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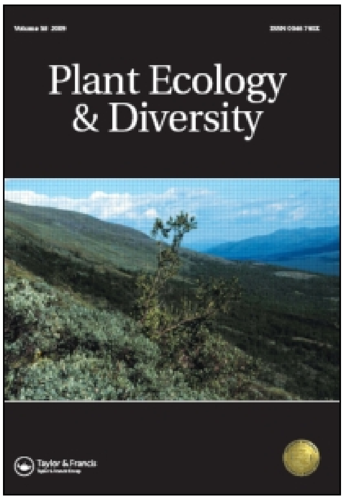

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Winter warming pulses affect the development of planted temperate grassland and dwarf-shrub heath communities

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Background: Winter conditions are changing considerably due to climate change. Resulting alterations in the frequency of soil freeze–thaw cycles (FTCs) are ecologically important.
Aim: We quantified the impact of winter soil-warming pulses on the community structure of temperate plant communities.
Methods: The cover of vascular plant species in two vegetation types, each at three diversity levels, was recorded 1 year before to 3 years after an FTC-manipulation that added five additional FTCs. Changes in species abundance patterns (Bray–Curtis similarity) were analysed by linear mixed effect models.
Results: Communities exposed to additional FTCs showed less change in their species abundance patterns than the reference plots. Community development in the grassland differed between the FTC-manipulation and the reference plots in the first growing season after the FTC-manipulation, but such effects disappeared over time, whereas the divergence from the reference plots in the dwarf-shrub heath started in the second year after the FTC-manipulation and effects grew over time. Responses to FTCs were related to growth forms: some grasses increased after the FTC-manipulation, whereas the cover of dwarf shrubs was reduced. There was less change in species abundance distributions in the more diverse communities with legumes present.
Conclusions: Winter climate change is a critical driver of temperate ecosystems. Short-term climatic events can have long-term implications on the structure of ecosystems. Community composition regulates alterations in the development and competitive balance of plant communities caused by soil warming pulses.

Keywords: diversity–stability; EVENT-experiment; freeze–thaw cycles; freezing–thawing; legume effect; soil frost; winter ecology

Introduction

Winter has predominantly been viewed as the dormant season in temperate ecosystems. However, some plants remain photosynthetically active (Starr and Oberbauer 2003; Steenberg-Larsen et al. 2007) and are capable of taking up nutrients (Bilbrough et al. 2000; Grogan et al. 2004; Andresen and Michelsen 2005) even under winter conditions. Many ecological processes that strongly affect the environment of plants, such as mineralisation, nutrient leaching, physical changes to soil properties, or CO_2 losses during the subsequent growing season are related to snow cover and soil frost regimes (Edwards et al. 2007; Öquist and Laudon 2008). Climate change in winter can therefore be expected to impact plant communities and ecosystem functioning in boreal and arctic, but also in temperate, ecosystems (Kreyling 2010). The magnitude of climate change in winter is projected to be greater than in other seasons (Solomon et al. 2007). The frequency of soil freeze–thaw cycles (FTCs), for instance, is expected to increase under reduced snow cover in winter as a result of a decrease in the insulation of the soil by snow (Groffman et al. 2001). Observations (Henry 2008) and climate modelling (Venalainen et al. 2001) have confirmed an expected increase in the frequency of FTCs, which are known to cause nitrogen (N) flushes, and to temporally increase N availability and nitrate leaching (DeLuca et al. 1992; Fitzhugh et al. 2001; Groffman et al. 2001; Monson et al. 2006; Matzner and Borken 2008). This may have implications for vegetation dynamics, as higher N availability facilitates species turnover (Tilman 1987).

Temperate grasslands can increase their productivity in the growing season after an increased frequency of FTCs (Kreyling et al. 2008). Tracer experiments after a final thaw indicated a rapid uptake and allocation of N into aboveground organs by grasses, whereas in shrubs the N-tracer was found in the root systems only (Grogan et al. 2004). The capacity to use the mobilised nutrients may therefore differ substantially between growth forms, such as grasses, forbs, and dwarf shrubs. This may be reflected in considerable differences in the response to increased FTCs between vegetation types, with grassland benefiting from FTC-events in terms of biomass production and dwarf-shrub heath being adversely affected – a pattern that has been linked to N deficiency in dwarf-shrub heaths (Kreyling et al. 2010).

