

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.

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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
95 1951) with snow cover for most of the year, cool summers, and relatively mild, snow-rich
96 winters. Mean annual temperatures ranged from -2.0 to -2.7°C between 1993 and 1999, with
97 winter minima of -27.3 to -21.7°C . Mean annual precipitation during this time period was 808
98 mm, with individual years ranging from a low 605 mm in 1996 up to 990 mm in 1993. The
99 warmest temperatures come in July, which had mean temperatures ranging from $+5.4^{\circ}\text{C}$ in 1992
100 to $+9.9^{\circ}\text{C}$ in 1997.

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

108 *vitis-idaea* were present in every plot in the meadow community, while *Polygonum viviparum* and
109 *D. octopetala* were present in 75% or more plots.

110 *Experimental design*

111 In July 1995, 20 plots (1 x 1 m) with homogenous vegetation cover were chosen in the meadow
112 plant community and randomly assigned to treatments in a factorial design. There were 8 control
113 (CTR) plots and 4 plots for each of the experimental treatments: warming (T for temperature
114 enhancement), nutrient addition (N) and combined warming and nutrient addition (TN). Warming
115 was induced by Open Top Chambers (OTCs) that increase temperature by 1.5 to 3°C compared to
116 control plots with ambient temperature (Marion *et al.* 1997; Molau & Alatalo 1998). Nutrient
117 addition consisted of 5 g of nitrogen (as NH_4NO_3) and 5 g of phosphorus (P_2O_5) per m^2 , dissolved
118 in 10 L of meltwater. In 1995 all plots were analyzed with a point–frame method (Walker 1996)
119 to determine the species occurrences under natural conditions before implementing the
120 experimental treatments. The OTC's were then left on plots with warming treatments year-
121 around, and nutrient addition was applied directly after the initial vegetation analyses in 1995 and
122 a few days after snow melt in the subsequent years (1996-2001).

123 *Measurements*

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

131 *Data analysis*

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

137 For each response variable, normality and homogeneity of variance were assessed using
138 standard diagnostic procedures. All statistical analyses were performed in R version 2.15.3 (R
139 Core Team 2013). A linear model with fixed factors of nutrient and temperature manipulation,
140 random factors of year and plot was used to analyze responses in total cover, species richness,
141 diversity, and evenness for the whole community using the lme4 package (Bates, Maechler &
142 Bolker 2012), using restricted maximum likelihood (REML). A generalized model using Poisson
143 errors was used for total cover and species richness, while diversity and evenness were normally
144 distributed and a generalized model was not necessary. Backward model selection was performed
145 using second-order AIC (AICc) scores (Mazerolle, 2013) due to the small sample size. For model
146 validation, we examined residuals and q-q plots. Where the interaction of the fixed factors was
147 significant, general linear hypotheses were set manually for each combination of factor levels and
148 tested within the model (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 showing a different response than the nutrient treatment (Figure 1A). A total of 51
171 species were observed in plots over the course of the seven-year experiment, with individual
172 counts per plot ranging from 6 to 21 species at a given time point. Only the warming treatment
173 had an effect on species richness, with no additional effect of nutrient manipulation or interaction
174 between the two treatments. However, the difference between species richness in warmed and
175 unwarmed plots was only marginal (linear comparisons, $p=0.07$; Figure 1B). This corresponded
176 to no significant effects of any of the treatments on either Shannon diversity (Figure 1C) or
177 Pielou's evenness (Figure 1D).

178 Drastic shifts in dominance structure were observed in the nutrient and combined
179 temperature and nutrient manipulation plots over the course of the 7-year experiment (Figure 2),
180 with grasses increasing in the nutrient and nutrient plus warming treatments, while sedges and
181 deciduous shrubs decreased in cover.

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

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

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

198 Grass cover responded to a significant interaction between the nutrient and temperature
199 manipulation. Grass cover increased in the nutrient treatment compared to the control treatment
200 (linear comparisons, $p = 0.004$), with intermediate abundance in the other plots (Figure 3E). By
201 1999, seven of the treatment plots had increased in richness but none of the control plots had
202 changed in richness, which represented a significant effect of the perturbations (Fisher's exact

203 test, $p=0.002$; Figure 5B). By 2001, additional gain and loss of species richness had negated this
204 effect (Fisher's exact test, $p>0.05$). Sedge cover increased significantly in the plots receiving
205 nutrient amendment (linear comparisons, $p=0.01$), especially in 1999 although the effect had
206 waned by 2001 (Figure 3F). The majority of plots either decreased in species richness or
207 maintained the same number of species by 1999 and 2001, and the distribution of changes among
208 the treatments was not different than that which would be predicted by the global mean (Fisher's
209 exact test, $p>0.10$; Figure 5C).

