.5 in the upper and pH = 6.2 in the lower soil layer (measured in 1 M KCl).

### The physical environment – drought and heavy rainfall

The weather manipulations consisted of extreme drought, heavy rainfall and ambient conditions for control. Intensity of the treatments was based on the local 100-year extreme event in each category. Vegetation periods (March to September) 1961–2000 were used as the reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100-year recurrence events were calculated. Drought was defined as the number

of consecutive days with less than 1 mm daily precipitation. Accordingly, a drought period of 32 days and a rainfall extreme of 170 mm over 14 days were applied in the experiment during peak growing season in June 2005 and 2006. Maximum values in the local climate data set were 33 days without rain during June and July 1976 and 152 mm of precipitation during 14 days in June 1977.

Drought was simulated using rain-out shelters that permitted nearly 90% penetration of photosynthetically active radiation. Near-surface air temperature was slightly (mean 2005: +1.2°C; mean 2006 +1.4°C; mean 2007 +1.3°C) increased by the roofs during the weather manipulation period. Strong greenhouse effects were avoided by starting the roof at 80 cm height, allowing for near-surface air exchange.

Heavy rainfall was realized using portable irrigation systems. The whole amount of added water was divided into two applications per day to constantly ensure high soil water saturation. If natural precipitation occurred, then the amount of rain was subtracted from the respective dose. Lateral surface flow was avoided by the application of small plastic sheet pilings around treated plots.

### The resident community – community composition and diversity

Overall, ten plant species were used to install experimental plant communities of various diversity levels, which represent naturally occurring species combinations in Germany (Table 1). Two richness levels (two and four species) and three functional diversity levels (2<sup>-</sup>: one growth form, 4<sup>-</sup>: two growth forms, and 4<sup>+</sup>: two growth forms with a legume being present) were created. Species were chosen with respect to their belonging to one of the desired functional groups (grasses, herbs, legumes, dwarf shrubs), to their life-span (perennials), to their overall importance in nearby and central European grassland systems, and to the fact that they can naturally occur on substrate similar to the one used in this experiment. We use only very abundant species on comparable soil substrate. One hundred individual plants per plot were planted from pre-grown, even-aged individuals in a systematic hexagonal grid with 20 cm distance between neighbors in April 2005. All grasses and herbs were grown from seeds in autumn 2004, the three dwarf shrub species were two years old

Table 1. Communities of two vegetation types (grassland, heath) are used in three functional diversity levels, resulting in six species combinations (Abbreviations: G: grassland, H: heath, 2/4: number of species, <sup>-</sup>: without legume, <sup>+</sup>: with legume).

| Abbreviation    | Vegetation type | Diversity level | Description  | Species   |
|-----------------|-----------------|-----------------|--|---|
| G2 <sup>-</sup> | grassland       | 2 <sup>-</sup>  | two species, one functional group (grass)                                | <i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i>  |
| G4 <sup>-</sup> | grassland       | 4 <sup>-</sup>  | four species, two functional groups (grass, herb)                        | <i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Geranium pratense</i>      |
| G4 <sup>+</sup> | grassland       | 4 <sup>+</sup>  | four species, three functional groups (grass, herb, legume herb)         | <i>Arrhenatherum elatius</i> , <i>Holcus lanatus</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i>     |
| H2 <sup>-</sup> | heath           | 2 <sup>-</sup>  | two species, one functional group (dwarf shrub)                          | <i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i>  |
| H4 <sup>-</sup> | heath           | 4 <sup>-</sup>  | four species, two functional groups (dwarf shrub, grass)                 | <i>Calluna vulgaris</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i>  |
| H4 <sup>+</sup> | heath           | 4 <sup>+</sup>  | four species, three functional groups (dwarf shrub, legume shrub, grass) | <i>Genista tinctoria</i> , <i>Vaccinium myrtillus</i> , <i>Agrostis stolonifera</i> , <i>Deschampsia flexuosa</i> |

when transferred to the experimental site.

For the grassland plots, ANPP (aboveground net primary productivity) was determined by two aboveground harvests per year (one week after the weather manipulations ended, and in September) resembling local agricultural routines. For the heath plots, destructive sampling was not feasible due to the absence of such a disturbance in their natural environments and the chamaephytic life form of the key species. Instead, a set of non-destructive biometric measures were calibrated by multiple regression analysis against harvested individuals from outside the central plots, but inside the weather manipulations. For each species, a coefficient of correlation of  $r^2 > 0.8$  was reached by a combination of two or three biometric measures.

Aboveground cover of the resident communities was quantified by a pin-point method, recording the presence of plant organs at 100 vertically inserted steel needles. These values were treated as percent cover. The measurement was repeated three times over the course of a vegetation period.

### The traits of the invaders – response parameters

Invasibility of the experimental communities was recorded three times per year: before and after the weather manipulations in early summer, and in fall. Invading plant individuals were collected from the inner square meter of each plot, and subsequently separated by species. Removal took place only after the first true leaves (after the cotyledons) emerged, but most specimens were considerably older than this and clearly established in the stand. At this point in development, we expected that number of individuals give a measure of established invaders rather than chance germinations. All grasses were grouped together into one aggregate due to difficulties in determining the species of small grass seedlings. For each plot, the number of individuals per species was determined. The ten target species of the experiment were removed from the subsequent analysis, their offspring was removed only from those plots where they were not designed to be in the target species mix. All invading specimens stem from outside the experiments, as the spaces between the plots were planted with one easily recognizable species (*Lolium perenne*) and regularly mowed before this species could flower. The matrix vegetation surrounding the experiment is highly heterogeneous, including agricultural meadows, roadside vegetation, forest patches, wetlands, allotments and the botanical garden of the University, within 200 m distance. Quantitative data is not available, but the species pool consists of several hundred species.

Here, we only analyze the data from the second and third year of the experiment, as we were interested in newly dispersed seeds from the matrix vegetation. Tests confirmed that germination from the soil seed bank was negligible after one year. Furthermore, this insured a high degree of establishment of the resident communities.