Any species- or growth form-specific differences in nutrient uptake and productivity after increased FTCs could

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lead to changes in competitive balance and, ultimately, to altered community composition as was reported by Joseph and Henry (2008) for a temperate site in Canada. In arctic or alpine environments winter may play a far greater role in shaping communities compared with temperate settings (e.g. temperature extremes, timing of FTCs). For instance, Bokhorst et al. (2009) reported damage to subarctic vegetation after mid-winter warming pulses, again with species-specific differences. Snow depth and the time of snowmelt are further known to affect composition and diversity in alpine snowbeds (Schoeb et al. 2009) or competitive interactions in subarctic tundra (Wipf et al. 2006). Existing community composition (functional types) may therefore be an important driver of the vegetation response to FTCs.

More diverse communities are generally expected to be more resilient to external perturbations than less diverse ones (Tilman et al. 2006). However, it is highly controversial as to which facet of diversity (species richness, functional group richness, key species with the special importance of dominants, the presence of specific functional groups, such as legumes) is responsible for the observed diversity effects (Hooper et al. 2005). None of the empirical evidence in the diversity–stability debate originates from the study of winter climate parameters, but the general expectation that more diverse communities are more stable when exposed to perturbations should also hold true here.

In this study, we evaluated the effects of experimentally increased frequency of FTCs on grassland and dwarf-shrub heath communities – expressed as changes in species abundance distribution on experimental plots – over the three growing seasons that followed the FTC-manipulation. Synthetic grassland and dwarf-shrub heath communities were subjected to winter warming pulses by a combination of below-ground heating cables and above-ground plastic tunnels during the winter of 2005/2006. We then examined the response of the communities through the 2006, 2007 and 2008 growing seasons. We hypothesised that (1) increased FTCs induced measurable changes in the composition of plant communities in comparison with the reference plots. We expected that (2) the functional composition of the plant community determined the direction and magnitude of changes in species abundance distributions due to different responses by growth forms (grasses, forbs, and dwarf shrubs); and (3) higher functional diversity increased resilience against FTCs. Previous reports on this experiment have focused on above- and below-ground productivity and enzyme activity in grasslands within one growing season after the FTC-manipulation (Kreyling et al. 2008) and on differences in above-ground productivity between grasslands and dwarf-shrub heath communities (Kreyling et al. 2010). The focus here is on the response of community composition and species abundance patterns as a function of initial species/functional group composition.

Materials and methods

Experimental site

This study was part of the EVENT-experiment (Jentsch et al. 2007) located in the Ecological-Botanical Garden of the University of Bayreuth, Germany (49° 55′ 19″ N, 11° 34′ 55″ E; 365 m a.s.l.; mean annual temperature: 7.9 °C; mean annual precipitation: 724 mm; data: German Weather Service, 1971–2000). The soil of the experimental site was established in February 2005 from homogenised regional soil (depth ca. 80 cm) underlain by drainage facilities to avoid water-logging. The texture of the soil is loamy sand (82% sand, 13% silt, 5% clay) with a pH of 4.5 in the upper layer and a pH of 6.2 in the lower layer (measured in 1M KCl).

Technical details on the freeze–thaw manipulation are described in Kreyling et al. (2010). In short, the experiment was carried out in a three-factorial design manipulating (1) freeze–thaw cycles (FTC-manipulation and reference), (2) vegetation types (grassland and dwarf-shrub heath), and (3) community compositions (three diversity levels, see Table 1). Five true replicates of the freeze–thaw treatment block and the reference block were established. Within each of the 10 blocks, six plant communities (two vegetation types with three community compositions differing in functional diversity) were replicated with a random assignment of location in the treatment block (Jentsch et al. 2007). Each of the 60 plots was 2 m × 2 m in size and was initially planted in April 2005 with 100 pre-grown individuals of the same age. All non-planted species were removed by periodic weeding.

FTC-manipulation

Soil temperature was manipulated by using buried heating wires (deviflex DTIP, DEVI, Vejle, Denmark) installed at a depth of 7 cm at 20 cm spacing, achieving an average heating of 100 W m^{-2}. This facility allowed short-term manipulations of frost including that of the soil while differing little from natural warming events (Peterjohn et al. 1993). Installation was completed during the establishment of the soil substrate prior to the planting of the experimental communities. One FTC was considered to be completed when the 0 °C level was crossed twice, i.e. temperature remained below zero before thawing, above zero, and then below zero again, each for at least 48 hours. With our setup we could only apply FTCs during natural frost periods lasting at least 6 days. The plots were covered from above using transparent plastic sheets during the heating periods, so that the air temperature also increased (Figure 1; for details see Kreyling et al. (2010)).

