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Diversity-Stability Relationships of an Alpine Plant Community under Simulated Environmental Change

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Abstract

We examined the relationship between plant community diversity (species richness, evenness) and stability in an alpine *Dryas octopetala* heath exposed to four years of warming (open top chambers) and nutrient addition at Finse, southern Norway. Furthermore, we examined if different functional types responded differently to the interaction between environmental change and initial community diversity. We used the temporal change in species composition, calculated as the sum of change in sample scores in detrended correspondence analyses, as a measure of variability (opposite of stability). Under ambient conditions, a high initial species richness was associated with less stability of the total species composition. Under experimental warming, initial high species richness and evenness were associated with a more stable subsequent vascular species composition. Vascular stability decreased, however, with higher species richness under nutrient addition. When warming and nutrient addition were combined, high initial evenness was associated with more stable bryophyte composition, whereas high species richness was associated with reduced lichen stability. Thus, the degree and direction of the diversity-stability relationship depended on the type of environmental perturbation, the responding functional type, and on the diversity parameter used. The large variation in diversity-stability relationships is likely an outcome of complex species interactions and environmental factors influencing community diversity.

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Introduction

The accelerating loss of global biodiversity has highlighted the question of the functional importance of diversity in ecosystems (Loreau et al., 2002). Moreover, a long-lasting debate has discussed to what extent diversity can stabilize ecosystems in the face of changing environmental conditions (see Loreau et al., 2002; Hooper et al., 2005). Several ecologists have hypothesized that high species diversity increases ecosystem stability (e.g. Elton, 1958; McNaughton, 1977; see also Tilman et al., 2001, and Hooper et al., 2005). Different species in a community may vary in their functional attributes. Therefore, they may respond differently to changes in the abiotic environmental conditions, which may enhance the ability of the particular system to resist changes (Yachi and Loreau, 1999; Hooper et al., 2005). This was shown for the first time when Frank and McNaughton (1991) demonstrated that community composition of diverse grasslands was more resistant to drought than less diverse grasslands. Conversely, diversity may also function to destabilize population dynamics because a high diversity may increase the number of interactions and thus result in larger fluctuations in population densities (May, 1973; McNaughton, 1977; Tilman, 1996; see Loreau et al., 2002). A review by Hooper et al. (2005) concluded that in most cases, diversity affects stability, either positively or negatively, but that the underlying mechanisms are far from known. Furthermore, most diversity-stability studies are from grasslands, and only one of fifteen studies reviewed by Loreau et al. (2002) used a perturbation of intrinsically positive effect on the production of most species in the system (N-supply; Mellinger and McNaughton, 1975). Determinants of diversity may vary among commu-

nities of contrasting environmental conditions, and consequently the functional role of diversity may be different. Furthermore, environmental perturbations that increase community productivity may have different effects on species interactions, and subsequently on the community, than perturbations that decrease productivity. Thus, to fully understand the functional role of diversity on stability, we need studies of systems under a range of abiotic and biotic conditions imposed to different types of environmental perturbations (Loreau et al., 2002).

Climate change is predicted to be one of the most important drivers of biodiversity changes, particularly in habitats of low temperature, such as the alpine (Sala et al., 2000). In low-productive alpine plant communities, minor changes in the environmental conditions may result in large responses in production and subsequent species interactions and community dynamics (e.g. Klanderud and Totland, 2005a). Experimental studies have shown that individual species or functional types may respond with different speed and amplitude to environmental changes (e.g. Arft et al., 1999; Klanderud and Totland, 2005a; Walker et al., 2006), which may result in secondary changes in community composition (Hollister et al., 2005; Jónsdóttir et al., 2005; Wahren et al., 2005; Klanderud, 2008). Moreover, recent studies have shown that environmental changes can modify species interactions (Bret-Harte et al., 2004; Klanderud and Totland, 2005b; Brooker, 2006; Wipf et al., 2006). Consequently, we predict that the functional role of community diversity on stability may vary with the type of perturbation imposed on the community, and that different functional types may respond differently to the combined effect of environmental change and initial community

diversity. The aim of this paper is to examine (1) if there is a relationship between diversity and stability, measured as temporal change in species composition (variability; Loreau et al., 2002) in an alpine plant community subjected to four years of warming and/or nutrient addition; (2) whether diversity-stability relationship depends on the type of environmental perturbation; (3) whether the interactions between initial community diversity, environmental perturbation, and stability differ among functional types; and (4) the relative role of the number of species vs. their relative abundance (evenness) for stability.