### Data analysis

Linear models accounting for the split plot design with the six community compositions being blocked within the weather manipulations were combined with analysis of

variance (ANOVA) to test for significant differences between groups. Homogeneous groups were identified by Tukey HSD post hoc comparisons. Level of significance was set to  $p < 0.05$ . Prior to statistical analysis, data was log or square root transformed if conditions of normality were not met, or to improve homogeneity of variances. Both characteristics were tested by examining the residuals versus fitted plots and the normal qq-plots of the linear models (Faraway 2005). For the regression between resident cover and invasibility, a large variety of linear and non-linear models was fitted with least-squares regression. The model with the highest  $r^2$  was kept.

In order to test for differences in invading species sets between factorial groups, we conducted multi response permutation procedures (MRPP). In the case of significant differences, pair-wise comparisons with Bonferroni corrections of the significance level were performed between all levels of the factor. MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more a priori groups. Test statistics describe the separation between the groups. Sørensen index was used as the dissimilarity measure due to its robustness with vegetation data (Faith et al. 1987). MRPP was applied according to the method described by McCune and Grace (2002) using the function `mrpp` of package `vegan` for the R statistics system. An unconstrained ordination was applied to illustrate the similarity between invading species compositions of each plot. We used non-metrical multidimensional scaling (NMDS) according to the procedure recommended by Minchin (1987) using the function `metaMDS` of package `vegan` for the R statistics system.

In order to examine the affinity of particular species to different weather manipulations or community compositions, we conducted an indicator species analysis (Dufrene and Legendre 1997) on abundance data with the function `duleg` of package `labdsv` for the R statistics system.

The inhibition of invaders by functionally similar resident species was evaluated by two approaches. First, invasion success of the functional groups was compared between communities where this functional group was present or absent. Significance of difference in mean was evaluated by a permutation procedure of 1000 permutations with the function `diffmean` of package `simba` for the R statistics system, because data points were not independent and number of observations per compared group was unequal. Second, cover of broad functional groups (grasses, forbs, shrubs, legumes) within the resident communities was correlated with the number of invaders from the same functional group and of all other functional groups with least-squares linear regression of the log-transformed number of invading individuals.

## Results

Overall, 6543 individuals of 65 species or aggregates were found in 2006, 3051 individuals of 49 species in 2007. All invading species also occurred in the vicinity of the experimental site and comprise common grassland and some ruderal species (Appendix 1).

## The physical environment – drought and heavy rainfall

Even though the applied weather manipulations led to strong changes in soil moisture (Fig. 1), total resident cover as well as biomass remained surprisingly stable in face of repeated weather events of 100 year recurrence (Fig. 2).

The drought manipulation, nevertheless, decreased invasibility by about one third, whereas the heavy rainfall manipulation nearly doubled invasibility in both years (Fig. 3). This effect was not visible in spring before the weather manipulation, significant directly after the manipulation in summer, and most pronounced in autumn (data not shown).

## The resident community – community composition and diversity

Invasibility was enhanced with decreasing community diversity (Fig. 3). The differences between diversity levels, however, were only significant between the least diverse level ( $2^-$ ) and the two other levels ( $4^-$  and  $4^+$ ; Tukey HSD post hoc comparison).

Higher invasibility was generally found for the heath communities compared to the grassland communities. The two vegetation types also exhibited a difference in their diversity effect (see interaction between vegetation type and diversity level in Fig. 3). This interaction effect between vegetation type and diversity level was due to the extremely high invasibility of the least diverse heath community. However, both vegetation types showed the same general decline of invasibility with increasing diversity, with only the slope of this decline differing.

## Interaction between the physical environment and the resident community

The decreased invasibility due to increasing diversity and the changes in invasibility due to the extreme weather manipulations were additive, as no significant interaction between these two factors were found (Fig. 3). This means that changes in the physical environment had the same effects irrespective of vegetation type or diversity level. And, vice versa, diversity resistance to invasion remained constant even under fluctuating conditions in the physical environment.