Five experimental FTCs were applied in the winter of 2005/2006, in addition to the three natural FTCs that occurred (Figure 1). Thus, the reference plots were exposed to three FTCs, whereas the FTC-manipulation plots experienced eight FTCs. Deviations in soil temperature between the treatment and the reference in early winter and early

Table 1. Experimental plant communities of two vegetation types (grassland, dwarf-shrub heath) were used at three diversity levels, resulting in six communities.

Abbreviation	Vegetation type	Description	Species
G2$^-$	Grassland	Two species, one functional group (grass)	*Arrhenatherum elatius*, *Holcus lanatus*
G4$^-$	Grassland	Four species, two functional groups (grass, forb)	*A. elatius*, *H. lanatus*, *Plantago lanceolata*, *Geranium pratense*
G4$^+$	Grassland	Four species, three functional groups (grass, forb, legume forb)	*A. elatius*, *H. lanatus*, *P. lanceolata*, *Lotus corniculatus*
S2$^-$	Dwarf-shrub heath	Two species, one functional group (dwarf shrub)	*Calluna vulgaris*, *Vaccinium myrtillus*
S4$^-$	Dwarf-shrub heath	Four species, two functional groups (dwarf shrub, grass)	*C. vulgaris*, *V. myrtillus*, *Agrostis* sp., *Deschampsia flexuosa*
S4$^+$	Dwarf-shrub heath	Four species, three functional groups (dwarf shrub, legume shrub, grass)	*Genista tinctoria*, *V. myrtillus*, *Agrostis* sp., *D. flexuosa*

G, grassland; S, dwarf-shrub heath; 2 or 4, number of species; $^-$, without legumes; $^+$, with legumes.

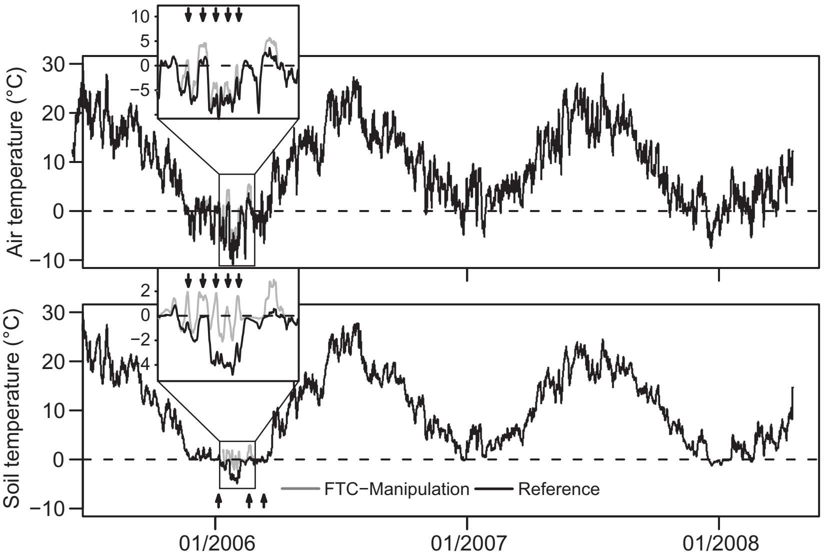

Figure 1. Air and soil temperature during the experiment. Upper panel: air temperature measured at +5 cm in two treatment blocks; lower panel: soil temperature measured at −4 cm on each plot (lines represent the means of the FTC-manipulation and the reference plot temperatures). The arrows which point downwards indicate the five experimentally-induced freeze–thaw cycles (FTC), in addition to three natural FTCs marked by arrows which point upwards (each arrow marks the second crossing of 0 °C per cycle).

spring were due to warming pulses that were stopped when reference plots thawed naturally. During the winter, maximum snow depth was less than 5 cm and snow cover did not last more than 1 day. No ice encasement occurred in any treatment.