Study System and Methods

This paper is based on a study conducted in a *Dryas octopetala* heath at ~1500 m elevation on Sandalsnuten, Finse, northern part of Hardangervidda (~60°N, 7°E), the alpine region of southwestern Norway. Mean monthly temperature during June, July, and August at 1200 m elevation at Finse is 6.3°C (Aune, 1993), and mean monthly precipitation during the same months is 89 mm (Førland, 1993). An experiment on simulated environmental change effects on plant community parameters was initiated in 2000 and sampled in 2003 (see Klanderud and Totland [2005a] for details on experimental design, and Klanderud [2008] for details on species composition before and after the treatments). Temperature treatment (T), nutrient addition (N), temperature and nutrient addition (TN), and controls (C, no treatment) were allocated to four 1 × 1 m plots with ten replicates (blocks). We increased temperature by using open-top chambers (OTCs; Marion et al., 1997; Hollister and Webber, 2000), and increased nutrient availability by adding slow-release granular NPK once early in season (~10 g N, 2 g P, and 8 g K per m²/growing season). Open top chambers increased summer air temperature ~5 cm above ground by ~1.5°C, and soil temperature ~5 cm below ground by ~1°C (Klanderud and Totland, 2005a).

To disentangle initial variability among treatment plots from experimental effects, we analyzed the variability in initial species composition, richness, and evenness before treatments in 2000. We used redundancy analysis (RDA; ter Braak and Šmilauer, 2002) to examine differences in initial species composition by testing each of the treatment variables and blocks (T, N, block; environmental variables) in a forward selection with 9999 unrestricted permutations. We used analysis of variance (ANOVA) to examine the variability of initial diversity parameters (response variables; species richness, evenness) with treatment as a fixed factor and block as a random factor. To be able to separate the functional role of diversity parameters from factors that determine the actual diversity in this system, we measured important environmental factors, such as the cover of the dominant species *Dryas octopetala* and soil parameters. We collected two soil samples from ~5 cm below ground in each plot by the end of August 2000. We mixed the samples from each plot properly before analyses. The soil was weighed and dried at 105°C for 24 hours to estimate water content, and then combusted at 550°C for 12 hours to measure the organic matter content via weight loss on ignition (LOI). An electrode was used to measure pH. Extractable soil nitrogen (NH₄⁺ + NO₃⁻) was measured by extraction with KCl and analyzed by Flow Injection Analysis at the Department of Plant and Environmental Sciences, Norwegian University of Life Sciences, Ås. We used correlation analysis to examine the relationship between community diversity parameters and the different environmental factors.

We recorded plot species richness (number of species) by counting the presence of all species within thirty-six 10 × 10 cm

subplots within the 1 × 1 m plot, and estimated the abundance by calculating the frequency of subplots where each of the species was present within each plot. This was done in 2000 (before treatments) and in 2003 (after four growing seasons of treatment). We calculated evenness (Pielou, 1975) indices for the 2000 data. We used the change in species composition, calculated as the total distances between the two samples scores from 2000 and 2003 along the first four axes in detrended correspondence analyses (DCA, ter Braak and Šmilauer, 2002), as a measure of variability. We did one DCA for the whole species composition, and one for each of the functional types, with the first four axes explaining 32.1%, 38.7%, 40.8%, and 57.5% of the total variation explained, for the whole species composition, vascular, bryophyte, and lichens, respectively. DCA arranges species according to reciprocal averaging, and the magnitude of change remains relative and vegetation changes appear as ranks. A large amount of abundance change will not lead to displacement of plots in an ordination, i.e. not all compositional change is reflected as displacement along ordination axes. Thus, this is a conservative method for detecting changes. See Klanderud (2008) for environmental interpretation of the DCA axes.

