

Dominance hierarchies, diversity and species richness of vascular plants in an alpine meadow: contrasting short and medium term responses to simulated global change

We studied the impact of simulated global change on a high alpine meadow plant community. Specifically, we examined whether short-term (5 years) responses are good predictors for medium-term (7 years) changes in the system by applying a factorial warming and nutrient manipulation to 20 plots in Latnjajaure, subarctic Sweden. Seven years of experimental warming and nutrient enhancement caused dramatic shifts in dominance hierarchies in response to the nutrient and the combined warming and nutrient enhancement treatments. Dominance hierarchies in the meadow moved from a community being dominated by cushion plants, deciduous, and evergreen shrubs to a community being dominated by grasses, sedges, and forbs. Short-term responses were shown to be inconsistent in their ability to predict medium-term responses for most functional groups, however, grasses showed a consistent and very substantial increase in response to nutrient addition over the seven years. The non-linear responses over time point out the importance of longer-term studies with repeated measurements to be able to better predict future changes. Forecasted changes to temperature and nutrient availability have implications for trophic interactions, and may ultimately influence the access to and palatability of the forage for grazers. Depending on what anthropogenic change will be most pronounced in the future (increase in nutrient deposits, warming, or a combination of them both), different shifts in community dominance hierarchies may occur. Generally, this study supports the productivity-diversity relationship found across arctic habitats, with community diversity peaking in mid-productivity systems and degrading as nutrient availability increases further. This is likely due the increasing competition in plant-plant interactions and the shifting dominance structure with grasses taking over the experimental plots, suggesting that global change could have high costs to biodiversity in the Arctic.

2 Juha M. Alatalo^{1*}, Chelsea J. Little¹, Annika K. Jägerbrand² and Ulf Molau³

3 ¹Department of Ecology and Genetics, Uppsala University, Campus Gotland, 621 67 Visby,
4 Sweden, ²VTI, Swedish National Road and Transport Research Institute, Box 55685, 102 15
5 Stockholm, Sweden, ³Department of Biological and Environmental Sciences, University of
6 Gothenburg, PO Box 461, 405 30 Gothenburg, Sweden.

7 *Corresponding author: Juha M Alatalo, Department of Ecology and Genetics, Uppsala
8 University, Campus Gotland, SE-621 67 Visby, Sweden

9 Phone: +46 (0)18 471 8357

10 E-mail: juha.alatalo@ebc.uu.se

11 Introduction

12 Global change is expected to lead to widespread biome and biodiversity shifts across spatial
13 scales, from the regional to the global (Sala, Chapin & Armesto 2000; Grimm *et al.* 2013). Many
14 of the fastest changes in physical conditions are predicted to occur in polar and alpine
15 ecosystems, including increasing growing season length, permafrost degradation, and increasing
16 nutrient mobilization, due to a climate warming that is unprecedented in the last two millennia
17 (IPCC 2007; Kaufman *et al.* 2009). As a result, these ecosystems are assumed to be particularly
18 vulnerable to climate change (Callaghan & Jonasson 1995), with some species even going extinct
19 (Klein, Harte & Zhao 2004). Observational studies have already shown shifts in plant community
20 structure over the last several decades of climate warming in high-latitude and high-elevation
21 tundra, particularly the proliferation of shrubs and grasses (Capers & Stone 2011; McManus *et*
22 *al.* 2012; Callaghan *et al.* 2013).

23 Ecosystem responses to global change are complex, nonlinear, and spatially and
24 temporally heterogeneous. Warming is predicted to be the largest driver of change in arctic,
25 alpine, and boreal regions, but nitrogen deposition is also expected to have a large effect,
26 especially in alpine ecosystems (Sala *et al.* 2000). Within a single landscape, warming and
27 nutrient amendment may change in their relative importance from low to high elevations (Graglia
28 *et al.* 2001). The effects of both have been examined experimentally. Early analyses and meta-
29 analyses of experimental warming in alpine and arctic systems found immediate phenological
30 changes, short-term responses in terms of plant growth, and medium- and long-term responses in
31 terms of plant reproduction and community structure (Arft *et al.* 1999; Van Wijk *et al.* 2004;
32 Hollister, Webber & Tweedie 2005). Nutrient enhancement in these systems also produced short-
33 term growth responses but were sometimes followed by declines in abundance (Dormann &
34 Woodin 2002; Campioli, Leblans & Michelsen 2012). There are many potential explanations for
35 the complexity of these responses. The changes themselves create biotic effects such as increased

36 plant competition and changes in litter accumulation, which may in turn affect demography
37 (Foster & Gross 1998; Olsen & Klanderud 2014). Species also exhibit different degrees of
38 phenotypic plasticity, and may thus vary in their ability to succeed, survive and thrive under the
39 anticipated changing conditions (Capioli *et al.* 2012). More recent meta-analyses of
40 temperature manipulation experiments have shown that responses vary sizes to warming
41 treatments and may increase over time, likely due to a combination of all of these factors
42 (Elmendorf *et al.* 2012). Longevity may also play a role, as short lived species have been
43 predicted to be more sensitive to climate change than more long-lived species (Morris *et al.*
44 2008). This implies that many alpine and Arctic plant species could buffer against climate change
45 due to their long-lived nature. In the longer run, however, the long life span of arctic and alpine
46 plants in combination with their capacity for sexual reproduction will determine their fate as
47 evolutionary adaptation is a slow process in comparison with the projected pace of warming
48 (Molau 1993). It is questionable whether evolution can keep pace with climate change on global
49 scale, thus increasing the extension risk (Jump & Peñuelas 2005; Parmesan 2006).

50 While dividing plant species by functional type may not always yield consistent results
51 within a group (Dormann & Woodin 2002), the size and speed of responses to simulated global
52 change may nonetheless be somewhat generalizable by plant functional type. For instance,
53 grasses are commonly increasing in abundance under both warming and nutrient treatments
54 (Graglia *et al.* 2001; Klanderud & Totland 2005; Capioli *et al.* 2012). Shrubs have also been
55 detected as expanding in the arctic in recent years (McManus *et al.* 2012). Another important
56 functional group is cushion plants, which have great influence on ecosystems in polar and high
57 alpine areas throughout the world as they often function as facilitator species across trophic levels
58 (Cavieres & Arroyo 2002; Molenda, Reid & Lortie 2012; Roy *et al.* 2013). Unfortunately, there
59 are very few experimental studies on climate change impact on cushion plants, but the few that
60 exist have shown contrasting responses to warming (Day *et al.* 2009; Alatalo & Little 2014). The

61 ability of functional groups to compete for light, nutrients, and other resources varies, and the
62 responses may depend on interactions with co-inhabiting species; for instance, the most abundant
63 (“dominant”) species or functional group in a community can have a strong influences on the
64 biotic conditions of the other species by either negative, competitive interactions or by positive,
65 facilitative interactions (Grime 1998; Klanderud & Totland 2004). For instance, an increase in
66 shrub cover may lead to a decrease in species richness (Pajunen, Oksanen & Virtanen 2011)
67 while the presence of nitrogen-fixing legumes facilitates a richer plant community (Olsen,
68 Sandvik & Totland 2013). With changes in abiotic conditions, dominant species in more
69 productive alpine plant communities may monopolize added N and P at the expense of their
70 neighbors (Onipchenko *et al.* 2012), or may show changes in both their competitive response and
71 competitive effect under experimental warming (Niu & Wan 2008). Thus the redistribution of
72 vegetation types in arctic and alpine ecosystems can create major shifts in dominance hierarchies
73 (Klanderud & Totland 2005), resulting in feedback loops accelerating changes in ecosystem
74 structure and functioning (Graglia *et al.* 2001).

75 There are a growing number of studies on simulated global change effects on alpine plant
76 communities at the community level, by warming and by nutrient addition. However, at present
77 there are only a few factorial studies with experimental warming and nutrient addition on alpine
78 plant communities (for example, Chapin *et al.* 1995; Alatalo 1998; Klanderud & Totland 2005;
79 Jägerbrand *et al.* 2009; Campioli *et al.* 2012), and not one of them attempts to assess if short term
80 (<5 years) responses are consistent with medium (6-10 years) or longer term (>10 years)
81 responses. This represents a notable gap in knowledge, as an Alaskan study suggests that short
82 term responses are poor indicators of longer term studies (Hollister *et al.* 2005). We used a
83 factorial experimental design to assess community and functional group response of vascular
84 plants to warming and nutrient perturbations in northern Sweden over a period of seven years.
85 The abundance of lichens, bryophytes, and vascular plants have already been shown to have

86 changed after five years of manipulations in this experiment (Alatalo 1998; Molau & Alatalo
87 1998; Jägerbrand *et al.* 2009). In this study, we examine whether short-term responses are good
88 predictors for longer-term changes in the system, i.e are short-term responses consistent with
89 longer-term responses.