Response parameters

The above-ground cover of each species was quantified for the central 1 m^{-2} of each plot to avoid any edge effects. We used the point quadrat method to estimate the cover of each species at 100 vertically inserted steel needles. The recording was repeated three times (May, July, and September) in each of four growing seasons (2005 to 2008). The soil temperature at −4 cm on every plot and the air temperature at +5 cm in two treatment blocks were measured at 10-minute intervals by using thermistors (B57863-S302-F40, EPCOS) connected to a data-logger (dl2, Delta).

Data analysis

Above-ground species cover was used to evaluate changes in species abundance patterns. At the beginning of the experiment, all replicates of each plant community had nearly identical species abundance patterns. We evaluated the compositional development of each individual plot by comparing its species abundance pattern to its initial species abundance pattern (5 weeks after planting) at each time step (three times in each of 4 years). Linear mixed effects models (FTC-manipulation, vegetation type, community composition, and all interactions) were used to test whether the FTC-manipulation significantly affected community development over time. Such models enable a statistical treatment of repeated measures by including time as a random factor (Pinheiro and Bates 2004). In addition to the FTC-manipulation as a fixed factor, block identity was used as a random factor to account for the blocking of communities within the treatment blocks. The significance of differences was evaluated by a Markov Chain Monte Carlo sampling of 10,000 permutations (Baayen et al. 2008). Data were log-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 models.

We used the Bray–Curtis dissimilarity coefficient to quantify community similarity. The Bray–Curtis coefficient, due to its semi-metric nature, is a good measure of ecological distance along gradients (Faith et al. 1987; Oksanen and Tonteri 1995) and it enables the detection of the deviation and turnover in the dominance structure of plant communities in response to a treatment before local extirpations occur, and expresses such changes with a single metric (Brosofske et al. 2001; Jurasinski and Kreyling 2007). In contrast to more common species-specific observations or population-oriented analyses and community gross-totals, this approach enables the community-wise evaluation of treatment effects. Here, the similarity index reflected the degree of dominance shift within the planted species composition, as all non-planted species were weeded out. All statistical analyses were performed using R (R Development Core Team 2008) with the additional packages simba, vegan, lme4, languageR, and gplots.

Results

The FTC-manipulation affected the species abundance patterns of the synthetic plant communities in subsequent years, with the response being determined by vegetation type and species composition (Table 2, Figure 2). The change in dissimilarity between the species abundance distribution at each time step and the initial species abundance distribution after the FTC-manipulation decreased in the grassland plots (Figure 2). Only the least diverse dwarf-shrub heath community (S2$^-$) displayed greater changes in the species abundance distribution in the FTC-manipulated plots than in the reference plots in the last year of the study period (mixed model $P = 0.005$ for 2008). This was related to the dying-off of many individuals of *Calluna vulgaris* and *Vaccinium myrtillus* in some plots of the FTC-manipulation (Figure 3).

The two vegetation types differed strongly in their response to the FTC-manipulation. When comparing the FTC-manipulation with the reference plots, the dissimilarity in species abundance distribution increased sharply in the year following the FTC-manipulation in the grassland plots without legumes (G2$^-$, G4$^-$). However, in the two-species grassland plots (G2$^-$), this was a transient effect and pre-manipulation levels of dissimilarity were restored in the following growing season. For the four-species grassland community (G4$^-$), differences between treatment and reference plots disappeared by the third year after the FTC-manipulation. In contrast, no differentiation in the dominance structure between the treatment and the reference plots of dwarf-shrub heath communities (S2$^-$, S4$^-$) was found in the first year after the manipulation (Figure 2, right-hand side). However, in the longer-term the community structure of manipulated and reference dwarf-shrub heath plots diverged steadily over the second and third years, indicating a delayed response to the FTC-manipulation.

The most diverse experimental plant communities that contained legumes (G4$^+$, S4$^+$) neither showed a clear trend in changes in species dominance patterns nor did the dissimilarity between the manipulated plots and the reference plots increase considerably over time after the FTC-manipulation (Figure 2, lower panels).