We used analysis of covariance (ANCOVA) to assess if there was a relationship between initial diversity parameters (species richness, evenness) and the change in community species composition (variability), and if such relationships differed among treatments (C, T, N, TN). We used temperature treatment (T) and nutrient addition treatment (N) as fixed factors; block as a random factor; the initial diversity parameter as a co-variable; and change in total (all functional types combined), vascular, bryophyte, or lichen species composition (variability) as dependent variables (one model for each variable). Significant interactions between treatments and diversity parameter indicated contrasting relationship between treatments, so we used simple linear regressions with initial species richness or evenness as the predictors, and change in species composition as the dependent variable to examine the slope of the relationships of each treatment separately. Changes in species composition-parameters (variability) were log transformed to fulfill the assumptions of normality and equal variances before analyses. DCAs and RDAs were computed in CANOCO 4.5, all other analyses were done in SYSTAT 10.

Results

ANOVAs showed no variability in species richness ($F_{3,36} = 0.33$, $P = 0.804$) or evenness ($F_{3,36} = 0.19$, $P = 0.902$) among the plots before the treatments were conducted in 2000. The RDA showed that there was no before-treatment difference in species composition among plots (T: $F = 0.72$, $P = 0.923$; N: $F = 0.95$, $P = 0.520$). There were no correlations between any of the environmental variables measured and the diversity parameters (Pearson Corr. Coef. < 0.39, in all cases), except for pH, which correlated negatively with species richness (Pearson Corr. Coef. = -0.62, $P = 0.002$) and evenness (Pearson Corr. Coef. = -0.57, $P = 0.013$).

A significant interaction between the temperature treatment (T), nutrient addition (N), and initial species richness on the variability of the total (all functional types combined) species composition, suggested contrasting richness-stability relationships among treatments (Table 1). Simple linear regressions for each of the treatments separately showed a positive relationship between species richness and variability ($R^2 = 0.64$, Std. Coef. = 0.80, $P = 0.005$) in the control plots, suggesting that a high initial species richness was associated with more variability in the total species

TABLE 1

General Linear Models (GLMs) ANCOVA on the effects of temperature (T), nutrient addition (N) (fixed factors), block (random factor), initial species richness (Sp richn) and evenness (co-variables), and their interactions on the change (Δ) in the total species composition, or vascular, bryophyte, or lichen species composition (variability; dependent variables) in alpine southern Norway. $F_{d,r}$ - and P -values are shown. Significant values are in bold.

Parameters	Δ total species composition		Δ vascular species composition		Δ bryophyte species composition		Δ lichen species composition	
	F	P	F	P	F	P	F	P
T	17.98 _{1, 23}	< 0.001	10.52 _{1, 23}	0.004	5.34 _{1, 23}	0.030	0.64 _{1, 23}	0.432
N	12.83 _{1, 23}	0.002	0.58 _{1, 23}	0.453	1.46 _{1, 23}	0.239	0.11 _{1, 23}	0.747
Block	1.14 _{9, 23}	0.374	2.66 _{9, 23}	0.028	1.20 _{9, 23}	0.341	0.82 _{9, 23}	0.605
Sp richn	1.96 _{1, 23}	0.175	7.52 _{1, 23}	0.012	0.00 _{1, 23}	0.983	3.52 _{1, 23}	0.074
T \times N	7.79 _{1, 23}	0.010	4.13 _{1, 23}	0.054	1.89 _{1, 23}	0.182	2.15 _{1, 23}	0.166
T \times Sp richn	12.32 _{1, 23}	0.002	9.43 _{1, 23}	0.005	1.50 _{1, 23}	0.232	1.26 _{1, 23}	0.274
N \times Sp richn	2.24 _{1, 23}	0.148	0.36 _{1, 23}	0.554	0.20 _{1, 23}	0.660	0.23 _{1, 23}	0.636
T \times N \times Sp richn	8.07 _{1, 23}	0.009	4.49 _{1, 23}	0.045	0.13 _{1, 23}	0.724	4.53 _{1, 23}	0.044
T	2.82 _{1, 23}	0.107	4.82 _{1, 23}	0.039	4.20 _{1, 23}	0.052	1.85 _{1, 23}	0.187
N	1.66 _{1, 23}	0.211	0.23 _{1, 23}	0.634	5.65 _{1, 23}	0.026	0.20 _{1, 23}	0.663
Block	0.95 _{9, 23}	0.501	1.01 _{9, 23}	0.464	1.29 _{9, 23}	0.295	0.47 _{9, 23}	0.879
Evenness	0.02 _{1, 23}	0.896	1.00 _{1, 23}	0.327	0.34 _{1, 23}	0.565	0.43 _{1, 23}	0.518
T \times N	2.25 _{1, 23}	0.147	0.33 _{1, 23}	0.570	5.42 _{1, 23}	0.029	1.29 _{1, 23}	0.267
T \times Evenness	2.56 _{1, 23}	0.124	4.66 _{1, 23}	0.042	3.64 _{1, 23}	0.069	1.98 _{1, 23}	0.173
N \times Evenness	1.19 _{1, 23}	0.287	0.12 _{1, 23}	0.732	5.15 _{1, 23}	0.033	0.12 _{1, 23}	0.241
T \times N \times Evenness	2.20 _{1, 23}	0.152	0.32 _{1, 23}	0.576	4.86 _{1, 23}	0.038	1.45 _{1, 23}	0.241