90 **Materials & Methods**

91 *Study area*

92 Fieldwork took place at the Latnjajaure Field Station (LFS) in northern Sweden, at 1000 m
93 elevation in the valley of Latnjavagge (68°21'N, 18°29'E). Continuous climate data were
94 provided from the early spring of 1992 onwards. Climate is classified as sub-arctic (Polunin 1951) with
95 snow cover for most of the year, cool summers, and relatively mild, snow-rich winters. Mean annual temperatures
96 ranged from -2.0 to -2.7°C between 1993 and 1999, with winter minima of -27.3 to -21.7°C . Mean annual
97 precipitation during this time period was 808 mm, with individual years ranging from a low 605 mm in 1996 up to
98 990 mm in 1993. The warmest temperatures come in July, which had mean temperatures ranging from +
99 5.4°C in 1992 to $+9.9^{\circ}\text{C}$ in 1997.

100 Physical conditions in the valley vary from dry to wet and poor and acidic to base-rich,
101 with a variety of plant communities to match. This field experiment focused on a meadow
102 community. Previous work in the valley has shown that despite a geographic situation of
103 subarctic-alpine, vegetation of the area is more representative of the Low Arctic, with *Cassiope*
104 *tetragona*, *Dryas octopetala*, and *Carex bigelowii* among the dominant species (Molau & Alatalo
105 1998). At the beginning of this field experiment, the plots were characterized by sedges, shrubs,
106 and cushion plants: *C. tetragona*, *C. bigelowii*, *Carex vaginata*, *Silene acaulis* and *Vaccinium*
107 *vitis-idaea* were present in every plot in the meadow community, while *Polygonum viviparum* and
108 *D. octopetala* were present in 75% or more plots.

109 *Experimental design*

110 In July 1995, 20 plots (1 x 1 m) with homogenous vegetation cover were chosen in the meadow
111 plant community and randomly assigned to treatments in a factorial design. There were 8 control
112 (CTR) plots and 4 plots for each of the experimental treatments: warming (T for temperature
113 enhancement), nutrient addition (N) and combined warming and nutrient addition (TN). Warming
114 was induced by Open Top Chambers (OTCs) that increase temperature by 1.5 to 3°C compared to
115 control plots with ambient temperature (Marion *et al.* 1997; Molau & Alatalo 1998). Nutrient
116 addition consisted of 5 g of nitrogen (as NH₄NO₃) and 5 g of phosphorus (P₂O₅) per m², dissolved
117 in 10 L of meltwater. In 1995 all plots were analyzed with a point–frame method (Walker 1996)
118 to determine the species occurrences under natural conditions before implementing the
119 experimental treatments. The OTCs were then left on plots with warming treatments year-around,
120 and nutrient addition was applied directly after the initial vegetation analyses in 1995 and a few
121 days after snow melt in the subsequent years (1996-2001).

122 *Measurements*

123 All vascular plants in the plots were identified to species level and cover of each species was
124 assessed using a 1 x 1 m frame with 100 grid points (Walker 1996) in the middle of the 1995,
125 1999, and 2001 growing seasons. To ensure accuracy and reproducibility, the same grid frame
126 was used for each measurement, and fixed points at the corner of each plot allowed the frame to
127 be placed in the same position within the plot at each different measuring point. Only the first hit
128 of each species was recorded. This method has been shown to be accurate in detecting changes in
129 tundra vegetation (May & Hollister 2012).

130 *Data analysis*

131 From the point-frame data, we summed the number of touches to pins within each plot to produce
132 plot-level cover measures for each species, which were aggregated into total cover for each plot.
133 Species richness was tallied as the total number of species present at the 100 points within the
134 plot. The cover data, showing the number of hits for each species, were used to calculate the
135 Shannon diversity index and Pielou's evenness index in each plot (Oksanen et al., 2012).

136 For each response variable, normality and homogeneity of variance were assessed using
137 standard diagnostic procedures. All statistical analyses were performed in R version 2.15.3 (R
138 Core Team 2013). A mixed-effects model with fixed factors of nutrient and temperature
139 manipulation, random factors of year and plot was used to analyze responses in total cover,
140 species richness, diversity, and evenness for the whole community using the lme4 package
141 (Bates, Maechler & Bolker 2012), using restricted maximum likelihood (REML). A generalized
142 linear mixed-effects model using Poisson errors was used for total cover and species richness.
143 Diversity and evenness were normally distributed and a generalized model was not necessary.
144 Backward model selection was performed using second-order AIC (AICc) scores (Mazerolle,
145 2013) due to the small sample size. For model validation, we examined residuals and q-q plots.
146 Where the interaction of the fixed factors was significant, multiple comparisons were performed
147 within the generalized linear model framework using the glht function of the multcomp package
148 (Hothorn et al., 2008).

149 We also analyzed responses for each of six functional groups: cushion plants, deciduous
150 shrubs, evergreen shrubs, forbs, grasses, and "sedges" (including both *Juncaceae* and
151 *Cyperaceae*). We used each species' pin-hits to calculate each functional group's cover, and from
152 this its relative cover as a percentage of the total cover in each plot. Functional group cover was
153 analyzed using the same generalized linear model as total cover, described above. Shannon
154 diversity was calculated separately for the deciduous shrub, evergreen shrub, and forb functional
155 groups and analyzed using mixed-effects models as described above. Cushion plant, grass, and

156 sedge functional groups rarely had more than one or two species present in a plot, and as a result
157 analyzing the Shannon diversity lacked utility. Instead, for each plot we used the more simplistic
158 measure of species richness for these three functional groups, categorizing the change from 1995
159 to 1999 and from 1995 to 2001 as either losing species richness, maintaining the same number of
160 species, or gaining species richness. The distribution of these responses between treatment groups
161 was compared to what would be expected based on cell size and the global mean using Fisher's
162 exact test, with p-values based on 10,000 replicates of Monte Carlo simulation.

163 **Results**

164 The model selection results for mixed-effects models of all total community and
165 functional group responses are summarized in Table 1. Treatment effects from linear comparisons
166 within the selected model are described below.

167 Seven years of experimental warming and nutrient addition had a significant interactive
168 effect on total cover of vegetation in the plots. All experimental treatments showed cover
169 differences from the control plots, with the temperature and combined temperature and nutrient
170 treatments decreasing compared to the control plots while the nutrient-only treatment showed a
171 cover increase compared to the control plots (Figure 1A). A total of 51 species were observed in
172 plots over the course of the seven-year experiment, with individual counts per plot ranging from
173 6 to 21 species at a given time point. The difference between species richness in warmed and
174 unwarmed plots was only marginal (linear comparisons, $p=0.07$; Figure 1B). This corresponded
175 to no significant effects of any of the treatments on either Shannon diversity (Figure 1C) or
176 Pielou's evenness (Figure 1D).

177 Drastic shifts in dominance structure were observed in the nutrient and combined
178 temperature and nutrient manipulation plots over the course of the 7-year experiment (Figure 2),

179 with grasses increasing in the nutrient and nutrient plus warming treatments, while sedges and
180 deciduous shrubs decreased in cover.

181 Cover of cushion plants responded to a significant interaction between the nutrient and
182 temperature manipulations, with the cover in the combined treatment plots significantly lower
183 than in any of the other plots (linear comparisons, $p < 0.001$; Figure 3A). In both 1999 and 2001,
184 20% of plots across the entire experiment had decreased in species richness compared to 1995,
185 whereas the rest had maintained the original number of species (Figure 5A). No plots gained
186 species of cushion plants. The distribution of the losses between treatment types was not different
187 than that expected by chance (Fishers exact test, $p > 0.20$)

188 The effect of nutrient manipulation was included in the best model for cover of both
189 deciduous and evergreen shrubs. For deciduous shrubs, there was no significant difference
190 between cover in plots with and without the nutrient treatment (linear comparisons, $p = 0.07$,
191 Figure 3B), however diversity declined significantly in the plots which had added nutrients
192 (linear comparisons, $p < 0.001$; Figure 4A). Conversely, evergreen shrub cover decreased
193 significantly with the nutrient manipulation (linear comparisons, $p < 0.001$, Figure 3C), but
194 diversity of evergreen shrubs showed no response to any of the treatments (Figure 4B).

195 Forb cover (Table 2, Figure 3D) and diversity (Figure 4C) in the plots was unaffected by
196 any of the manipulations.