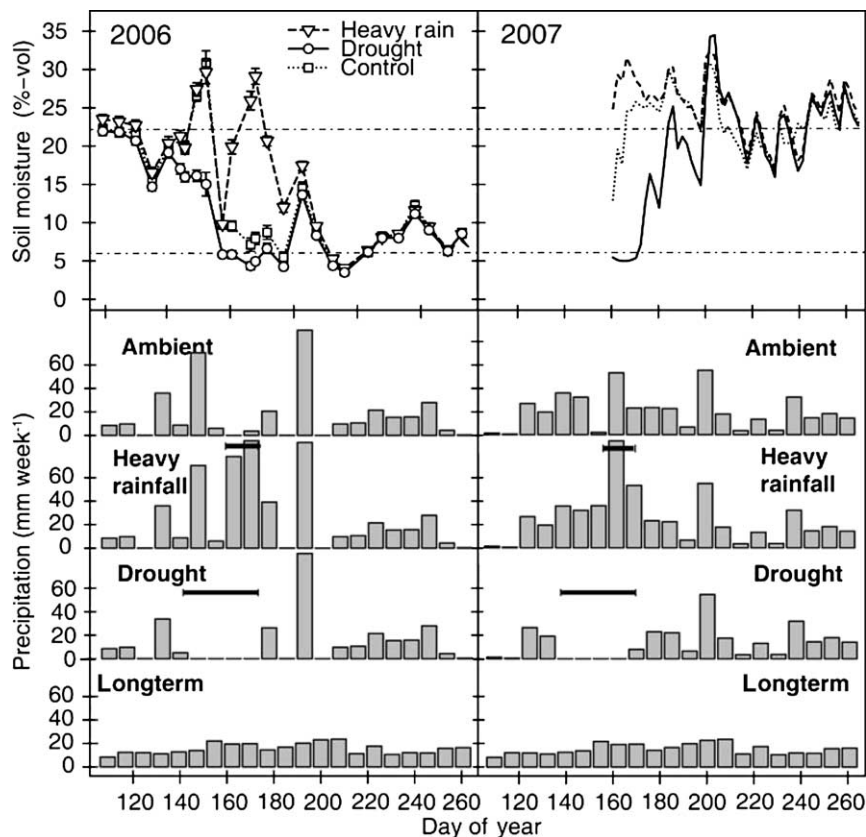


Figure 1. Soil moisture and precipitation in the EVENT experiment during manipulation and recovery after extreme drought and heavy rainfall events. Mean values and standard errors of TDR tube access probe measurements at  $-10$  cm are given for 2006. For 2007, 48 h mean values of hourly measurements by FD-sensors between  $-5$  and  $-10$  cm are given ( $n = 5$  per weather manipulation). Upper dot-dashed line indicates field capacity ( $pF = 1.8$ ), lower dot-dashed line indicates permanent wilting point ( $pF = 4.2$ ) of the soil substrate (AG Boden 1996). Grey bars show weekly precipitation for the weather manipulations in comparison with ambient conditions (control) and the long term mean precipitation 1961–2000 (data: German Weather Service, Station Bayreuth). Timing and duration of the weather manipulations is indicated by black vertical bars.

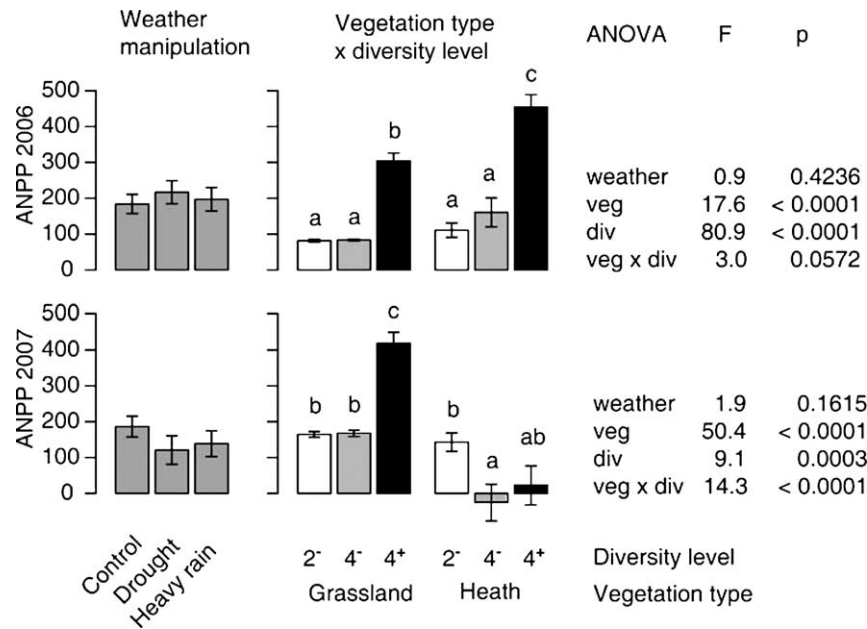


Figure 2. Annual above-ground productivity of experimental communities. Shown are mean values and standard errors in  $g\ m^{-2}$ . Letters display homogenous groups of the interaction between vegetation type and diversity level according to Tukey HSD post hoc comparisons. No significant effect of weather manipulations or interaction with weather manipulation was found at any time, ANOVA results are provided next to barplots.

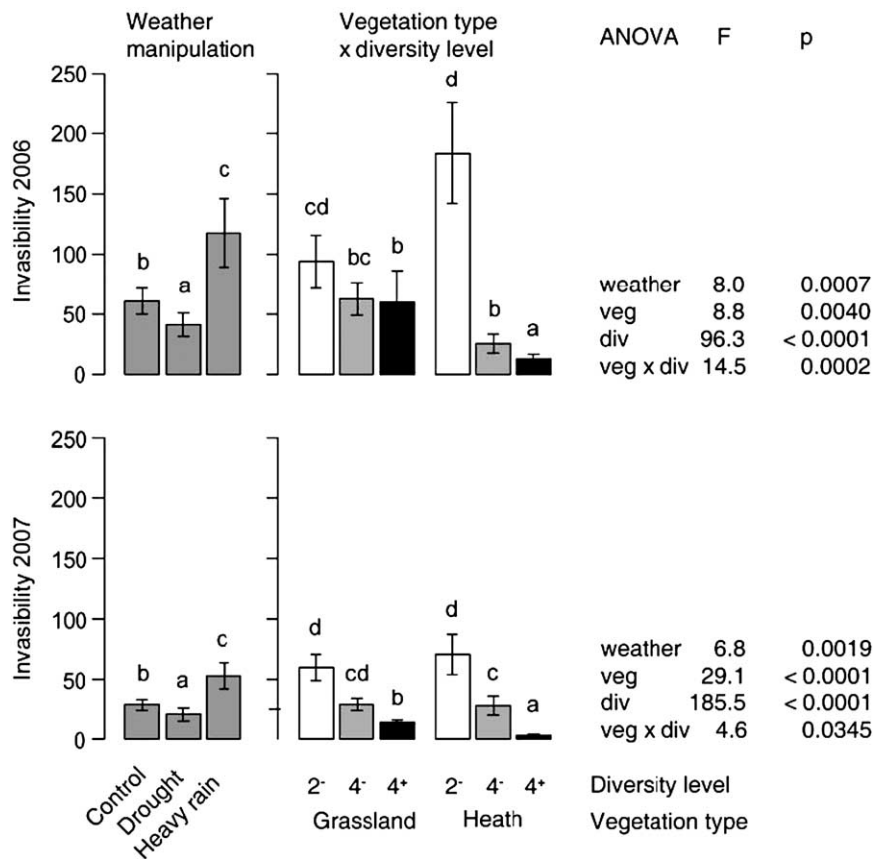


Figure 3. Total invasibility in 2006 and 2007. Shown are mean numbers and standard errors of invading individuals  $m^{-2}$ . Letters display homogenous groups of weather manipulations and of the interaction between vegetation type and diversity level according to Tukey HSD post hoc comparisons. No significant interaction with weather manipulation was found at any time, other ANOVA results are provided next to barplots.