composition between 2000 and 2003. Under experimental warming, a T \times species richness interaction (Table 1), together with a negative direction of the slope in the T-treatment regression (Fig. 1a), suggested that high initial species richness was associated with less variability in the total species composition. There were no significant interactions between any treatments and evenness on community stability (Table 1, Fig. 1b). When responses to initial community diversity parameters and environmental perturbations were analyzed separately for each functional type, significant interactions between treatments and initial diversity parameters suggested that the diversity-stability relationship depended on the type of perturbation, diversity parameter, and functional type (Table 1). For the vascular species, a T \times N \times species richness interaction suggested contrasting directions of the richness-stability relationship among treatments (Table 1). High initial species richness was associated with more variability in the control plots and in plots with nutrient addition, but less variability in plots with experimental warming (Fig. 1c). A T \times evenness interaction suggested that also high evenness was associated with less variability of the vascular species composition in plots with experimental warming (Table 1, Fig. 1d). For the bryophytes, there was no relationship between initial species richness and variability (Table 1, Fig. 1e). However, a T \times N \times evenness interaction, and a negative evenness-stability relationship in the TN-plots ($R^2 = 0.45$, $P = 0.034$; Fig. 1f) suggested that high initial evenness was associated with less variability of the bryophyte composition in plots with warming combined with nutrient addition. Conversely, for the lichens, a T \times N \times species richness interaction, and a slightly positive, although not significant ($R^2 = 0.34$, $P = 0.079$; Fig. 1g) richness-variability relationship in the TN-plots, suggested that high initial species richness was associated with more lichen variability. There were no significant interactions between treatments and evenness for lichen stability (Table 1, Fig. 1h).

Discussion

Plant community diversity was associated with stability, measured as temporal change in species composition, in the alpine

Dryas heaths at Finse, southern Norway. The degree and the direction of the diversity-stability relationship, however, depended substantially on the nature of the environmental perturbation imposed on the community, and on the responding functional type. Indeed, the interactions between stability, initial diversity, and environmental change were far more complex than suggested previously.

Under experimental warming the stability of the vascular species composition was positively related to initial species richness and evenness. This is fully in line with the hypothesis of greater stability in diverse systems (Elton, 1958), and with a growing volume of literature predicting that because species differ in their ecological attributes, they respond differently to environmental changes. Consequently, more species in a system can enhance the ability of the system to resist any change (see Hooper et al., 2005). However, when nutrients were added to the *Dryas* community, stability of the vascular species composition decreased with higher initial species richness. Furthermore, when warming was combined with nutrient addition (TN-plots), high evenness was associated with a more stable bryophyte composition, whereas, on the contrary, a high species richness was associated with reduced stability in lichen composition. Although diversity is predicted to increase ecosystem stability, the population density of individual species might be destabilized (May, 1973; Tilman et al., 2006). More species in a system increases the likelihood that the most responsive (negatively or positively) or interacting (competitive or facilitative) species are present. This 'sampling effect' (Huston, 1997; Tilman et al., 1997) enhances the potential for species interactions that may subsequently affect community composition (May, 1973; Tilman, 1996). When the *Dryas* heath was exposed to nutrients (N), and experimental warming combined with nutrients (TN), the changes in the abiotic conditions resulted in extensive changes in the biotic environment due to a substantial increase in vascular biomass production (Klanderud and Totland, 2005a). Species respond differently to warming, fertilization, and changes in the surrounding vegetation. Thus, high initial diversity parameters in these plots might have increased the possibilities for both positive and negative plant-plant interactions, with different outcomes among functional