197 Grass cover responded to a significant interaction between the nutrient and temperature
198 manipulation. Grass cover increased in the nutrient treatment compared to the control treatment
199 (linear comparisons, $p = 0.004$), with intermediate abundance in the other plots (Figure 3E). By
200 1999, seven of the treatment plots had increased in richness but none of the control plots had
201 changed in richness, which represented a significant effect of the perturbations (Fisher's exact
202 test, $p = 0.002$; Figure 5B). By 2001, additional gain and loss of species richness had negated this
203 effect (Fisher's exact test, $p > 0.05$). Sedge cover increased significantly in the plots receiving

204 nutrient amendment (linear comparisons, $p=0.01$), especially in 1999 although the effect had
205 waned by 2001 (Figure 3F). The majority of plots either decreased in species richness or
206 maintained the same number of species by 1999 and 2001, and the distribution of changes among
207 the treatments was not different than that which would be predicted by the global mean (Fisher's
208 exact test, $p>0.10$; Figure 5C).

209 **Discussion**

210 Total vascular plant cover in the alpine meadow increased significantly with nutrient perturbation
211 over the seven-year experiment, maintaining the direction of its short-term response into the
212 medium-term. The most notable responses to simulated global change came at the functional
213 group level, where cover and diversity of some functional groups showed consistent short- and
214 medium-term responses to perturbations (nutrient addition, warming and combined nutrient
215 addition and warming) while after seven years of perturbations others showed either recovery
216 from their initial responses, or intensification of those responses. In particular, the nutrient and
217 the combined warming and nutrient treatment caused changes in the dominance structure in the
218 meadow. Cover of grasses increased dramatically in the nutrient and the combined warming and
219 nutrient enhancement treatments in the meadow community, with response increasing over the
220 course of several years. This increased their relative dominance compared to the previously
221 shown shorter-term responses (Alatalo 1998; Jägerbrand *et al.* 2009). These results are in line
222 with other studies, as graminoids have been reported to increase dramatically in abundance in
223 response to nutrient addition in several previous studies in alpine and arctic communities
224 (Theodose & Bowman 1997; Klanderud & Totland 2005; Calvo *et al.* 2005; Campioli *et al.* 2012;
225 Onipchenko *et al.* 2012). Sedges that traditionally have been incorporated into the “graminoids”
226 functional group in many previous studies showed a contrasting pattern, with abundance
227 decreasing among years in all treatments in the meadow community. This is in contrast to other

228 studies that have indicated that sedges may have more positive responses than grasses (Bowman
229 *et al.* 1993; Walker *et al.* 2001; Soudzilovskaia & Onipchenko 2005; Bassin *et al.* 2007). These
230 studies have suggested that the positive response is because traits such as lower nutrient losses
231 and slow turnover rates are more important in nutrient limited habitats for competitive success
232 (Aerts 1999). Furthermore, it has previously been reported that species respond differently to
233 temperature and nutrient perturbations at different sites (Elmendorf *et al.* 2012, Press *et al.* 1998),
234 thus the species composition of the “functional group” at a specific site may influence the
235 community’s responses. Indeed, the functional group designation has not always yielded
236 consistent results in global change experiments (Dormann & Woodin, 2002). In that case, a
237 possible explanation for our contrasting results may be that the sedge species found in our
238 meadow community might not be as responsive as the sedge species from other sites reporting a
239 positive response for the functional group.

240 Previous short-term studies have found positive short-term responses of forbs to nutrient
241 addition (Henry, Freedman & Svoboda 1986; Bowman *et al.* 1993; Calvo *et al.* 2005;
242 Onipchenko *et al.* 2012), including a five-year study in this same community (Jägerbrand *et al.*
243 2009). However, we found that this response had disappeared after seven years of perturbations.
244 In all treatments, mean forb cover decreased to a level near or below its initial starting value.
245 Warming also caused contrasting short- and longer-term responses: after seven years of warming
246 the forbs had declined their cover, while having previously not responded to shorter-term
247 treatment (Jägerbrand *et al.* 2009). Contrasting responses were also found in a short-term study in
248 the Swiss Alps, where species-specific responses of different forbs to nutrient addition varied
249 between negative, neutral and positive (Bassin *et al.* 2007).

250 Evergreen shrubs showed a significant and complex response to nutrient addition. After
251 seven years the cover of evergreen shrubs had recovered from the short-term negative response to
252 the combined warming and nutrient addition that was reported in a previous study (Jägerbrand *et*

253 *al.* 2009), gaining their previous relative share of the dominance hierarchy in terms of cover.
254 However, cover had increased in the control and temperature treatments over seven years, an
255 effect which seemed to be dampened by the nutrient perturbation. Nevertheless, the appearance
256 of a recover by evergreen shrubs is interesting as, for instance, in a four-year study in Norway the
257 evergreen shrub *Dryas octopetala* lost its dominant position in the community to graminoids in
258 response to nutrient addition and combined warming and nutrient addition (Klanderud & Totland
259 2005). It has been suggested that evergreen shrubs are more likely to decline in response to
260 nutrient addition, while deciduous shrubs are likely to increase due to the same perturbation
261 (Chapin *et al.* 1995). The potential recovery of evergreen shrubs in our results is a novel finding,
262 and should be further examined in other long-term studies. Furthermore, we found no support for
263 a deciduous shrub increase. Rather, deciduous shrubs cover decreased in response to both the
264 nutrient and combined warming and nutrient addition treatments. This was caused by an initial
265 short-term response (Jagerbrand *et al.* 2009), since their relative share of the cover did not
266 continue to decline after the five years. These results reinforce previous experimental findings
267 that diversity of both types of shrubs are negatively affected by increasing nutrient availability
268 (Press *et al.* 1998; Klanderud & Totland 2005).

269 Cushion plants decreased in cover in response to nutrient and the combined warming and
270 nutrient addition. Similarly, in high Arctic Svalbard, 5 years of nutrient addition caused
271 significant decrease of *Saxifraga oppositifolia* (Robinson *et al.* 1998), while *Silene acaulis* has
272 been shown to respond in contrasting manner to short and medium term nutrient addition (Alatalo
273 & Little 2014). If cushion plants begin to decrease in larger numbers in severe environments, this
274 could potentially impact a wide array of species in ecosystems where they are found due to their
275 importance as facilitator species (Cavieres & Arroyo 2002; Molenda, Reid & Lortie 2012).

276 Total species richness declined over the seven years of warming, while species richness,
277 diversity, and evenness showed nonsignificant decreases in the combined nutrient and warming

278 treatment. The largest decline in species diversity after seven years of perturbation was found in
279 deciduous shrubs in response to nutrient addition and the combined warming and nutrient
280 addition. In contrast grasses increased their species richness, almost tripling in response to the
281 combined warming and nutrient addition, and sedges showed a nonsignificant trend of increasing
282 species richness in response to the nutrient addition but decreasing in response to warming. A
283 decrease in species richness due to simulated global change has also been reported in other
284 studies. A 9-year study with experimental warming and nutrient addition in Alaskan tundra found
285 that species richness declined by 30-50% due to losses primarily of rarer species, but this was
286 mainly caused by loss of bryophytes, lichens and forbs (Chapin *et al.*, 1995). In alpine Norway,
287 four years of combined warming and nutrient addition caused a significant decline in total species
288 richness, caused by a decline in bryophytes and lichens, while the same perturbation increased
289 species richness of graminoids (Klanderud & Totland 2005). In the same study species richness
290 of forbs increased in response to nutrient addition. The contrasting results of species richness of
291 forbs ranging from negative (Chapin *et al.* 1995), neutral (this study), to positive (Klanderud &
292 Totland 2005), suggest that the responses may be highly species-specific.

293 Community diversity has been shown to decrease in arctic and alpine meadows in
294 response to nutrient addition (Theodose & Bowman 1997; Wardle *et al.* 2013) and in particular in
295 response to combined warming and fertilization (Press *et al.* 1998; Klanderud & Totland 2005).
296 Generally, this study supports the productivity-diversity relationship found across arctic habitats,
297 with community diversity peaking in mid-productivity systems and crashing as nutrient
298 availability increases further (Virtanen *et al.* 2013). This is likely due to the increasing
299 competition in plant-plant interactions and the shifting dominance structure with grasses taking
300 over the experimental plots and suggests that global change in the arctic could entail not only
301 redistribution of vegetation types, but also significant costs to biodiversity.