## The traits of the invaders

Significant differences in the composition of the invading species sets within the three factors (extreme weather event, diversity level, vegetation type) were found by the multi response permutation procedure, but these differences were small and no clear grouping occurred in the ordination (Fig. 4). In particular, the differences in species composition within weather manipulations (Fig. 4A) and within vegetation types (Fig. 4C) were subtle, although significant. Higher compositional differences in the invading species sets were found between diversity levels of the resident communities, where total difference in the invading species sets was already 12% (Fig. 4B). In the pair-wise comparisons of diversity levels, the lowest level differed significantly from both other levels. The interaction between vegetation type and diversity level accounted for 18% differences in the invading species compositions, with the lowest diverse and the highest diverse heath community being most strongly distinguished from each other and from the other communities (Fig. 4D).

Several invading species showed significant affinities to one weather manipulation (Table 2). In general, species with high affinity to the heavy rainfall treatment are known to also occur naturally in moist conditions, whereas the

species with significant affinity to the drought manipulation commonly occur in drier habitats (see Ellenberg indicator values in Table 2). There were also species with significant affinity to one or more of the experimental plant communities (Table 3). The general pattern of decreased invasibility into the more diverse communities is displayed by the fact that grouping by diversity level also resulted in significant indicator values. But even though most species showed highest relative abundances in the least diverse communities, there are also two species, *Trifolium repens* and *Sonchus* sp. with significant affinity to the four species community without legumes.

No general trend towards stronger inhibition of functionally similar invaders was found. Presence of grasses in the resident community led to a strongly reduced invasion success by grasses, but this relationship was inverted for forbs. No significant effect was found for shrubs and legumes (Fig. 5A). These effects, however, were similar for members of the other functional groups (Fig. 5B). Legumes and shrubs in the resident communities even suppressed non-allied species stronger than members of their functional groups. Generally, no strong correlations between cover of the functional group in the resident community and invasion success were found even though linear regressions were significant for all but the models containing resident forbs

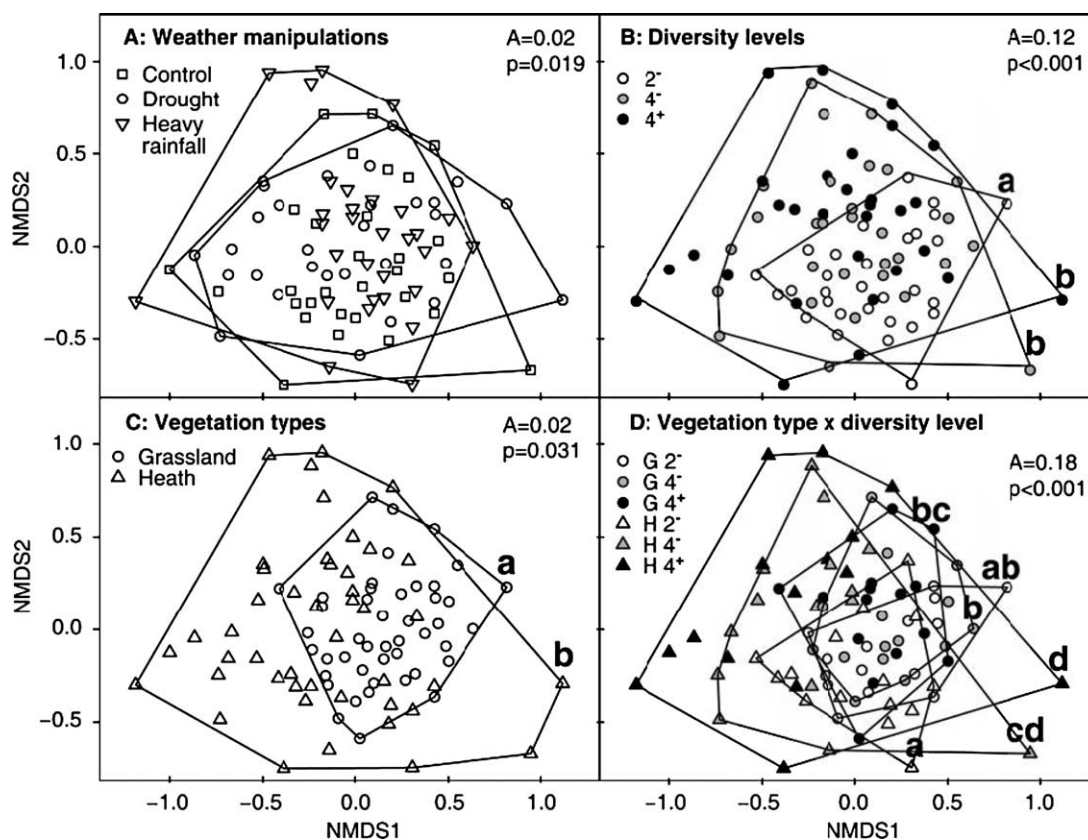


Figure 4. Ordination of species sets invading the experimental plant communities. Shown is the output of a non-metrical multi-dimensional scaling ordination (NMDS) of invading species compositions after 20 random starts of a two-dimensional solution (final stress = 26.78, rmse = 0.0783, max residual = 0.36). Outlines of the positions of the three factors (weather manipulation, diversity level, vegetation type) and the interaction between vegetation type and diversity level (abbreviations see Table 1) in ordination space (shortest distance) are shown in the four panels. Within-group homogeneity (A) and significance of differences between groups (p) are based on a multi response permutation procedure (MRPP). Letters next to the outlines indicate homogenous groups within the factor according to pair-wise MRPP comparisons with Bonferroni corrections between all factor levels.