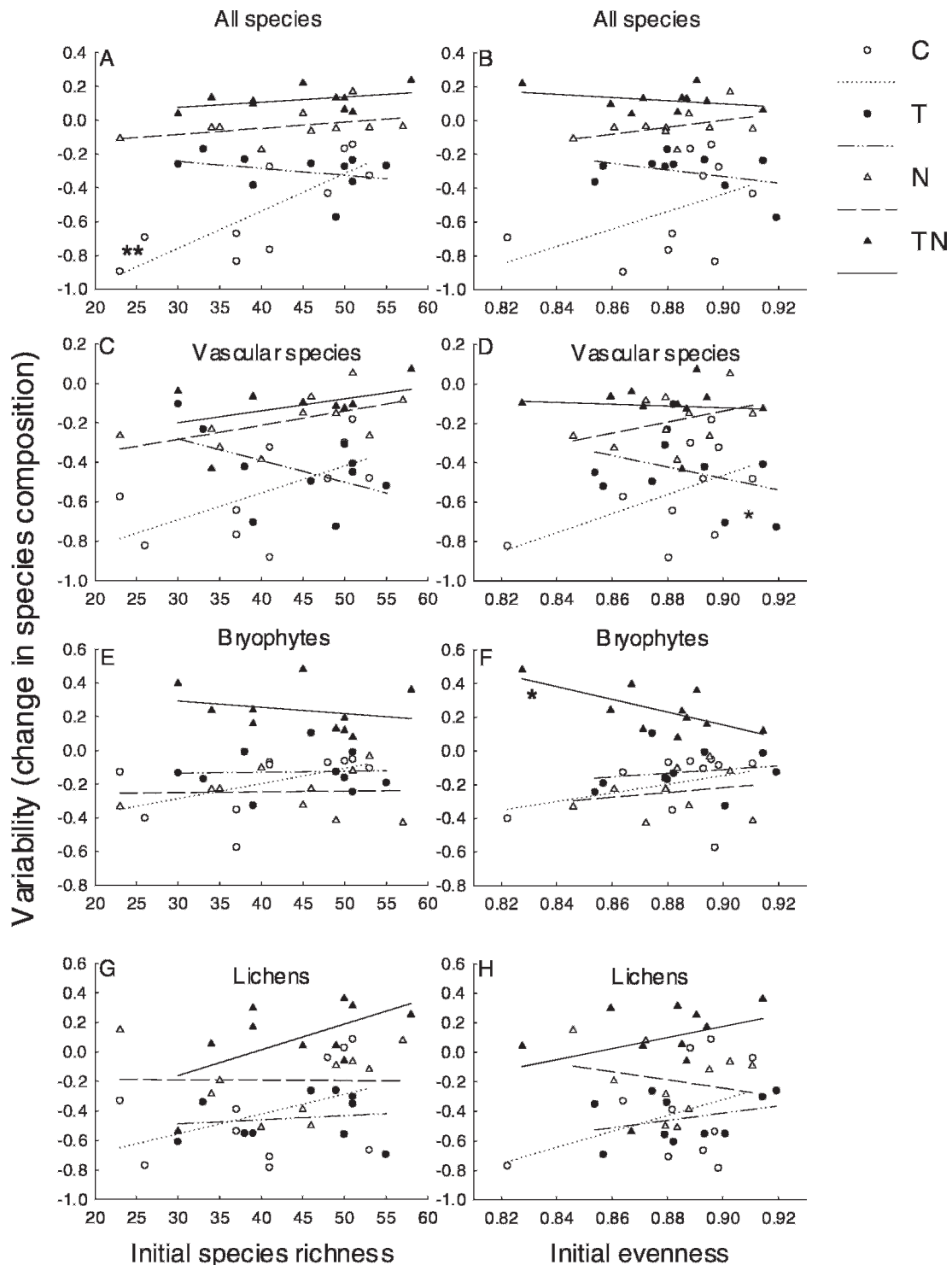


FIGURE 1. Linear regressions of initial species richness and evenness and the change in species composition (variability) from 2000 to 2003 (DCA sample scores 2003 minus DCA sample scores 2000) of an alpine plant community exposed to warming (T), nutrient addition (N), warming combined with nutrient addition (TN), or no perturbations (control; C). Significant regressions are indicated by asterisks: **, $P \leq 0.01$; *, $P \leq 0.05$.

types. Individual vascular species differ to a large extent in their responses to nutrients, and high initial species richness likely increased the possibilities for both strong and weak competitors to be present. Subsequently, this might have increased the chances for species interactions in plots receiving nutrients, which again decreased stability in vascular species composition. The significantly higher biomass in plots with warming combined with nutrient addition (Klanderud and Totland, 2005a) resulted in

decreased abundances of individual bryophytes and lichens (Klanderud, 2008). Thus, the changes in bryophyte and lichen composition shown in this study are to a large extent likely caused by decreased rather than increased abundances of individual species. The higher stability of the bryophyte composition, i.e. less decrease in abundance, with higher initial evenness in the TN-plots, is in line with the classical hypothesis that diversity enhances stability (Elton, 1958). Lichens, on the other hand, appear to be

particularly vulnerable to increases in vascular plant biomass (e.g. Cornelissen et al., 2001; Jägerbrand et al., 2006). Thus, high initial community species richness might have intensified interspecific competition for light and space when biomass increased as a result of warming and nutrient addition.

For the vascular species composition at Finse, a negative diversity-stability relationship in the control plots changed to a positive relationship in plots with experimental warming. This shows that environmental changes may modify the role of species interactions on community dynamics, which is in line with removal experiments in arctic (Bret-Harte et al., 2004; Wipf et al., 2006) and alpine (Klanderud, 2005; Klanderud and Totland, 2005b) plant communities. Experimental warming resulted in a dryer soil surface in the *Dryas* heath at Finse (K. Klanderud, personal