302 **Conclusions**

303 The different perturbations caused shifts in dominance hierarchies in the alpine meadow. Nutrient
304 addition drove the community to become more dominated by grasses, sedges and forbs. Short-
305 term responses were shown to be inconsistent in their ability to predict medium-term responses
306 for sedges, shrubs, cushion plants and forbs. However, grasses showed consistent and very
307 substantial response to nutrient addition over the whole period of seven years. The non-linear
308 responses over time point out the importance of longer-term studies with repeated measurements
309 to be able to better predict future changes. The non-linear responses also have important
310 implications for improving modeling the future changes to global change. The different changes
311 to warming and nutrient addition will likely have implications for trophic interactions, and may
312 ultimately influence the access to and palatability of the forage for grazers. Depending on what
313 anthropogenic change will be most pronounced in the future (increase in nutrient deposits,
314 warming, or a combination of them both), different shifts in community dominance hierarchies
315 may occur.

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320 **References**

- 321 Aerts, R. (1999) Interspecific competition in natural plant communities: mechanisms, trade-offs
322 and plant-soil feedbacks. *Journal of Experimental Botany*, **50**, 29–37.
- 323 Alatalo, J.M. (1998) *Climate Change: Impacts on Structure and Biodiversity of Subarctic Plant*

- 324 *Communities*. Göteborg University, Sweden.
- 325 Alatalo, J.M. & Little, C.J. (2014) Simulated global change: contrasting short and medium term
326 growth and reproductive responses of a common alpine/Arctic cushion plant to experimental
327 warming and nutrient enhancement. *SpringerPlus*, **3**, 157.
- 328 Arft, A.M., Walker, M.D.M., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M.,
329 Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jónsdóttir, I.S., Laine, K., Lévesque,
330 E., Marion, G.M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C.H.,
331 Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, P.L., Walker, L.J., Webber, P.J.,
332 Welker, J.M. & Wookey, P.A. (1999) Responses of tundra plants to experimental warming:
333 meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491–511.
- 334 Bassin, S., Volk, M., Suter, M., Buchmann, N. & Fuhrer, J. (2007) Nitrogen deposition but not
335 ozone affects productivity and community composition of subalpine grassland after 3 yr of
336 treatment. *The New phytologist*, **175**, 523–34.
- 337 Bates, D., Maechler, M. & Bolker, B. (2012) lme4: Linear mixed-effects models using S4 classes.
- 338 Bowman, W.D., Theodose, T.A., Schardt, J.C. & Conant, R.T. (1993) Constraints of Nutrient
339 Availability on Primary Production in Two Alpine Tundra Communities. *Ecology*, **74**, 2085–
340 2097.
- 341 Callaghan, T. V & Jonasson, S. (1995) Implications for changes in arctic plant biodiversity from
342 environmental manipulation experiments. *Arctic and alpine biodiversity: patterns, causes
343 and ecosystem consequences* (eds F.S.I. Chapin & C. Körner), pp. 151–166. Springer, Berlin.
- 344 Callaghan, T. V, Jonasson, C., Thierfelder, T., Yang, Z., Hedenås, H., Johansson, M., Molau, U.,
345 Van Bogaert, R., Michelsen, A., Olofsson, J., Gwynn-Jones, D., Bokhorst, S., Phoenix, G.,

- 346 Bjerke, J.W., Tømmervik, H., Christensen, T.R., Hanna, E., Koller, E.K. & Sloan, V.L.
347 (2013) Ecosystem change and stability over multiple decades in the Swedish subarctic:
348 complex processes and multiple drivers. *Philosophical transactions of the Royal Society of*
349 *London. Series B, Biological sciences*, **368**.
- 350 Calvo, L., Alonso, I., Fernández, A. & De Luis, E. (2005) Short-term study of effects of
351 fertilisation and cutting treatments on the vegetation dynamics of mountain heathlands in
352 Spain. *Plant Ecology*, **179**, 181–191.
- 353 Campioli, M., Leblans, N. & Michelsen, A. (2012) Twenty-two years of warming, fertilisation
354 and shading of subarctic heath shrubs promote secondary growth and plasticity but not
355 primary growth. *PloS one*, **7**, e34842.
- 356 Cavieres, L. & Arroyo, M. (2002) Nurse effect of *Bolax gummifera* cushion plants in the alpine
357 vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science*, **13**, 547–554.
- 358 Chapin, F.S., Bret-Harte, M.S., Hobbie, S.E. & Zhong, H. (1996) Plant functional types as
359 predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation*
360 *Science*, **7**, 347–358.
- 361 Chapin, F.I., Shaver, G., Giblin, A., Nadelhoffer, K. & Laundre, J. (1995) Responses of arctic
362 tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.
- 363 Day, T.A., Ruhland, C.T., Strauss, S.L., Park, J.H., Krieg, M.L., Krna, M.A. & Bryant, D.M.
364 (2009) Response of plants and the dominant microarthropod, *Cryptopygus antarcticus*, to
365 warming and contrasting precipitation regimes in Antarctic tundra. *Global Change Biology*,
366 **15**, 1640–1651.
- 367 Dormann, C. & Woodin, S. (2002) Climate change in the Arctic : using plant functional types in a

- 368 meta-analysis of field experiments. *Functional Ecology*, **16**, 4–17.
- 369 Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Alatalo, J., Björk, R.G., Bjorkman, A.D.,
370 Callaghan, T. V, Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T. A, Fosaa, A.M.,
371 Gould, W. A, Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F.,
372 Jónsdóttir, I.S., Keuper, F., Klanderud, K., Klein, J. A, Koh, S., Kudo, G., Lang, S.I.,
373 Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H.,
374 Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M., Shaver,
375 G.R., Stenström, A., Tolvanen, A., Totland, O., Troxler, T., Wahren, C.-H., Webber, P.J.,
376 Welker, J.M. & Wookey, P. A. (2012) Global assessment of experimental climate warming on
377 tundra vegetation: heterogeneity over space and time. *Ecology letters*, **15**, 164–75.
- 378 Foster, B.L. & Gross, K.L. (1998) Species richness in a successional grassland: effects of
379 nitrogen enrichment and plant litter. *Ecology*, **79**, 2593–2602.
- 380 Graglia, E., Jonasson, S., Michelsen, A., Schmidt, I.K., Havstroim, M. & Gustavsson, L. (2001)
381 Effects of environmental perturbations on abundance of subarctic plants after three, seven
382 and ten years of treatments. *Oikos*, **24**, 5–12.
- 383 Grime, J. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects.
384 *Journal of Ecology*, **86**, 902–910.
- 385 Grimm, N.B., Chapin, F.S., Bierwagen, B., Gonzalez, P., Groffman, P.M., Luo, Y., Melton, F.,
386 Nadelhoffer, K., Pairis, A., Raymond, P. A, Schimel, J. & Williamson, C.E. (2013) The
387 impacts of climate change on ecosystem structure and function. *Frontiers in Ecology and the*
388 *Environment*, **11**, 474–482.
- 389 Henry, G.H.R., Freedman, B. & Svoboda, J. (1986) Effects of fertilization on three tundra plant

- 390 communities of a polar desert oasis. *Canadian Journal of Botany*, **64**, 2502–2507.
- 391 Hollister, R.D., Webber, P.J. & Tweedie, C.E. (2005) The response of Alaskan arctic tundra to
392 experimental warming: differences between short- and long-term responses. *Global Change*
393 *Biology*, **11**, 525–536.
- 394 Hothorn, T., Bretz, F., & Westfall, P. (2008) Simultaneous inference in general parametric
395 models. *Biometrical Journal*, **50**, 346-363.
- 396 IPCC. (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability: Working Group II*
397 *Contribution to the Fourth Assessment Report of the IPCC Intergovernmental Panel on*
398 *Climate Change*. Cambridge.
- 399 Jägerbrand, A.K., Alatalo, J.M., Chrimes, D. & Molau, U. (2009) Plant community responses to 5
400 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site.
401 *Oecologia*, **161**, 601–10.
- 402 Jump, A.S. & Peñuelas, J. (2005) Running to stand still: adaptation and the response of plants to
403 rapid climate change. *Ecology Letters*, **8**, 1010–1020.
- 404 Kaufman, D.S., Schneider, D.P., McKay, N.P., Ammann, C.M., Bradley, R.S., Briffa, K.R.,
405 Miller, G.H., Otto-Bliesner, B.L., Overpeck, J.T. & Vinther, B.M. (2009) Recent warming
406 reverses long-term arctic cooling. *Science*, **325**, 1236–9.
- 407 Klanderud, K. & Totland, Ø. (2004) Habitat dependent nurse effects of the dwarf-shrub *Dryas*
408 *octopetala* on alpine and arctic plant community structure. *Euroscience*, **11**, 410–420.
- 409 Klanderud, K. & Totland, Ø. (2005) Simulated climate change altered dominance hierarchies and
410 diversity of an alpine biodiversity hotspot. *Ecology*, **86**, 2047–2054.