Table 2. Invading species with significant indicator values for weather manipulations according to an indicator species analysis of all species which were found with more than 10 individuals in 2006. Shown are relative abundance values in each group and the significance p. Highest relative abundance values between groups are set off bold. Ellenberg indicator values of ecological behaviour for moisture run from 1 – extreme dryness – to 9 – often water saturated – (Ellenberg et al. 2001). If identification was not successful to the species level, values are given in parenthesis as range between the possible species.

|                             | Control | Heavy rainfall | Drought     | p     | Ellenberg moisture |
|-----------------------------|---------|----------------|-------------|-------|--------------------|
| <i>Juncus bufonius</i>      | 0.23    | <b>0.73</b>    | 0.03        | 0.011 | 7                  |
| <i>Epilobium spec</i>       | 0.24    | <b>0.67</b>    | 0.09        | 0.017 | (5–7)              |
| <i>Juncus spec</i>          | 0.28    | <b>0.64</b>    | 0.09        | 0.025 | (7–9)              |
| <i>Taraxacum officinale</i> | 0.26    | <b>0.62</b>    | 0.12        | 0.001 | 5                  |
| <i>Carex c.f. ovalis</i>    | 0.26    | <b>0.57</b>    | 0.17        | 0.025 | 7                  |
| <i>Trifolium repens</i>     | 0.26    | <b>0.48</b>    | 0.27        | 0.011 | 5                  |
| <i>Sonchus spec</i>         | 0.00    | 0.40           | <b>0.60</b> | 0.020 | (4–5)              |
| <i>Rumex acetosella</i>     | 0.17    | 0.31           | <b>0.52</b> | 0.027 | 3                  |

(Table 4). The slope of the significant regressions was similar for grasses and other species for the resident grasses. Shrubs showed a weak trend to inhibit woody plants more strongly than other functional groups. Legumes, however, inhibited other functional groups stronger than other legumes.

## Discussion

### The physical environment – drought and heavy rainfall

Application of weather events with 100 years recurrence did not alter resident above-ground cover, i.e. they did not provide changes in the invasibility by creating physical disturbance of the biomass or by creating bare ground in the first (Kreyling et al. in press) or the subsequent years of the weather manipulations in our experiment (Fig. 2). We find no significant correlation between invasibility and above-ground productivity or cover of the resident stand ( $r^2 = 0.04$  for a linear regression between number of invading individuals and aboveground cover of the resident plant communities). Compared to natural communities, productivity of the grassland plots is within the natural range of extensively managed grassland in the region (200–700 g ha<sup>-1</sup>), but at the lower productivity end.

Despite the missing effects of extreme weather events on above-ground resident productivity, the applied events

changed invasibility. The observed effects support expectations from the fluctuating resource hypothesis (Davis et al. 2000) or the environmental heterogeneity hypothesis (Melbourne et al. 2007) with increased invasibility during and after times of enhanced resource availability (heavy rainfall), and decreased invasibility during and after times of strong competition and resource limitation (drought). Fluctuating resources therefore challenge the competitive interaction between resident and invading species. The first experimental set-up to test the fluctuating resources hypothesis, in fact, applied weather manipulations remarkably similar to ours in an old field at Cedar Creek, USA (Davis and Pelsor 2001). Observational studies confirm the finding that climatic variability promotes invasibility by non-native species in years of low resource use by the resident community (Cleland et al. 2004).

Water is known to be the limiting resource for plant performance in semi-arid ecosystems, with increased soil moisture availability generally enhancing invasibility (Thomsen et al. 2006b). A review (Dukes and Mooney 1999) has shown that in dry regions, increase of water supply (whether by natural rainfall or by experimental additions) generally increases the invasibility, whereas imposed drought conditions decrease invasibility of the same communities.

It is somewhat surprising that water availability was able to act as the main determining factor in the temperate

Table 3. Invading species with significant indicator values for community compositions (vegetation type × diversity level) according to an indicator species analysis of all species which were found with more than 10 individuals in 2006. Shown are relative abundance values in each group and the significance  $p_{veg \times div}$ . Highest relative abundance values between groups are set off bold.  $p_{veg}$  indicates significance between vegetation types and  $p_{div}$  between diversity levels.

|                              | Dispersal agent | Grassland       |                 |                 | Health          |                 |                 | $p_{veg \times div}$ | $p_{veg}$    | $p_{div}$    |
|------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|----------------------|--------------|--------------|
|                              |                 | G2 <sup>-</sup> | G4 <sup>-</sup> | G4 <sup>+</sup> | H2 <sup>-</sup> | H4 <sup>-</sup> | H4 <sup>+</sup> |                      |              |              |
| <i>Conyza canadensis</i>     | wind (pappus)   | <b>0.62</b>     | 0.26            | 0.09            | 0.01            | 0.01            | 0.00            | <b>0.009</b>         | <b>0.001</b> | 0.159        |
| <i>Gnaphalium uliginosum</i> | wind (pappus)   | <b>0.44</b>     | 0.25            | 0.25            | 0.06            | 0.00            | 0.00            | <b>0.011</b>         | <b>0.001</b> | 0.108        |
| <i>Taraxacum officinale</i>  | wind (pappus)   | <b>0.36</b>     | 0.14            | 0.16            | 0.25            | 0.08            | 0.02            | <b>0.013</b>         | <b>0.005</b> | <b>0.002</b> |
| <i>Sonchus spec</i>          | wind (pappus)   | 0.30            | <b>0.50</b>     | 0.00            | 0.20            | 0.00            | 0.00            | <b>0.004</b>         | 0.099        | 0.189        |
| <i>Trifolium repens</i>      | wind/vegetative | 0.12            | <b>0.31</b>     | 0.26            | 0.07            | 0.13            | 0.11            | <b>0.025</b>         | <b>0.002</b> | <b>0.010</b> |
| Lamiaceae spec               | ants            | 0.00            | 0.00            | 0.00            | <b>1.00</b>     | 0.00            | 0.00            | <b>0.017</b>         | 0.221        | 0.114        |
| <i>Cerastium glomeratum</i>  | wind/water      | 0.08            | 0.00            | 0.00            | <b>0.92</b>     | 0.00            | 0.00            | <b>0.002</b>         | <b>0.023</b> | <b>0.004</b> |
| <i>Spergula arvensis</i>     | wind            | 0.05            | 0.10            | 0.03            | <b>0.81</b>     | 0.00            | 0.01            | <b>0.001</b>         | 0.224        | <b>0.001</b> |
| <i>Rumex acetosella</i>      | unspecialized   | 0.18            | 0.08            | 0.11            | <b>0.58</b>     | 0.03            | 0.02            | <b>0.002</b>         | 0.666        | <b>0.001</b> |
| Poaceae aggregate            | wind            | 0.25            | 0.10            | 0.09            | <b>0.51</b>     | 0.04            | 0.02            | <b>0.001</b>         | 0.988        | <b>0.001</b> |
| <i>Viola arvensis</i>        | ants            | 0.08            | 0.17            | 0.00            | <b>0.42</b>     | 0.00            | 0.33            | <b>0.027</b>         | <b>0.026</b> | 0.465        |