observation), which likely decreased the abundances of individual species in this system (Klanderud, 2008). A high initial richness or evenness in these plots might have stabilized the vascular species composition by ameliorating the humidity. Facilitation by improved water absorption and retention has been documented in other studies, and likely explained the positive effects of a high diversity on bryophyte productivity in a temperate plant community exposed to drought (Mulder et al., 2001) and in the arctic tundra when water availability was secured (Rixen and Mulder, 2005). Furthermore, soil moisture was positively related to species establishment and diversity in a seed addition experiment in the *Dryas* heath at Finse, in particular in plots with experimental warming (Klanderud and Totland, 2007). This suggests that soil moisture may be an important factor for the actual diversity when this system is exposed to experimental warming.

Because diversity parameters were not manipulated in this study, it is difficult to separate diversity effects from the possible effects of environmental factors that determine diversity itself, such as resource availability and disturbance (Huston, 1997). However, the lack of before-treatment differences in species richness, evenness, and composition among the plots, suggests that there was no large environmental variability between the plots in this study. This suggests that the diversity-stability relationships shown are, to a large extent, due to the environmental perturbations and the initial diversity parameters. Nevertheless, factors influencing species richness, such as for example soil moisture and pH, are expected to also influence stability, and should therefore be taken into account in diversity-stability studies (Levine, 2000). In the natural community at Finse, which did not receive any perturbations (control plots), a high initial species richness was associated with a less stable species composition. This contrasted with the hypothesis of greater stability in diverse systems (Elton, 1958), but is in line with Levine (2000), who concluded that in natural systems, diverse communities were less stable due to factors co-varying with diversity. In homogenous experimental systems, such factors are most often eliminated, and therefore not taken into account in the diversity-stability discussion (Levine, 2000).