- 411 Klein, J. A., Harte, J. & Zhao, X.-Q. (2004) Experimental warming causes large and rapid species
412 loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, **7**, 1170–1179.
- 413 Marion, G., Henry, G.H.R., Freckrnan, D.W., Johnstone, I., Jones, G., Jones, M.H., Levesque, E.,
414 Molau, U., Molgaard, P., Parsons, A.N., Svoboda, J. & Virginia, R.A. (1997) Open-top
415 designs for manipulating field temperature in high-latitude ecosystems. *Global Change
416 Biology*, **3**, 20–32.
- 417 May, J.L. & Hollister, R.D. (2012) Validation of a simplified point frame method to detect change
418 in tundra vegetation. *Polar Biology*, **35**, 1815–1823.
- 419 Mazerolle, M.J. (2013) AICcmodavg: Model selection and multimodel inference based on
420 (Q)AIC(c). version 1.28. <http://cran.r-project.org/package=AICcmodavg>
- 421 McKendrick, J., Batzli, G., Everett, K. & Swanson, J. (1980) Some Effects of Mammalian
422 Herbivores and Fertilization on Tundra Soils and Vegetation. *Arctic and Alpine Research*, **12**,
423 565–578.
- 424 McManus, K.M., Morton, D.C., Masek, J.G., Wang, D., Sexton, J.O., Nagol, J.R., Ropars, P. &
425 Boudreau, S. (2012) Satellite-based evidence for shrub and graminoid tundra expansion in
426 northern Quebec from 1986 to 2010. *Global Change Biology*, **18**, 2313–2323.
- 427 Molau, U. (1993) Relationships between Flowering Phenology and Life History Strategies in
428 Tundra Plants. *Arctic and Alpine Research*, 391–402.
- 429 Molau, U. & Alatalo, J.M. (1998) Responses of Subarctic-Alpine Plant Communities to
430 Simulated Environmental Change: Biodiversity of Bryophytes, Lichens, and Vascular Plants.
431 *Ambio*, **27**, 322–329.
- 432 Molenda, O., Reid, A.M. & Lortie, C.J. (2012) The alpine cushion plant *Silene acaulis* as

- 433 foundation species: a bug's-eye view to facilitation and microclimate. *PloS one*, **7**, e37223.
- 434 Morris, W., Pfister, C., Tuljapurkar, S., Haridas, C. V., Boggs, C.L., Boyce, M.S., Bruna, E.,
435 Church, D., Coulson, T., Doak, D., Forsyth, S., Gaillard, J., Horwitz, C., Kalisz, S., Kendall,
436 B., Knight, T., Lee, C. & Menges, E.S. (2008) Longevity can buffer plant and animal
437 populations against changing climatic variability. *Ecology*, **89**, 19–25.
- 438 Niu, S. & Wan, S. (2008) Warming changes plant competitive hierarchy in a temperate steppe in
439 northern China. *Journal of Plant Ecology*, **1**, 103–110.
- 440 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L.,
441 Solymos, P., Stevens, M.H., & Wagner, H. (2012) vegan: Community ecology package.
442 version 2.0-5. <http://cran.r-project.org/package=vegan>
- 443 Olsen, S.L. & Klanderud, K. (2014) Biotic interactions limit species richness in an alpine plant
444 community, especially under experimental warming. *Oikos*, **123**, 71–78.
- 445 Olsen, S.L., Sandvik, S.M. & Totland, Ø. (2013) Influence of Two N-Fixing Legumes on Plant
446 Community Properties and Soil Nutrient Levels in an Alpine Ecosystem. *Arctic, Antarctic,
447 and Alpine Research*, **45**, 363–371.
- 448 Onipchenko, V.G., Makarov, M.I., Akhmetzhanova, A. A., Soudzilovskaia, N. A., Aibazova,
449 F.U., Elkanova, M.K., Stogova, A. V. & Cornelissen, J.H.C. (2012) Alpine plant functional
450 group responses to fertiliser addition depend on abiotic regime and community composition.
451 *Plant and Soil*, **357**, 103–115.
- 452 Pajunen, A. M., Oksanen, J. & Virtanen, R. (2011) Impact of shrub canopies on understorey
453 vegetation in western Eurasian tundra. *Journal of Vegetation Science*, **22**, 837–846.

- 454 Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual*
455 *Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- 456 Pearson, R.G., Phillips, S.J., Loranty, M.M., Beck, P.S. A., Damoulas, T., Knight, S.J. & Goetz,
457 S.J. (2013) Shifts in Arctic vegetation and associated feedbacks under climate change.
458 *Nature Climate Change*, **3**, 673–677.
- 459 Polunin, N. (1951) The real arctic: suggestions for its delimitation, subdivision, and
460 characterization. *Journal of Ecology*, **39**, 308–315.
- 461 Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T. V & Lee, J.A. (1998) Responses of a
462 subarctic dwarf shrub heath community to simulated environmental change. *Journal of*
463 *Ecology*, **86**, 315–327.
- 464 R Core Team. (2013) R: A language and environment for statistical computing.
- 465 Robinson, C., Wookey, P., Lee, J., Callaghan, T.V. & Press, M. (1998) Plant community responses
466 to simulated environmental change at a high arctic polar semi-desert. *Ecology*.
- 467 Roy, J., Albert, C.H., Ibanez, S., Saccone, P., Zinger, L., Choler, P., Clément, J.-C., Lavergne, S.
468 & Geremia, R.A. (2013) Microbes on the cliff: alpine cushion plants structure bacterial and
469 fungal communities. *Frontiers in microbiology*, **4**, 64.
- 470 Sala, O.E., Chapin, F. & Armesto, J. (2000) Global Biodiversity Scenarios for the Year 2100 .
471 *Science*, **287**, 1770–1774.
- 472 Soudzilovskaia, N. & Onipchenko, V.G. (2005) Experimental investigation of fertilization and
473 irrigation effects on an alpine heath, northwestern Caucasus, Russia. *Arctic, Antarctic, and*
474 *Alpine Research*, **37**, 602–610.

- 475 Theodose, T. & Bowman, W. (1997) Nutrient availability, plant abundance, and species diversity
476 in two alpine tundra communities. *Ecology*, **78**, 1861–1872.
- 477 Van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin, F.S.I.,
478 Cornelissen, J.H.C., Gough, L., Hobbie, S.E., Jonasson, S., Lee, J.A., Michelsen, A., Press,
479 M.C., Richardson, S.J. & Rueth, H. (2004) Long-term ecosystem level experiments at Toolik
480 Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem
481 and plant type responses to global change. *Global Change Biology*, **31**, 105–123.
- 482 Virtanen, R., Grytnes, J.-A., Lenoir, J., Luoto, M., Oksanen, J., Oksanen, L. & Svenning, J.-C.
483 (2013) Productivity-diversity patterns in arctic tundra vegetation. *Ecography*, **36**, 331–341.
- 484 Walker, M.D. (1996) Community baseline measurements for ITEX studies. *ITEX Manual (2nd*
485 *ed.)* (eds U. Molau & P. Miolgaard), pp. 39–41. Danish Polar Centre, Copenhagen, Denmark.
- 486 Walker, M.D., Walker, D., Theodose, T. & Webber, P.J. (2001) The vegetation: hierarchical
487 species-environment relationships. *Structure and function of an alpine ecosystem: Niwot*
488 *Ridge, Colorado* (eds W. Bowman & T. Seastedt), pp. 99–127. Oxford University Press,
489 Oxford.
- 490 Wardle, D.A., Gundale, M.J., Jaderlund, A. & Nilsson, M.-C. (2013) Decoupled long-term effects
491 of nutrient enrichment on aboveground and belowground properties in subalpine tundra.
492 *Ecology*, **94**, 904–919.

Figure 1

Total cover, species richness, Shannon's diversity, and Pielou's evenness within the meadow community

Figure 1. Total cover (A), species richness (B), Shannon's diversity (C), and Pielou's evenness (D) in the control (CTR), nutrient addition (N), warming (T), and combined nutrient addition and warming (TN) plots in the meadow community. Means are separated by measurement year, with a white bar for 1995, a grey bar for 1999, and a black bar for the final measurement in 2001. Labels for treatments in (A) represent groupings based on significant ($p < 0.05$) differences from multiple comparisons performed within the generalized linear mixed-effects model. There were no significant differences between treatments for the other response variables. Error bars represent one standard error of the mean within each treatment and year.