Individual species responded differently to the FTC-manipulation (Figure 3, Table 3). Apart from *Holcus lanatus*, which benefited to a large extent from the FTC-manipulation (Figure 3, Table 3), no other species from the grassland plots showed any significant long-lasting

Table 2. ANOVA table of mixed model results for differences in the dissimilarity of the species abundance distributions between each recording time and the initial conditions for each plot as a response parameter. The following three factors and their interactions were tested with respect to their influence: FTC-treatment (ftc: FTC-manipulation, reference), vegetation type (veg-type: grassland, dwarf-shrub heath), and diversity (div: 2$^-$, 4$^-$, 4$^+$). Results are provided over all evaluated time steps (overall) and for each year separately (i.e. the dissimilarity of species abundance distributions of each of the three cover measurements per year compared with the initial conditions). The FTC-manipulation took place in the winter of 2005/2006; data for 2005 display pre-treatment conditions.

	Overall		2005		2006		2007		2008	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
ftc	**12.9**	**< 0.001**	0.1	0.745	**14.5**	**< 0.001**	**9.7**	**0.002**	**2.0**	**0.016**
veg-type	**21.6**	**< 0.001**	**23.0**	**< 0.001**	**22.8**	**< 0.001**	**66.9**	**< 0.001**	**198.6**	**< 0.001**
div	**12.4**	**< 0.001**	**8.5**	**< 0.001**	**12.0**	**< 0.001**	**16.2**	**< 0.001**	1.5	0.233
ftc × veg-type	**5.7**	**0.020**	3.4	0.068	**16.0**	**< 0.001**	0.5	0.497	0.8	0.372
ftc × div	**6.6**	**< 0.001**	3.2	0.054	1.7	0.190	**5.0**	**0.008**	**7.2**	**0.001**
veg-type × div	**24.0**	**< 0.001**	**5.4**	**0.005**	**6.1**	**0.003**	**41.8**	**< 0.001**	**35.2**	**< 0.001**
ftc × veg-type × div	1.0	0.350	0.1	0.888	0.2	0.841	0.3	0.720	**10.2**	**< 0.001**

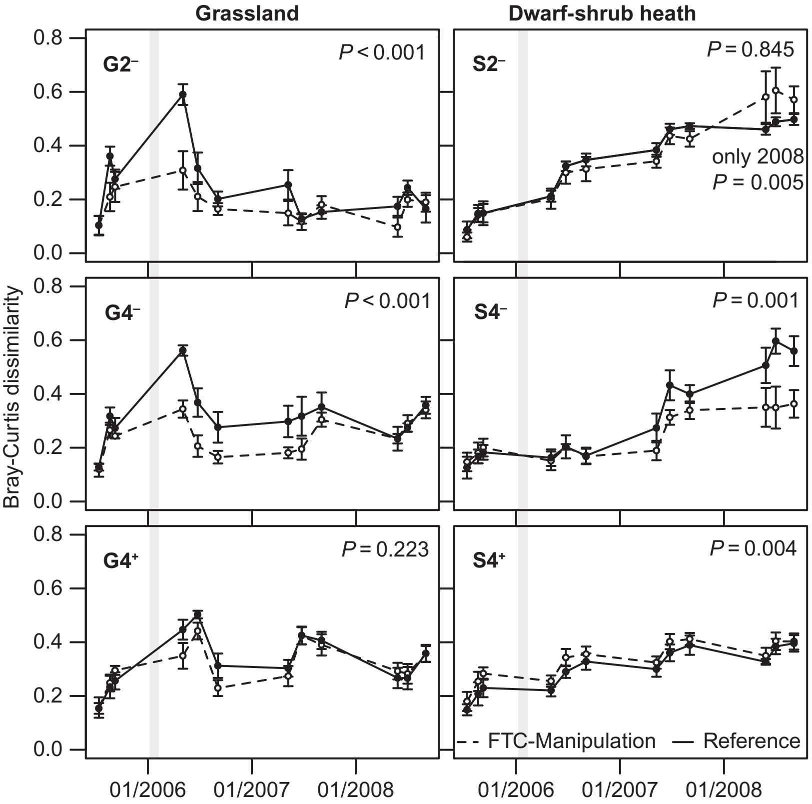

Figure 2. Temporal development of FTC-manipulation (open circles, dashed lines) and reference plots (filled circles, solid lines) for each of the six plant communities. The species abundance distribution at each time step was compared with the initial species abundance distribution (35 days after planting). Each plot (whether manipulated or reference) was only compared with its own initial composition using the Bray–Curtis dissimilarity coefficient, i.e. $n = 5$ in all cases. The symbols represent the mean, bars are one standard error. If the temporal development on the FTC-manipulation plots differed significantly from that on the reference plots over the whole study period was evaluated with mixed models (repeated measures ANOVA; for details see Table 2). The period of FTC-manipulation is shaded in grey.