It is predicted that different aspects of diversity may have different effects on community resistance to environmental change (Hooper et al., 2005). In our study, the number of species (species richness) was more often significantly related (positive or negative) to stability than the relative abundance of each of the species (evenness). The direction of the relationships, however, were similar for both components in all cases, suggesting that the combined effect of the number and abundance of the species (e.g. Shannon diversity) is likely more important for community stability than each of these parameters separately. The results of our study show that environmental changes caused by global

warming can modify the relationship between diversity parameters and alpine plant community stability, but that the direction of the responses may depend on the nature of the environmental change. It is predicted that the magnitude of stability can depend on the type of perturbation imposed on the system (Frank and McNaughton, 1991). This makes sense, because individual plant species respond in different directions to, for example, temperature, water deficit, nutrient availability, and to vegetation changes. This is, however, rarely shown, perhaps because most diversity-stability studies to date are done with perturbations of only one (often negative) direction to the system, such as for example water deficit (see Loreau et al., 2002). Our results also suggest that whether diversity stabilizes or destabilizes community composition is highly dependent on the responses among the different functional types. Thus, when changes in the community composition are analyzed with all functional types pooled, diversity-stability relationships may be hidden because contrasting directions of responses at the functional type level can neutralize each other at the community level. The complex interactions between stability, initial diversity, and simulated environmental change as seen at Finse, also indicate that different mechanisms of the diversity-function and different ecological processes might be operating within the same community. This is in line with diversity-manipulation experiments from grasslands, which have shown that alternative mechanisms are often not mutually exclusive (see Hooper et al., 2005). Moreover, our results suggest that the net outcome of diversity is the combined effects of species interactions, and the environmental conditions experienced by the community. To understand fully the relationship between diversity and stability, and the mechanisms underpinning it, we need a better understanding of which factors determine the actual diversity of the different systems.

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References Cited

- Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jónsdóttir, I. S., Laine, K., Lévesque, E., Marion, G. M., Molau, U., Mølgaard, P., Nordenhall, U., Raszhivin, V., Robinson, C. H., Starr, G., Stenstrom, A., Stenström, M., Totland, Ø., Turner, P. L., Walker, L. J., Webber, P. J., Welker, J. M., and Wookey, P. A., 1999: Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, 69: 491–511.
- Aune, B., 1993: *Temperaturnormaler: normalperiode 1961–1990*. Oslo: The Norwegian Meteorological Institute.
- Bret-Harte, M. S., García, E. A., Sacré, V. M., Whorley, J. R., Wagner, J. L., Lippert, S. C., and Chapin, F. S., III, 2004: Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *Journal of Ecology*, 92: 635–647.
- Brooker, R. W., 2006: Plant-plant interactions and environmental change. *New Phytologist*, 171: 271–284.
- Cornelissen, J. H. C., Callaghan, T. V., Alatalo, A., Michelsen, A., Graglia, E., Hartley, A. E., Hik, D. S., Hobbie, S. E., Press, M. C., Robinson, C. H., Henry, G. H. R., Shaver, G. R., Phoenix, G. K., Jones, D. G., Jonasson, S., Chapin, F. S., Molau, U., Neill, C., Lee, J. A., Melillo, J. M.,