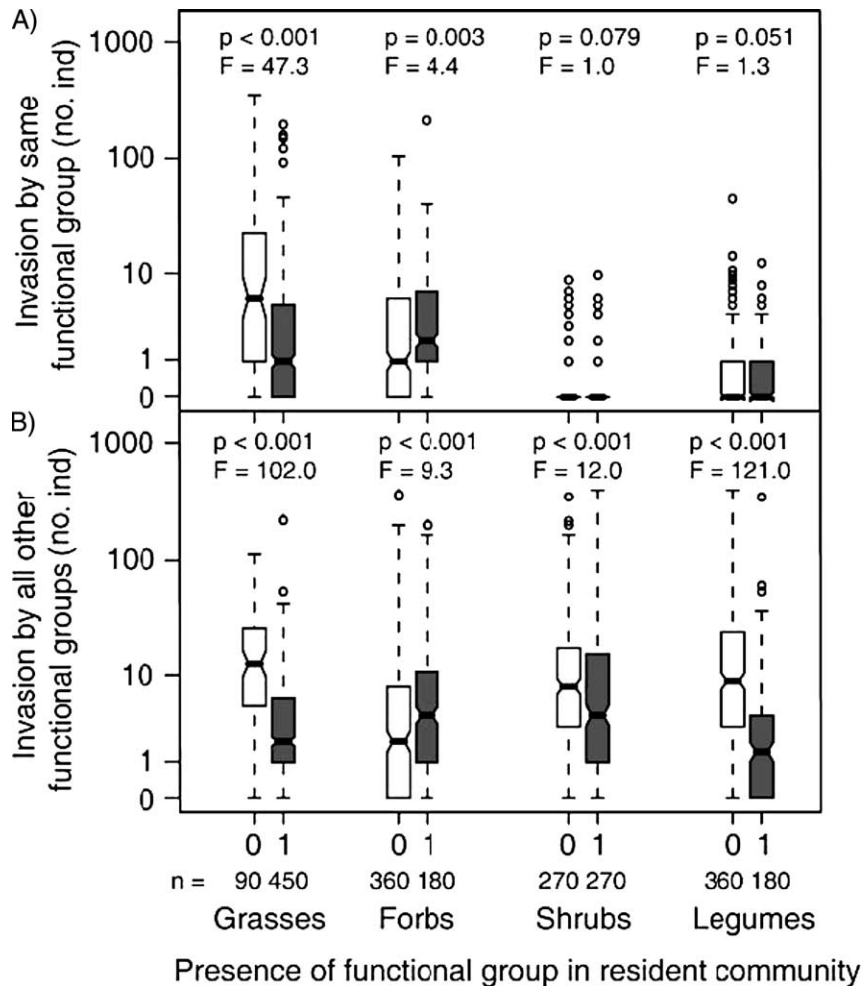


Figure 5. Invasion success separated by functional groups as function of presence or absence of the same group in the resident community. (A) Invasion success of same functional group, (B) invasion success of all other functional groups combined. For each pair of boxes  $n = 540$  (three dates in both years of 90 plots).

environment of our experiment. Even without changing total aboveground productivity of the resident stands, relative competitive ability between species might have been influenced (Kreyling et al. in press) and this can also alter invasibility (Fay et al. 2003). The sandy substrate may also play an important role here, leading to fast water percolation. Furthermore, indirect effects such as decreased mineralization may add to our findings (Davis and Pelsor 2001).

Besides the effects of the manipulations themselves, the temporal development of invasibility is remarkable. The

extreme weather effects were most significant in autumn, two months after the weather manipulations in June and after one removal of all initial invaders. Such a legacy of the effect is also described in another field experiment where fluctuations in water availability as short as a few weeks had a large impact on plant invasion success (survival and percentage cover) for up to one year following the fluctuations (Davis and Pelsor 2001). There, it was concluded that the primary reason for the legacy effect of wet or dry spells is their pronounced impact on the survival of the germinating seedlings. Even though we find a similar

Table 4. Significance,  $r^2$ , and parameters of linear regression between cover of functional groups in the resident communities and log number of invaders from the same and from all other functional groups.  $n = 540$  pairwise comparisons of three weeding actions both in 2006 and 2007.

| Resident group | Invading group | p      | Adj. $r^2$ | Intercept | Slope  |
|----------------|----------------|--------|------------|-----------|--------|
| Grasses        | grasses        | <0.001 | 0.11       | 1.80      | -0.011 |
|                | others         | <0.001 | 0.16       | 2.14      | -0.013 |
| Forbs          | forbs          | 0.180  | 0.00       | 1.27      | -0.003 |
|                | others         | 0.761  | 0.00       | 1.55      | -0.000 |
| Shrubs         | shrubs         | 0.026  | 0.01       | 0.16      | 0.001  |
|                | others         | <0.001 | 0.03       | 1.87      | 0.007  |
| Legumes        | legumes        | 0.007  | 0.01       | 0.51      | -0.002 |
|                | others         | <0.001 | 0.21       | 2.30      | -0.017 |

pattern, we cannot explain it by the proposed mechanism, because invaders present during the phase of precipitation manipulations were removed after the manipulations ended in July. A significant treatment effect, nevertheless, was still found in September. Thus, competitive balance of the resident community is affected longer than the short duration of the weather manipulation itself. Overall, our findings on invasibility related to changes in the physical environment can convincingly be explained by the fluctuating resource hypothesis.