210 Discussion

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

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

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

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

270 Cushion plants decreased in cover in response to nutrient and the combined warming and
271 nutrient addition. Similarly, in high Arctic Svalbard, 5 years of nutrient addition caused
272 significant decrease of *Saxifraga oppositifolia* (Robinson *et al.* 1998), while *Silene acaulis* has
273 been shown to respond in contrasting manner to short and medium term nutrient addition (Alatalo
274 & Little 2014). If cushion plants begin to decrease in larger numbers in severe environments, this

275 could potentially impact a wide array of species in ecosystems where they are found due to their
276 importance as facilitator species (Cavieres & Arroyo 2002; Molenda, Reid & Lortie 2012).

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

294 Community diversity has been shown to decrease in arctic and alpine meadows in
295 response to nutrient addition (Theodose & Bowman 1997; Wardle *et al.* 2013) and in particular in
296 response to combined warming and fertilization (Press *et al.* 1998; Klanderud & Totland 2005).
297 Generally, this study supports the productivity-diversity relationship found across arctic habitats,
298 with community diversity peaking in mid-productivity systems and crashing as nutrient
299 availability increases further (Virtanen *et al.* 2013). This is likely due to the increasing

300 competition in plant-plant interactions and the shifting dominance structure with grasses taking
301 over the experimental plots and suggests that global change in the arctic could entail not only
302 redistribution of vegetation types, but also significant costs to biodiversity.

303 **Conclusions**

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

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Figure 1

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

Fig 1 - Total cover (A), species richness (B), Shannon's diversity (C), and Pielou's evenness (D) within the meadow community. 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.