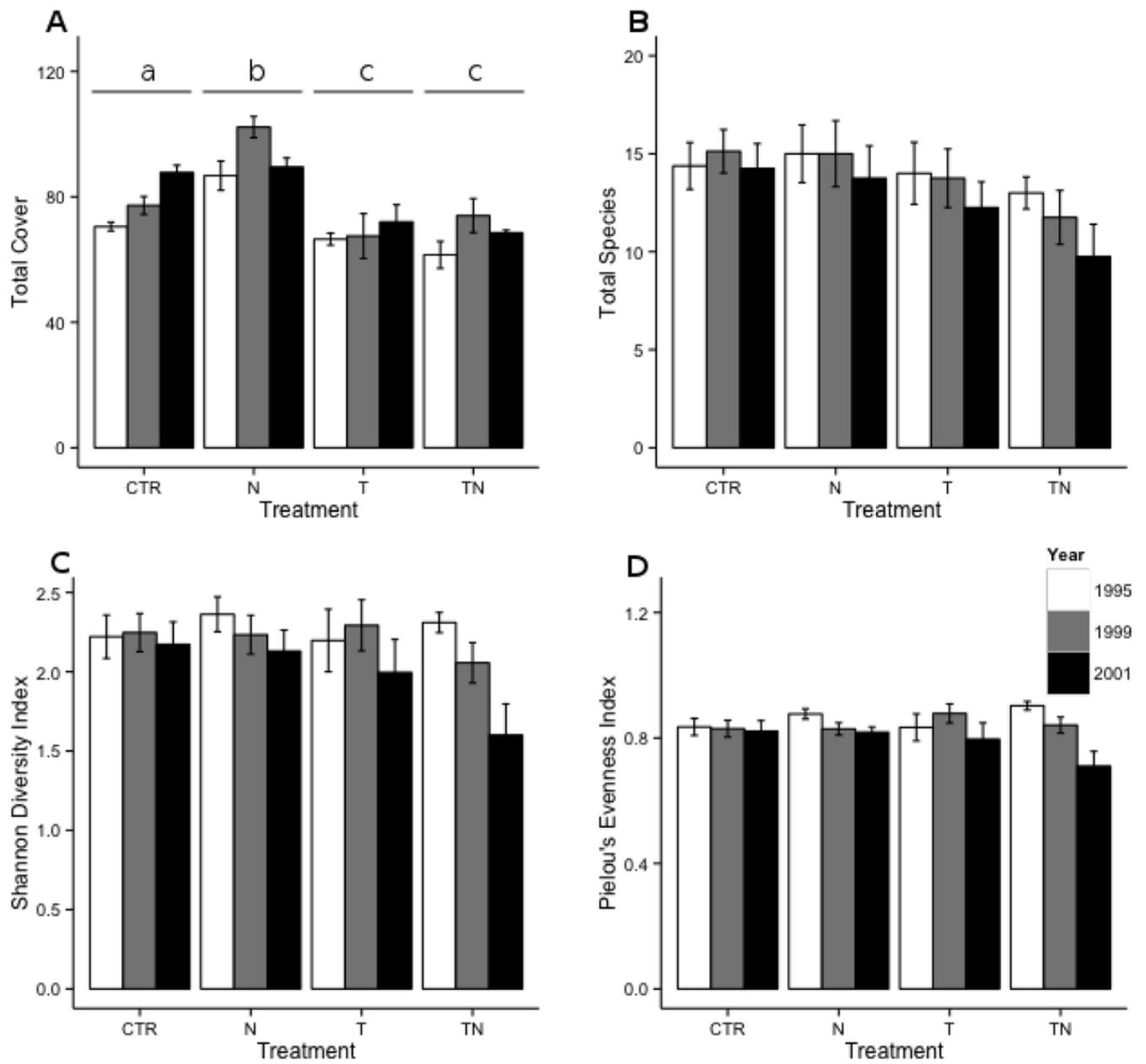


Figure 2

Cover of different functional groups, by treatment and year

Figure 2. Percentage of the total cover within the plots made up by six different functional groups, by treatment and year.

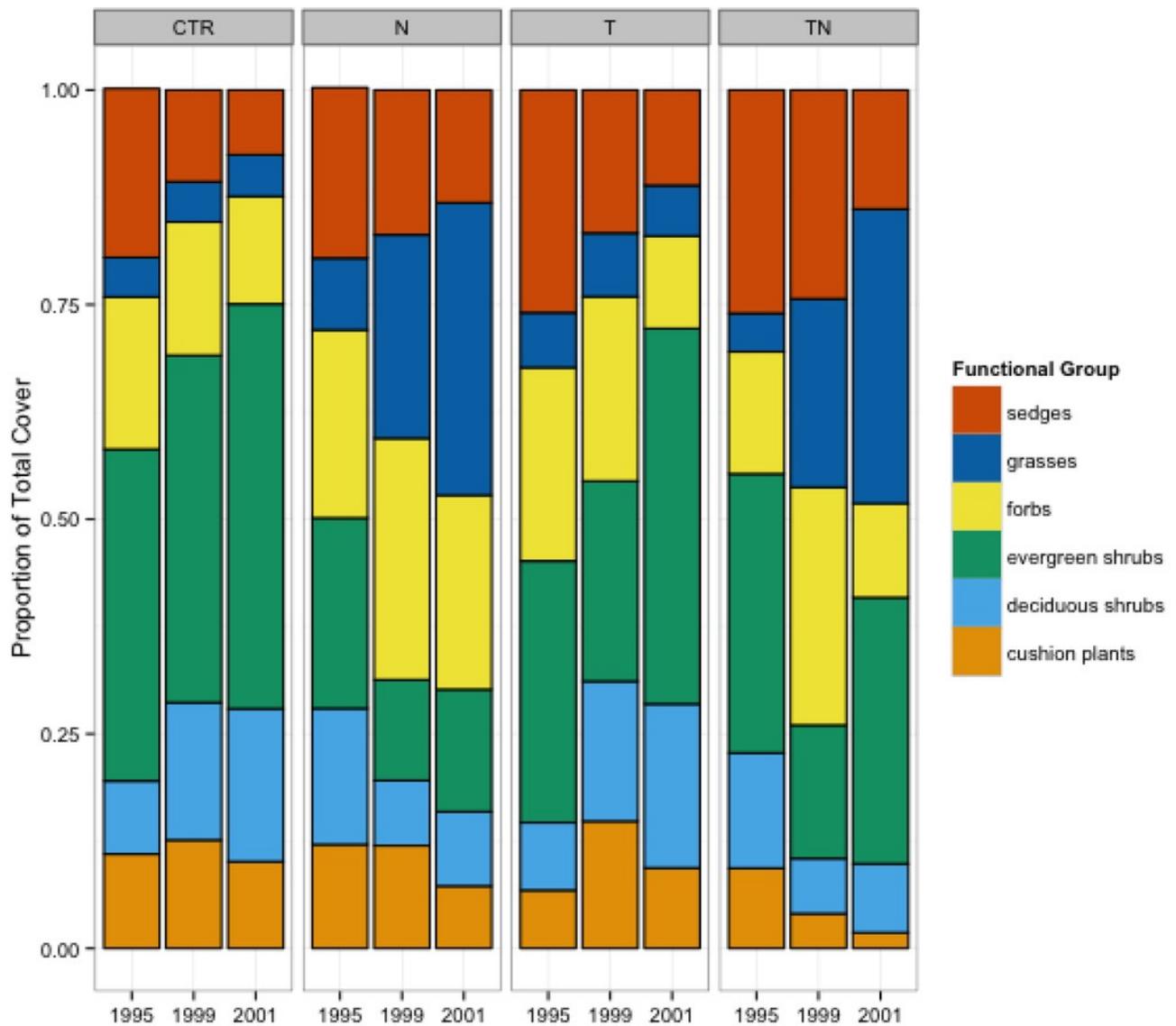


Figure 3

Total cover of cushion plants, deciduous shrubs, evergreen shrubs, forbs, grasses, and sedges.

Figure 3. Total cover of cushion plants (A), deciduous shrubs (B), evergreen shrubs (C), forbs (D), grasses (E), and sedges (F) within the plots. Bar colors and treatment codes are as in Figure 1. Letter labels above the bars for treatments, where present, indicate that linear comparisons performed within the generalized linear mixed-effects model showed significant ($p < 0.05$) differences between treatments. There were no significant differences between treatments for the other response variables. Error bars represent one standard error of the mean within each treatment and year.