effects over the whole study period (Table 3). However, most species showed strong short-term responses in the first and the second year after the manipulation. The cover of *Arrhenatherum elatius*, the other grass species in the grassland plots, decreased significantly in the vegetation period after the FTC-manipulation (Table 3). The same was true for the forbs *Plantago lanceolata* and *Geranium pratense* (Figure 3, Table 3). In the grassland, the legume *Lotus corniculatus* was the only species that did not display any significant reaction to the manipulation. All species in the dwarf-shrub heath plots except for the woody legume *Genista tinctoria*, were significantly affected by the FTC-manipulation when considering all three growing seasons (Table 3). However, the effects were not significant for any species within the first year after manipulation (Table 3, columns 5 to 7). In the second and third year, decreases in cover were found in *C. vulgaris*, *V. myrtillus*, and *Deschampsia flexuosa*, whereas *Agrostis* increased in the treatment plots (Figure 3, Table 3). This contributed to an increasing level of dissimilarity in the species abundance distribution between treatment and reference plots (S2$^-$, and S4- in Figure 2).

The performance of various species differed significantly among the three levels of functional diversity (2$^-$, 4$^-$, 4$^+$), and significant interactions between FTC-manipulation and community diversity were found for *V. myrtillus* (over all years) and *H. lanatus* in 2006 (Table 3).

Discussion

Research on the ecological importance of FTCs has been criticised for commonly applying unrealistic magnitudes and frequencies of FTCs (Henry 2007), and it has been suggested that the effects of realistic manipulations might be small (Grogan et al. 2004; Sjursen et al. 2005). Our temperature manipulation was within the natural variation recorded for the reference plots (Figure 1). For our site, the number of natural FTCs over 8 years ranged between zero and nine with a mean of 3.6 (Kreyling et al. 2010). Thus, the low frequency with at least 48 hours in each state and the low total number of FTCs in our study appear to represent a realistic magnitude and frequency of FTCs. Despite these modest manipulations we found strong and lasting effects in the development of the vegetation. These findings highlight the importance of winter climate change for vegetation dynamics in temperate ecosystems (Kreyling 2010).