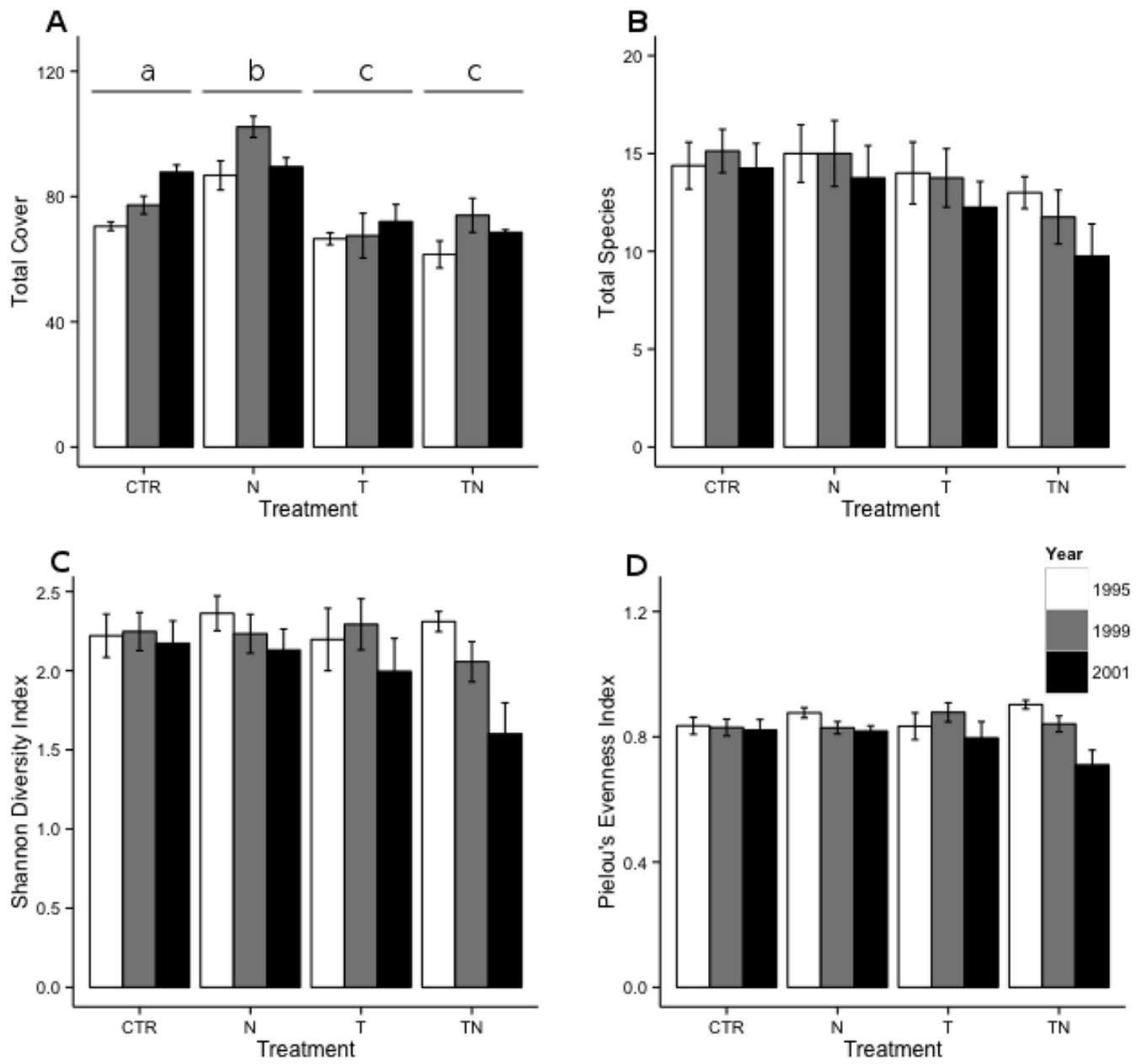


Figure 2

Cover of different functional groups, by treatment and year

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

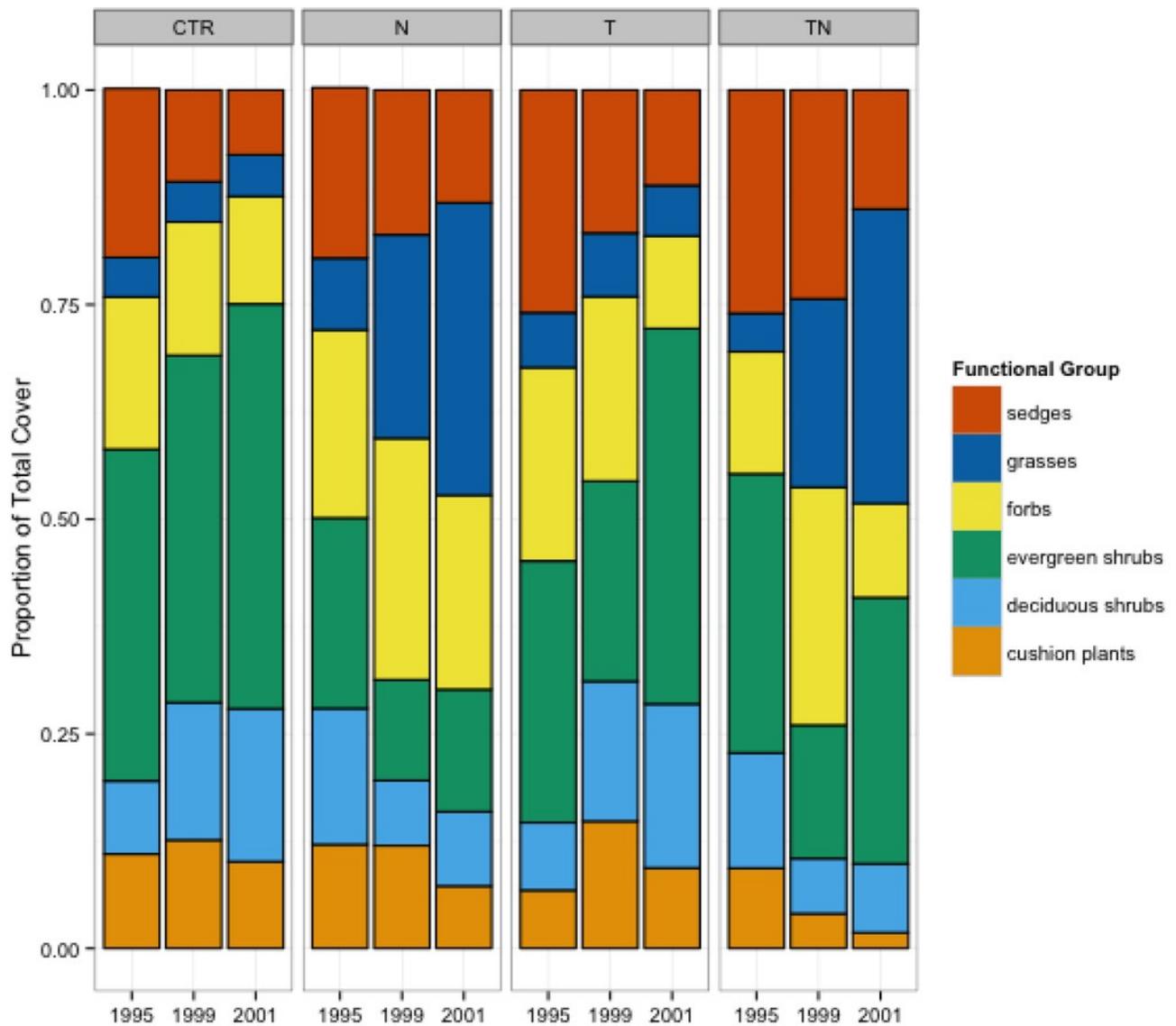


Figure 3

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

Fig 3 - Total cover of cushion plants (A), deciduous shrubs (B), evergreen shrubs (C), forbs (D), grasses (E), and sedges (F) within the plots. 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.