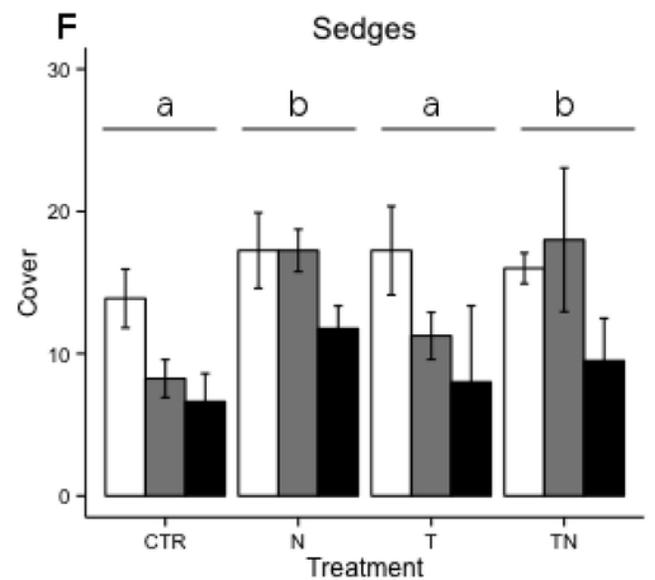
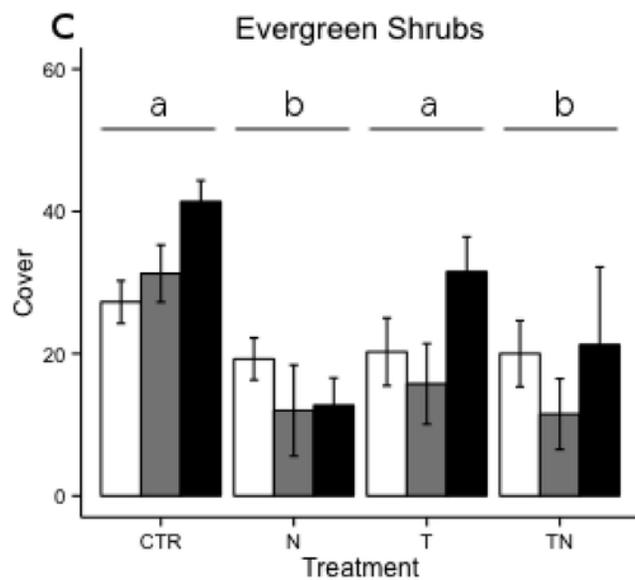
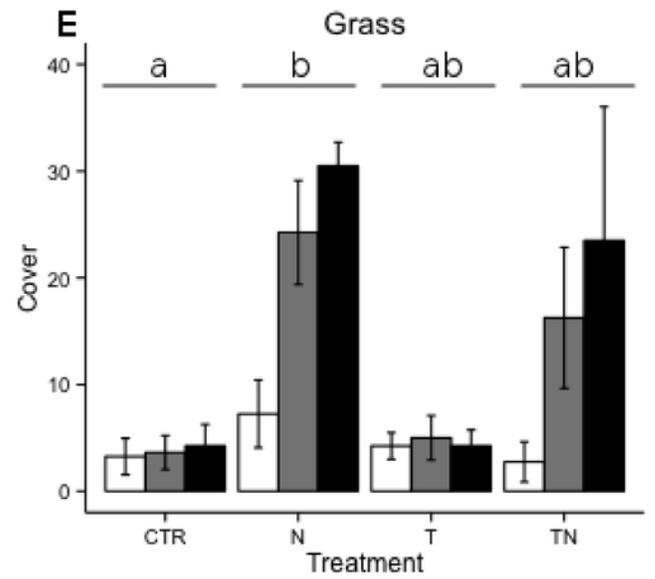
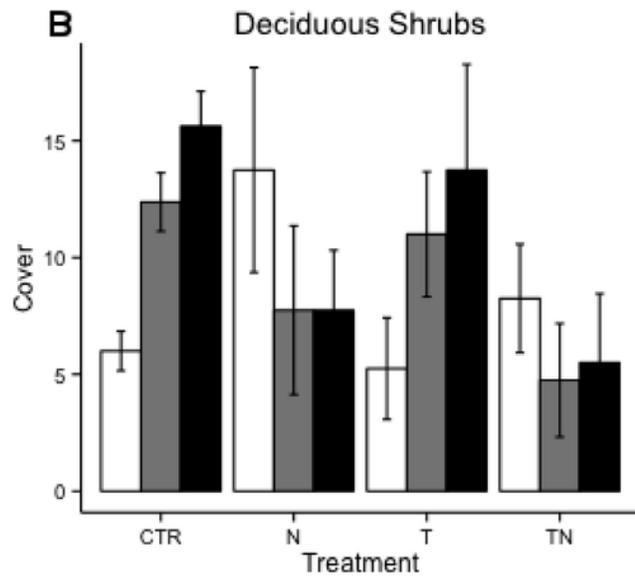
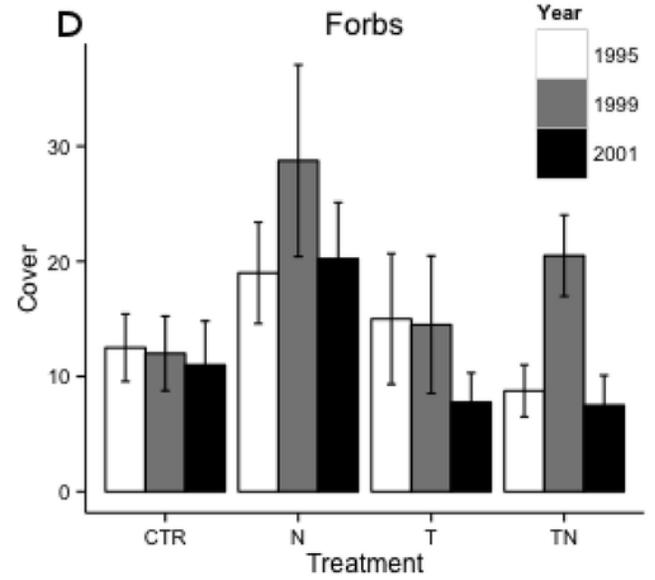
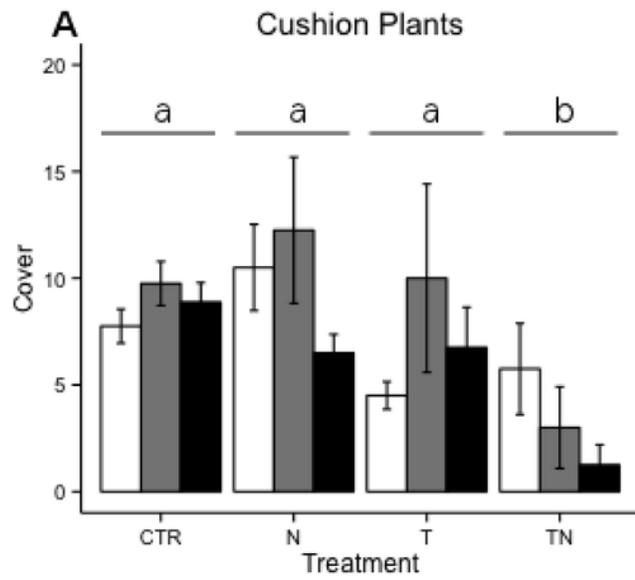


Figure 4

Shannon's diversity index for deciduous shrubs, evergreen shrubs, and forbs.

Figure 4. Shannon's diversity index for deciduous shrubs (A), evergreen shrubs (B), and forbs (C) within the plots. Bar colors and treatment codes are as in Figure 1. Letter labels above the bars for treatments in (A) indicate that linear comparisons performed within the linear mixed-effects model showed significant ($p < 0.05$) differences between treatments. There were no significant differences between treatments for (B) or (C). Error bars represent one standard error of the mean within each treatment and year.