### **The resident community – community composition and diversity**

The fluctuating resource hypothesis, however, does not necessarily imply a relationship between resident species diversity and its susceptibility to invasion (Davis et al. 2000). Like many other (experimental) studies (reviewed by Fridley et al. 2007), we observe a decrease in invasibility with increasing diversity level. Although not a true diversity experiment due to the fact that diversity levels were not repeated with different species sets, the consistency between two functionally different vegetation types in our experiment implies some generality of this pattern. Such a negative relationship between resident diversity and invasibility can be brought into accordance with the fluctuating resource hypothesis when viewed together with ideas in stochastic niche concepts or niche opportunities. These concepts predict higher niche filling in functionally more diverse communities, leading generally to low levels of unused resources (Shea and Chesson 2002, Tilman 2004). Accordingly, total biomass of introduced species is often positively correlated with levels of available (unconsumed) resources, such as nitrate, initial bare ground, or light transmittance (Fargione et al. 2003). Diversity levels within this experiment are low, but it is noteworthy in this context that the well-known diversity experiments of the last decade all have shown that the diversity effects occur mainly within the range between monocultures and three to five species (Hooper et al. 2005, Cardinale et al. 2006).

Within the ongoing debate about which facet of diversity is responsible for the overall diversity resistance effect (reviewed by Richardson and Pysek 2006), competitive dominance has been proposed to be of high importance (Wardle 2001). Heath communities are naturally restricted to nutrient-poor habitats in central Europe, and their plasticity in reacting to changing conditions may be limited due to their perennial, woody growth form. Under conditions of increased nutrient supply, grasses commonly out-compete dwarf-shrubs (Wessel et al. 2004). Thus, the particular growth form and life strategy may hint at a competitive disadvantage of the dwarf shrubs and could – rather than richness-help to explain the high levels of invasibility into the lowest diverse heath community, which is composed of only two dwarf shrubs.

Legumes generally increase nitrogen availability and their presence has therefore been related to increased invasibility (Maron and Jeffries 2001, Prieur-Richard et al. 2002). But other studies contradict this relationship: Removal of legumes does not change invasibility in a diverse Scandinavian grassland (Eriksson et al. 2006), and

experimentally increased levels of nitrogen availability does not influence competition between native and exotic grass species in California (Thomsen et al. 2006a). The observed decrease of invasibility in our communities containing legumes might therefore be explained by increased niche filling due to the presence of another functional group (Mwangi et al. 2007) rather than by changes in the nutrient status of the system caused by these species.

The highly artificial community set-up of even-aged and evenly distributed plant individuals could have had an effect on invasibility itself besides being different from natural communities, but recent findings suggest that evenness of resident communities has no effect on invasibility in grasslands (Mattingly et al. 2007). Our findings generally support the diversity resistance hypothesis, which can be explained by niche theory.

### **Interaction between the physical environment and the resident community**

The effects of fluctuating resources (due to the weather manipulations) and biotic resistance (due to community composition) were independent in our experiment, which means that the enhancement of biotic resistance due to higher diversity is not altered by fluctuating environmental conditions. No additional buffering in the more diverse communities the insurance hypothesis (Yachi and Loreau 1999) was apparent. Resource fluctuations and differences in diversity resistance had about the same effect on invasibility in our experiment (Fig. 3), but we assume that their net balance and relative importance will strongly, and maybe not even linearly, depend on differences in community composition (not only species richness) and magnitude of disturbance in natural communities. Furthermore, resident diversity and physical disturbance feed back on each other, with initial diversity, regeneration rate, and disturbance frequency determining the outcome (Hughes et al. 2007).

The observed pattern of diversity resistance in a fluctuating physical environment in our experiment can be explained by linking niche concepts and the fluctuating resource hypothesis. Whether environmental fluctuations increase or decrease invasibility depends further on the interaction in timing of fluctuations and response by residents and invaders (Schoolmaster and Snyder 2007). This is in accordance to Shea and Chesson (2002), who state that invaders must nevertheless have an advantage over residents in some places or times via different life-history traits. This contradicts neutral assembly theories, and we follow these ideas by having a closer look at community assembly processes and specific traits of the invaders.

### **The traits of the invaders**

Subtle, but significant differences between the invading species sets were found, with stronger differences between the experimental plant communities than between the applied weather manipulations. The indicator species analysis revealed several species with significantly higher affinity to one of the weather manipulations or resident community compositions. Species identity of the invading species

therefore mattered for their invasive success. This clearly contradicts expectations from neutral species assembly. Even short term resource fluctuations can therefore determine not only invasibility in general, but also invading species identity and, presumably, future community development.