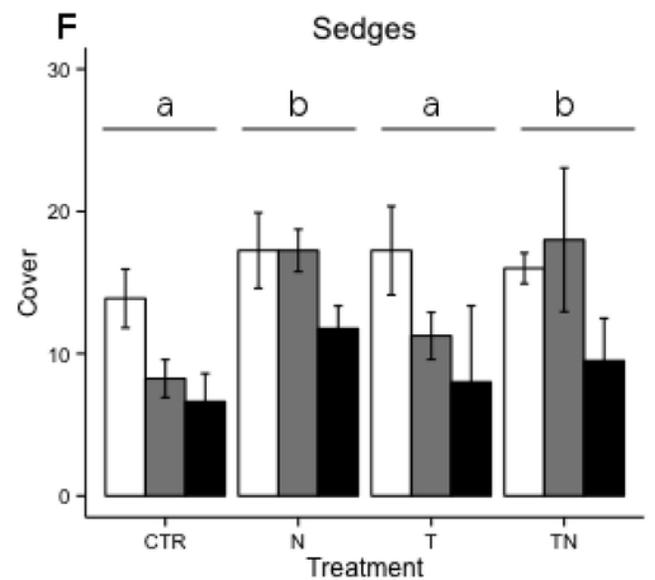
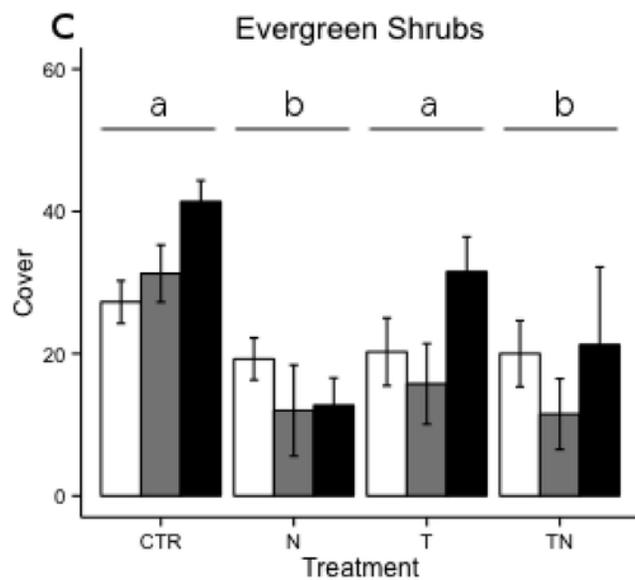
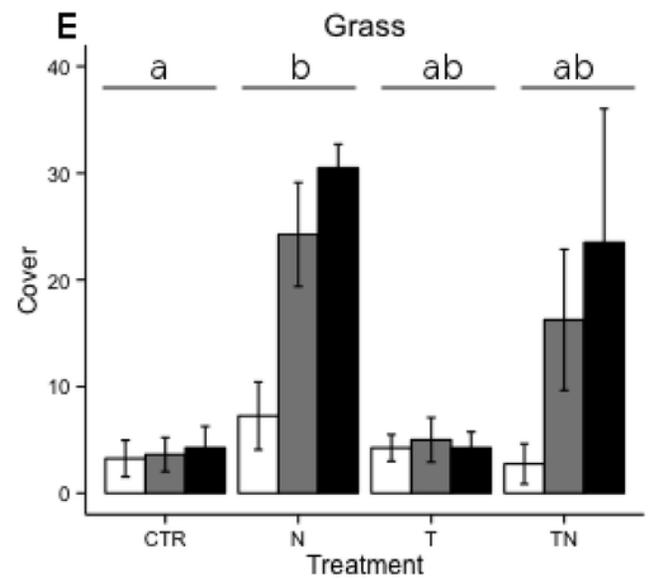
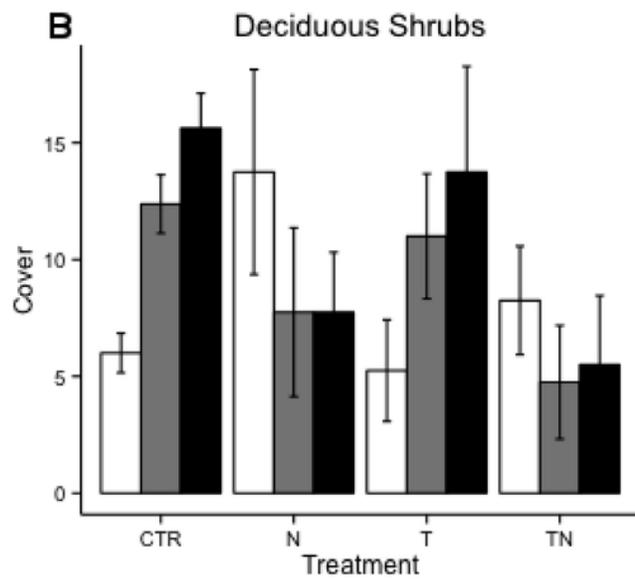
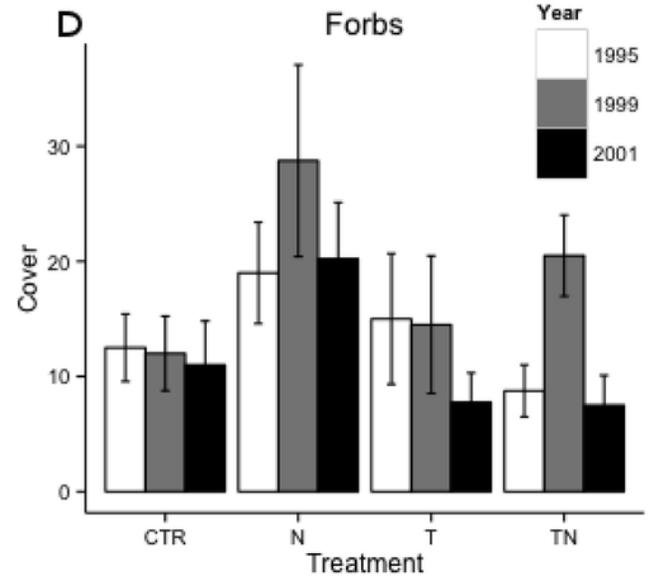
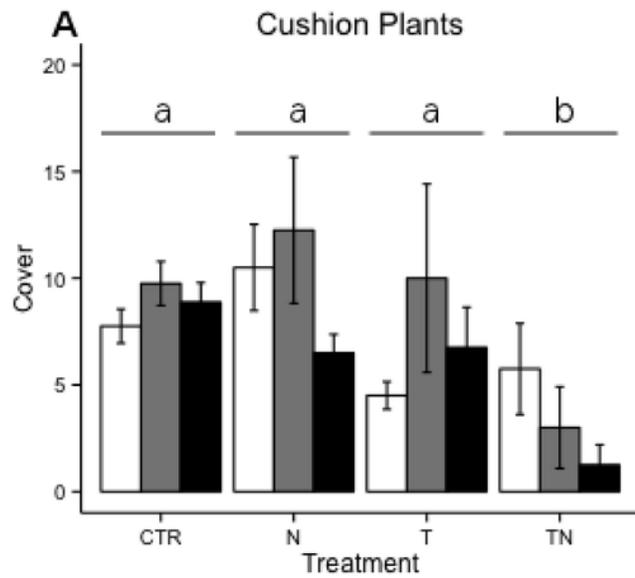


Figure 4

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

Fig 4 - Shannon's diversity index for deciduous shrubs (A), evergreen shrubs (B), and forbs (C) within the plots. 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.