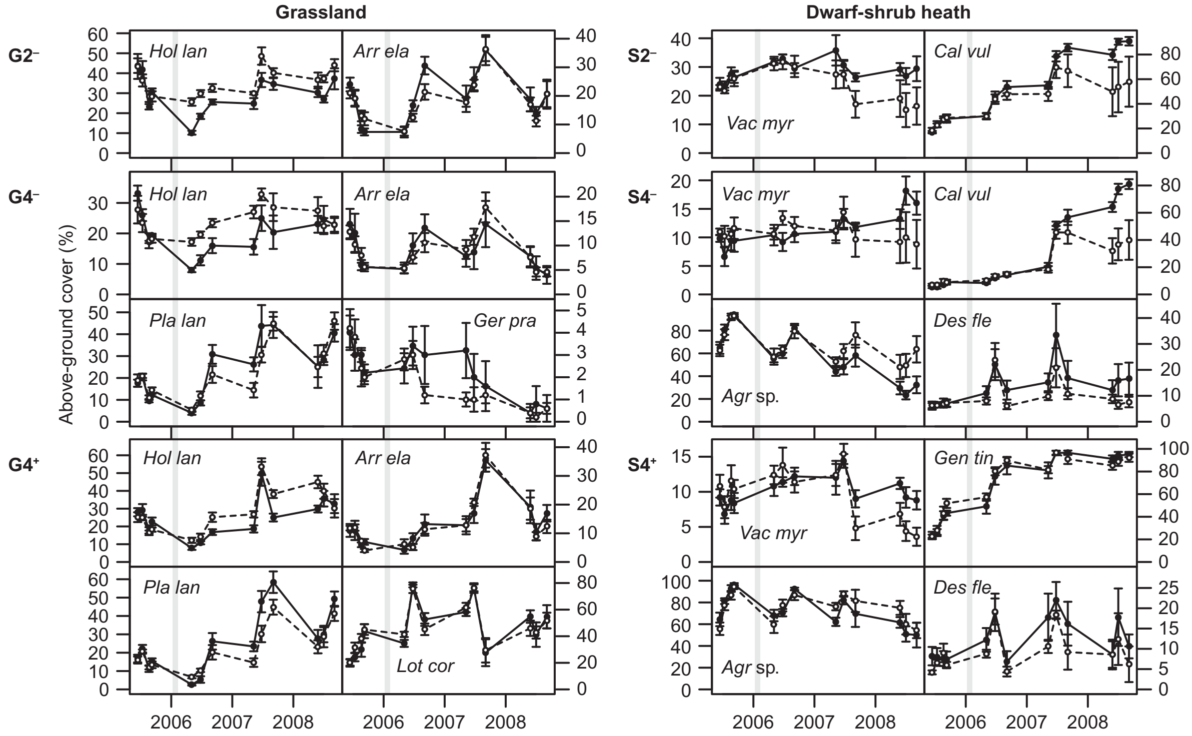

Figure 3. Above-ground cover of each single species for the FTC-manipulation (open circles, dashed lines) and reference plots (filled circles, solid lines) shown for the six plant communities (see Table 3 for statistical results). The period of FTC-manipulation is shaded in grey. The symbols depict the mean, bars are one standard error of the above-ground cover.

The development of plant communities during the 3 years following the FTC-manipulation were influenced by winter warming pulses (Hypothesis 1). In contrast to our expectation, the FTC-manipulation tended to reduce compositional change. The significant dissimilarity between the treatment and reference plots in three of the synthetic plant communities (G2$^-$, G4$^-$, S4$^-$; Figure 2) was caused more by an increasing deviation from the initial conditions in the reference plots rather than by the FTC-manipulation (Figure 2). Climatic forcing would impact all plots and cause their vegetation to change from their initial state. It appears that FTC-manipulation in these three communities has reset their state close to that at the start of the experiment. The other communities either showed no significant changes over the whole study period (G4+, S2-), or the difference between treatment and reference started before the manipulation and the pattern was not altered by the FTC-manipulation (S4+), thereby implying that the effect described above is no general feature, but depends on the specific community, thereby supporting our Hypothesis 2.

Calluna die-back due to winter processes has been linked elsewhere to desiccation during exceptionally cold periods (Hancock 2008). However, in our study the die-back occurred with time lags of more than 1 year and coldest temperatures occurred in the reference plots, not in the FTC-manipulation (due to one warming pulse during the coldest times of winter). We argue that root injury, possibly further allowing for pathogenic attacks, may be a possible explanation. Root injury due to soil frost has been identified as a major source of N-leaching (Robitaille et al. 1995; Tierney et al. 2001; Weih and Karlsson 2002; Gaul et al. 2008) and nitrate losses from ecosystems are more likely to be caused by reduced root uptake rather than by increased N net mineralisation (Matzner and Borken 2008).

In general, our results cannot be explained by the altered air temperature. Short-term air-warming events can increase frost injury in shoots due to dehardening and reduced snow insulation (Bokhorst et al. 2009). In our experiment, only *C. vulgaris* retained green foliage over winter, and personal observations did not show any above-ground injuries in this or in any other species. As no other species had green leaves, we can rule out that winter photosynthesis contributed to changes in FTC-manipulated plots. Furthermore, the observed plant responses appear not to be related to soil moisture, as no effects of the FTC-manipulation on soil moisture were found beyond the warming pulses (Kreyling et al. 2010).

Species abundance shifts after the FTC-manipulation in our experiment were related to the pre-treatment composition of the plant communities, supporting our Hypothesis 2. As discussed above, lasting effects were found for the dwarf-shrub heath plots, whereas the grassland plots exhibited a high level of resilience (i.e. the ability of a system to absorb a disturbance event and return to pre-disturbance characteristics after a short period of time). Our Hypothesis 3 was supported by our findings as more diverse communities were more stable against change and showed less deviation from the reference plots than less diverse communities. This finding supports the insurance

Table 3. ANOVA table of mixed model results for species-specific above-ground cover as a response parameter. The following two factors and their interactions were tested with respect to their influence: FTC-treatment (ftc: FTC-manipulation, reference), and diversity (div: 2^{-}, 4^{-}, 4^{+}). Diversity could only be tested if the respective species occurred at more than one diversity level. Results are provided over all evaluated time steps (overall) and for each year separately. The FTC-manipulation took place in the winter of 2005/2006; data for 2005 display pre-treatment conditions.