Our findings indicate that short term changes in water availability already differentiate between the invading species. Species show successful establishment under conditions that, although only during the short manipulation events, resemble the conditions of their natural environments (Table 2). The conditions at time of seedling establishment are therefore of high importance for the species composition of a given environment. As most removed individuals were well established with several developed leaves after the cotyledons, as no dead individuals of this age occurred within the three years of the study, and as total numbers rather than timing of occurrence were altered, the manipulations influenced establishment and not just the breaking of seed dormancy. The pattern can be explained in relation to niche theory; species with niche requirements poorly represented in relation to niche width at a given time may establish with relatively little resistance (Tilman 2004). From this study, however, we are not able to tell if these species, once they are established, would also survive in the long run, because they were removed after establishment. The removal of invaders causes inevitably minor soil disturbance, plots with higher numbers of invading individuals therefore also received a slightly increased density of soil disturbance. This potentially confounding factor is not further considered here.

Interestingly, all species with significant affinity to one of the grassland communities have a pappus (Table 3). Canopy roughness of grassland seems to favor this dispersal mode. In the heath communities, however, seeds with pappuses were often trapped in the more complex canopy of the stands, preventing them from reaching the ground (personal observation). Therefore, in heath, small sized wind dispersed species without winged organs are facilitated. Furthermore, ant dispersal seems to be especially successful in the heath systems. Again, this contradicts expectations from neutral species assembly and points at the importance of individual species traits for successful invasion (Funk and Vitousek 2007). The observed differences in invasion success warn furthermore that general conclusions about invasibility of communities should not be drawn from studies on single invading species (Emery 2007).

Several studies have shown that resident species inhibit the establishment and growth of species similar to them more strongly than they inhibit species with less similar functional traits (Fargione et al. 2003, Strauss et al. 2006, Mwangi et al. 2007). In our study, no general trend towards stronger inhibition of functionally similar invaders was found. The results imply, however, that some functional groups have stronger inhibitive power than others. Especially the grasses suppressed invasion by both, other grasses as well as members of the other functional groups. This finding points again towards the importance of key species with high competitive power in the control of invasibility (Wardle 2001).

One important interaction not considered in our study is propagule pressure or the availability of propagules at favorable times for invasion (Ejrnæs et al. 2006, Thomsen

et al. 2006b). Propagule pressure appears to be especially important for invasibility because at least natural temperate grassland communities are recruitment limited and rarely saturated with species (Tilman 1997). Furthermore, even communities of high resistance in terms of available resources and competition can be invaded if propagule pressure gets sufficiently high (D'Antonio et al. 2001).

## Conclusions

Increasing variability in precipitation and presumably also in other climate parameters are one important aspect of climate change (IPCC 2007). This development in the physical environment will have strong effects on plant community invasibility and therefore community development. In accordance to the fluctuating resource hypothesis, this implies that the predicted increase in variability of precipitation due to climate change may decrease resistance against invasion, or more general, that stochastic factors strongly influence invasibility.

On the other hand, our data support the notion that diversity resistance is additive to such effects and can be explained by the interplay between the fluctuating resource hypothesis and niche opportunities. This fact highlights the need to protect diversity as an important tool to mitigate unwanted changes in ecosystems.

Understanding the role of environmental variation in the assembly and maintenance of communities is vital to our ability to predict community development – and thereby maintain ecosystem services. Linking fields such as invasion biology, community ecology and global change research seems necessary to improve our understanding of plant community development in a changing world.

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## Appendix 1.

| Invading species                  | Invading species continued             |
|-----------------------------------|--|
| <i>Ajuga reptans</i>              | <i>Prunus</i> sp.                      |
| <i>Alchemilla</i> sp.             | <i>Quercus</i> sp.                     |
| <i>Anagallis arvensis</i>         | <i>Ranunculus</i> c.f. <i>flammula</i> |
| <i>Betula pendula</i>             | <i>Ranunculus</i> sp.                  |
| <i>Cardamine</i> sp.              | <i>Rubus</i> sp.                       |
| <i>Carex</i> c.f. <i>ovalis</i>   | <i>Rumex acetosella</i>                |
| <i>Cerastium glomeratum</i>       | <i>Salix</i> sp. 1                     |
| <i>Chenopodium album</i>          | <i>Salix</i> sp. 2                     |
| <i>Cirsium arvense</i>            | <i>Scleranthus annuus</i>              |
| <i>Conyza canadensis</i>          | <i>Solidago canadensis</i>             |
| <i>Daucus carota</i>              | <i>Sonchus</i> species                 |
| <i>Epilobium</i> sp.              | Sp. 1                                  |
| <i>Equisetum arvense</i>          | Sp. 2                                  |
| <i>Erica tetralix</i>             |  |
| <i>Erigeron annuus</i>            | Sp. 3                                  |
| <i>Galium mollugo</i>             | <i>Spergula arvensis</i>               |
| <i>Galium</i> sp.                 | <i>Spergularia rubra</i>               |
| <i>Geranium pusillum</i>          | <i>Stellaria media</i>                 |
| <i>Geranium robertianum</i>       | <i>Stellaria</i> sp.                   |
| <i>Gnaphalium uliginosum</i>      | <i>Tanacetum</i> sp.                   |
| <i>Hypericum perforatum</i>       | <i>Taraxacum officinale</i>            |
| <i>Hypochoeris</i> sp.            | <i>Trifolium arvense</i>               |
| <i>Juncus bufonius</i>            | <i>Trifolium dubium</i>                |
| <i>Juncus</i> c.f. <i>effusus</i> | <i>Trifolium pratense</i>              |
| <i>Lapsana communis</i>           | <i>Trifolium repens</i>                |
| <i>Leontodon autumnalis</i>       | <i>Tripleurospermum maritimum</i>      |
| <i>Lupinus polyphyllus</i>        | <i>Ulmus</i> sp.                       |
| <i>Luzula multiflora</i>          | <i>Urtica dioica</i>                   |
| <i>Myosotis arvensis</i>          | <i>Veronica officinalis</i>            |
| <i>Pinus sylvestris</i>           | <i>Vicia angustifolia</i>              |
| <i>Plantago major</i>             | <i>Viola arvensis</i>                  |
| Poaceaea sp.                      | <i>Viola odorata</i>                   |
| <i>Potentilla</i> sp.             |  |