- Sveinbjornsson, B., and Aerts, R., 2001: Global change and arctic ecosystems: is lichen decline a function of increase of vascular plants? *Journal of Ecology*, 89: 984–994.
- Elton, C. S., 1958: *The ecology of invasions of animals and plants*. London: Methuen.
- Frank, D. A., and McNaughton, S. J., 1991: Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. *Oikos*, 62: 360–362.
- Førland, E. J., 1993: *Precipitation normals, normal period 1961–1990*. Oslo: The Norwegian Meteorological Institute.
- Hollister, R. D., and Webber, P. J., 2000: Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology*, 6: 835–842.
- Hollister, R. D., Webber, P. J., and Tweedie, C. E., 2005: The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, 11: 525–536.
- Hooper, D. U., Chapin, F. S., III, Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A., 2005: Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75: 3–35.
- Huston, M. A., 1997: Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110: 449–460.
- Jägerbrand, A. K., Lindblad, K. E. M., Björk, R. G., Alatalo, J. M., and Molau, U., 2006: Bryophyte and lichen diversity under simulated environmental change compared with observed variation in unmanipulated alpine tundra. *Biodiversity and Conservation*, 15: 4453–4475.
- Jónsdóttir, I. S., Magnússon, B., Gudmundsson, J., Elmarsdóttir, Á., and Hjartarson, H., 2005: Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology*, 11: 553–563.
- Klanderud, K., 2005: Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, 93: 127–137.
- Klanderud, K., 2008: Species-specific responses of an alpine plant community under simulated environmental change. *Journal of Vegetation Science*, 19: 363–372.
- Klanderud, K., and Totland, Ø., 2005a: Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology*, 86: 2047–2054.
- Klanderud, K., and Totland, Ø., 2005b: The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, 93: 493–501.
- Klanderud, K., and Totland, Ø., 2007: The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos*, 116: 1279–1288.
- Levine, J. M., 2000: Species diversity and biological invasions: relating local process to community pattern. *Science*, 288: 852–854.
- Loreau, M., Downing, A., Emmerson, M., Gonzales, A., Hughes, J., Inchausti, P., Joshi, J., Norberg, J., and Sala, O., 2002: A new look at the relationship between diversity and stability. In Loreau, M., Naeem, S., and Inchausti, P. (eds.), *Biodiversity and ecosystem functioning. Synthesis and perspectives*. New York: Oxford University Press, 79–91.
- Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A. N., Svoboda, J., and Virginia, R. A., 1997: Open-top designs for manipulating field temperature in high latitude ecosystems. *Global Change Biology*, 3: 20–32.
- May, R. M., 1973: *Stability and complexity in model ecosystems*. Princeton, New Jersey: Princeton University Press.
- McNaughton, S. J., 1977: Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist*, 111: 515–525.
- Mellinger, M. V., and McNaughton, S. J., 1975: Structure and function of successional vascular plant communities in New York. *Ecological Monographs*, 45: 161–182.
- Mulder, C. P. H., Uliassi, D. D., and Doak, D. F., 2001: Physical stress and diversity-productivity relationships: the role of positive interactions. *Proceedings of the National Academy of Sciences*, 5: 6704–6708.
- Pielou, E. C., 1975: *Ecological diversity*. New York: Wiley.
- Rixen, C., and Mulder, C. P. H., 2005: Improved water retention links high species richness with increased productivity in arctic tundra moss communities. *Oecologia*, 146: 287–299.
- Sala, E. O., Chapin, F. S., III, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sandwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., LeRoy Poff, N., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H., 2000: Global biodiversity scenarios for the year 2100. *Science*, 287: 1770–1774.
- ter Braak, C. J. F., and Šmilauer, P., 2002: *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (Version 4.5)*. Ithaca: Microcomputer Power.
- Tilman, D., 1996: Biodiversity: population versus ecosystem stability. *Ecology*, 77: 350–363.
- Tilman, D., Lehman, C., and Thompson, K., 1997: Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, 94: 1857–1861.
- Tilman, D., Knops, J., and Wedin, D., et al., 2001. Experimental and observational studies of diversity, productivity, and stability. In Kinzig, A., Pacala, S., and Tilman, D. (eds.), *Functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton, New Jersey: Princeton University Press, 42–70.
- Tilman, D., Reich, P. B., and Knops, J. M. H., 2006: Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441: 629–632.
- Wahren, C. H., Walker, M. D., and Bret-Harte, M. S., 2005: Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, 11: 537–552.
- Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jónsdóttir, I. S., Klein, J. A., Magnússon, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., Suding, K. N., Thompson, C. C., Tolvanen, A., Totland, Ø., Turner, P. L., Tweedie, C. E., Webber, P. J., and Wookey, P. A., 2006: Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, 31: 1342–1346.
- Wipf, S., Rixen, C., and Mulder, C. P. H., 2006: Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Global Change Biology*, 12: 1496–1506.
- Yachi, S., and Loreau, M., 1999: Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences*, 96: 1463–1468.

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