	Overall			2005			2006			2007			2008		
Species	ftc	div	ftc × div	ftc	div	ftc × div	ftc	div	ftc × div	ftc	div	ftc × div	ftc	div	ftc × div
Arrhenatherum elatius^{g}	0.270	**0.001**	0.700	0.610	**0.001**	0.490	**0.006**	**0.001**	0.250	0.672	**0.001**	0.500	0.501	**0.001**	0.780
Holcus lanatus^{g}	**0.001**	**0.001**	0.510	0.772	**0.001**	0.405	**0.001**	**0.001**	**0.010**	**0.001**	**0.001**	0.940	**0.009**	**0.001**	0.220
Plantago lanceolata^{f}	0.927	0.877	0.669	0.761	0.661	0.131	**0.029**	0.129	0.084	**0.001**	0.210	0.200	0.759	0.815	0.192
Geranium pratense^{f}	0.102			0.914			0.322			**0.037**			0.490		
Lotus corniculatus$^{leg, f}$	0.740			0.072			0.715			0.714			0.461		
Calluna vulgaris^{ds}	**0.002**	**0.001**	0.360	0.780	**0.001**	0.169	0.404	**0.001**	0.062	**0.016**	**0.001**	0.399	**0.001**	0.582	0.705
Vaccinium myrtillus^{ds}	**0.001**	**0.001**	**0.003**	0.290	**0.001**	0.100	0.804	**0.001**	0.500	**0.004**	**0.001**	0.100	**0.001**	**0.001**	0.100
Agrostis sp.^{g}	**0.001**	**0.001**	0.100	0.535	0.715	0.372	0.791	**0.003**	0.493	**0.016**	**0.001**	0.699	**0.001**	**0.001**	0.063
Deschampsia flexuosa^{g}	**0.001**	0.219	0.524	0.831	0.257	0.354	0.274	0.297	0.862	**0.029**	0.385	0.696	**0.017**	0.364	0.331
Genista tinctoria$^{leg, ds}$	0.686			0.248			0.137			0.603			0.060		

^{g}, grass; ^{f}, forb; ^{leg}, legume; ^{ds}, dwarf shrub.

hypothesis (Yachi and Loreau 1999) for such bio-climatic processes, stating that communities which are more diverse in species or functional groups can be expected to be more stable against environmental perturbations. However, diversity levels were not replicated by different species compositions in our experiment except for the same levels occurring both in grassland and dwarf-shrub heath. Results of the diversity effects are therefore discussed as preliminary and no identification of the causal effects (species numbers, functional diversity, species identities) is possible here. With regard to the most diverse communities in our experiment, we cannot determine whether functional diversity alone or a legume effect occurred. Nevertheless, the similar results in two different vegetation types with legume species of two different growth forms imply some generality of the observed effect. Diversity experiments repeatedly point out that legumes are one of the most important determinants of community stability through increased N supply (Spehn et al. 2002; Beierkuhnlein and Nesshoever 2006).

Conclusions

In temperate ecosystems with a seasonal climate, soil freeze–thaw cycles are of high ecological importance. Their occurrence is expected to change drastically due to ongoing climate change, with some areas being subjected to increases and others to decreases in frequency of FTCs (Henry 2008). Moreover, given the spatial importance of FTCs whereby seasonally frozen ground currently covers about 55 million km^2 or 55% of the total land area of the Northern Hemisphere (Zhang et al. 2003), it seems necessary to develop a better understanding of such ecological processes that occur outside of the growing season. Here, we showed that short-term fluctuations in winter temperature have the potential to induce long-term ($>$3 years) shifts in the species abundance distribution of our experimental communities. Functional composition of the communities affected compositional development, with grasses being the only growth form that was able to benefit from the FTC-manipulation, whereas dwarf shrubs decreased in above-ground cover. Higher functional diversity or the presence of legumes appeared to make the system more resilient in this respect. Due to the fact that some plant functional types react negatively whilst others benefit, an indirect influence of winter climate change on competition, community composition, and even species distributions in temperate ecosystems may occur. However, we are far from a complete understanding of the causal processes behind such changes. Long-term effect-oriented field experiments in various natural communities as well as process-oriented laboratory studies are necessary to gain further understanding of ecological impacts due to altered frost regimes.

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