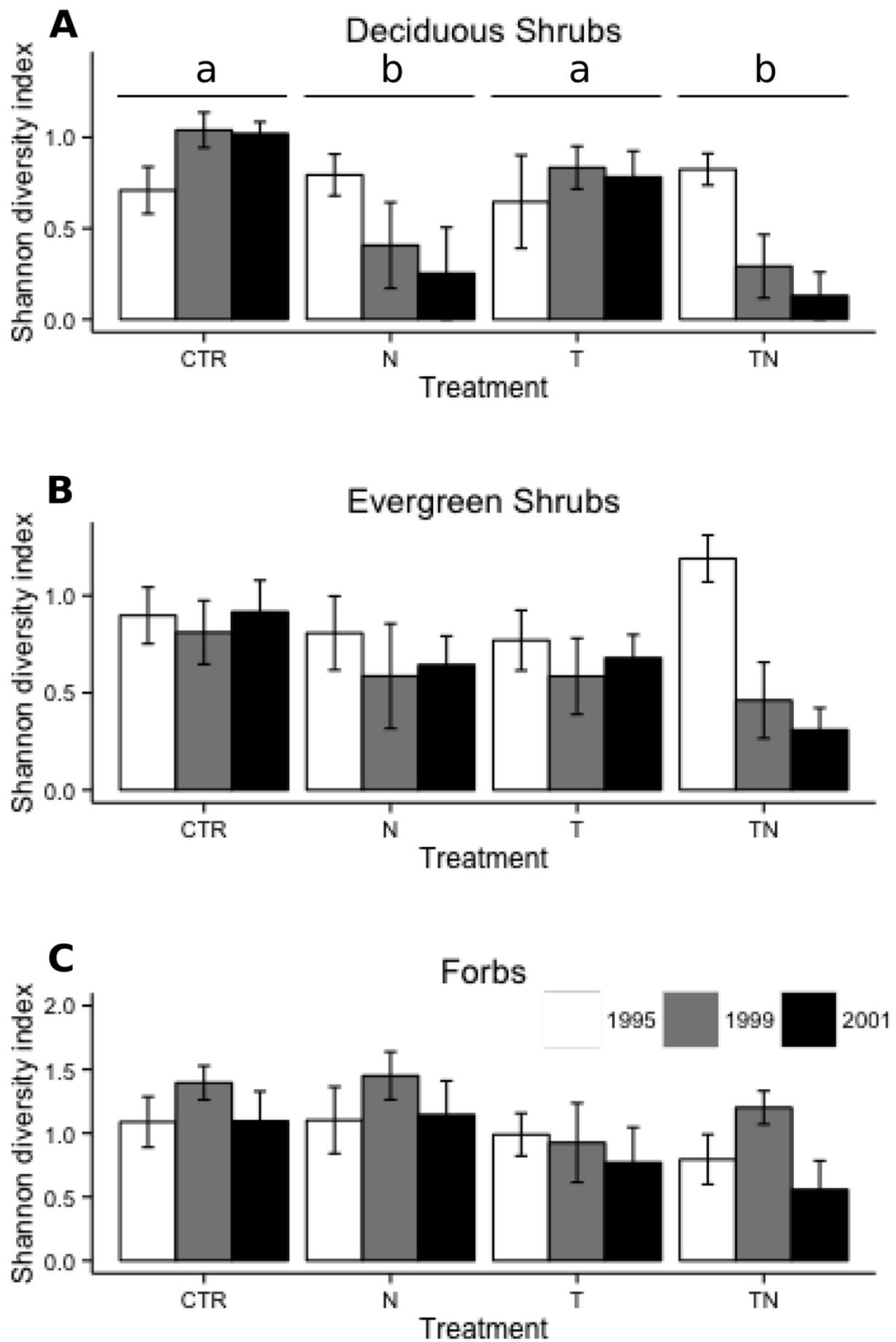


Figure 5

Changes in species richness from 1995 levels for the low-diversity functional groups of cushion plants, grasses, and sedges by treatment and year

Figure 5. Changes in species richness from 1995 levels for the low-diversity functional groups of cushion plants (A), grasses (B), and sedges (C) by treatment and year. Fisher's exact test showed that for grasses (B), treatment significantly ($p=0.002$) affected the gain or loss of species by 1999, but for the other functional groups the gain or loss of species within the treatments was not significantly different than predicted by the global mean.

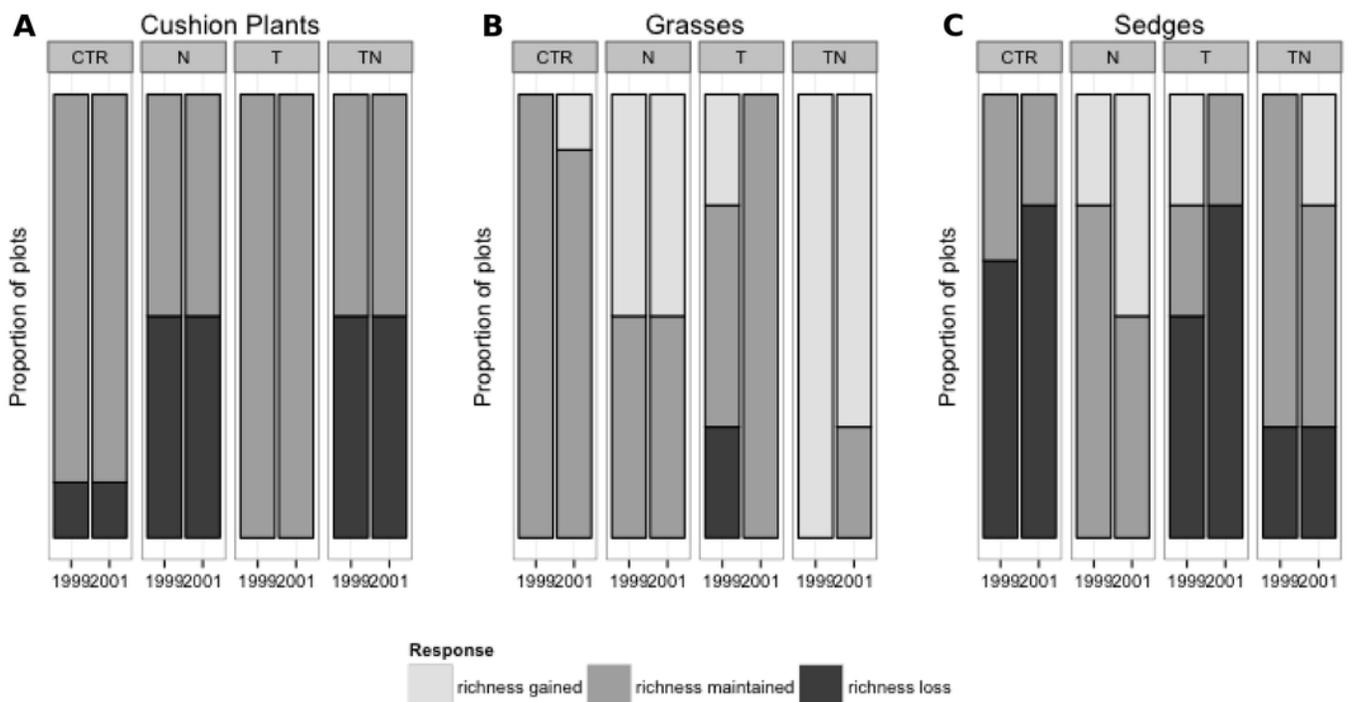


Table 1 (on next page)

Stepwise selection of generalized linear mixed-effects models for community responses to simulated global change, including plot and year as random factors

Table 1 - Stepwise selection of generalized linear mixed-effects models for community responses to simulated global change, including plot and year as random factors. AICc values for models are listed, beginning with the most complex model (factorial: nutrient x temperature manipulation) and moving backward until the best model is found. This process tests first an additive model (nutrient + temperature manipulation), then univariate models (nutrient manipulation only; temperature manipulation only) and finally a random effects model including only the random factors. The AICc of the best model is highlighted in bold, and the marginal R^2 (explaining variation from only the fixed factors) of the best model is also listed.

		AICc values for models in backward stepwise selection					Marginal R ² of Best Model
	Response	Factorial	Additive	Nutrient	Temperature	Random	
Total Community	Cover	73.53	76.92				0.45
	Richness	48.68	45.68	47.21	44.95	45.69	0.07
	Diversity	39.63	36.91	33.32	32.53	29.17	n.a.
	Evenness	-111.86	-117.98	-125.69	-125.73	-133.43	n.a.
Cushion Plants	Cover	123.52	125.79				0.41
Deciduous Shrubs	Cover	167.47	165.25	164.49	165.33	165.30	0.11
	Diversity	72.19	68.59	64.89	74.37	71.81	0.24
Evergreen Shrubs	Cover	200.60	199.21	197.77	205.27	204.55	0.32
	Diversity	63.43	60.77	57.07	57.08	53.67	n.a.
Forbs	Cover	160.80	159.16	157.18	159.26	157.09	n.a.
	Diversity	82.67	80.17	79.06	76.26	75.38	n.a.
Grasses	Cover	197.65	198.01				0.34
Sedges	Cover	154.35	152.76	150.74	155.64	154.14	0.15