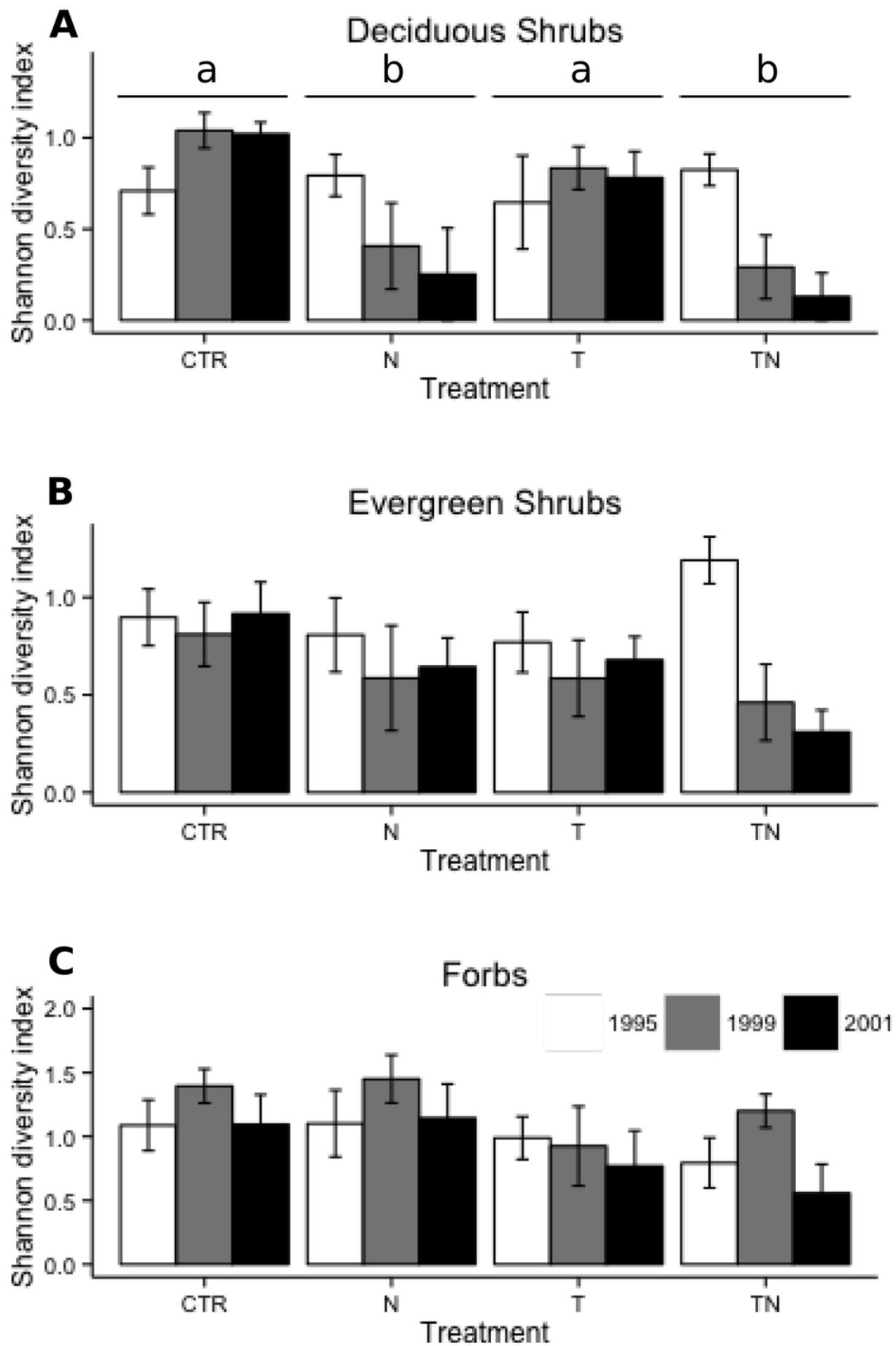


Figure 5

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

Fig 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.

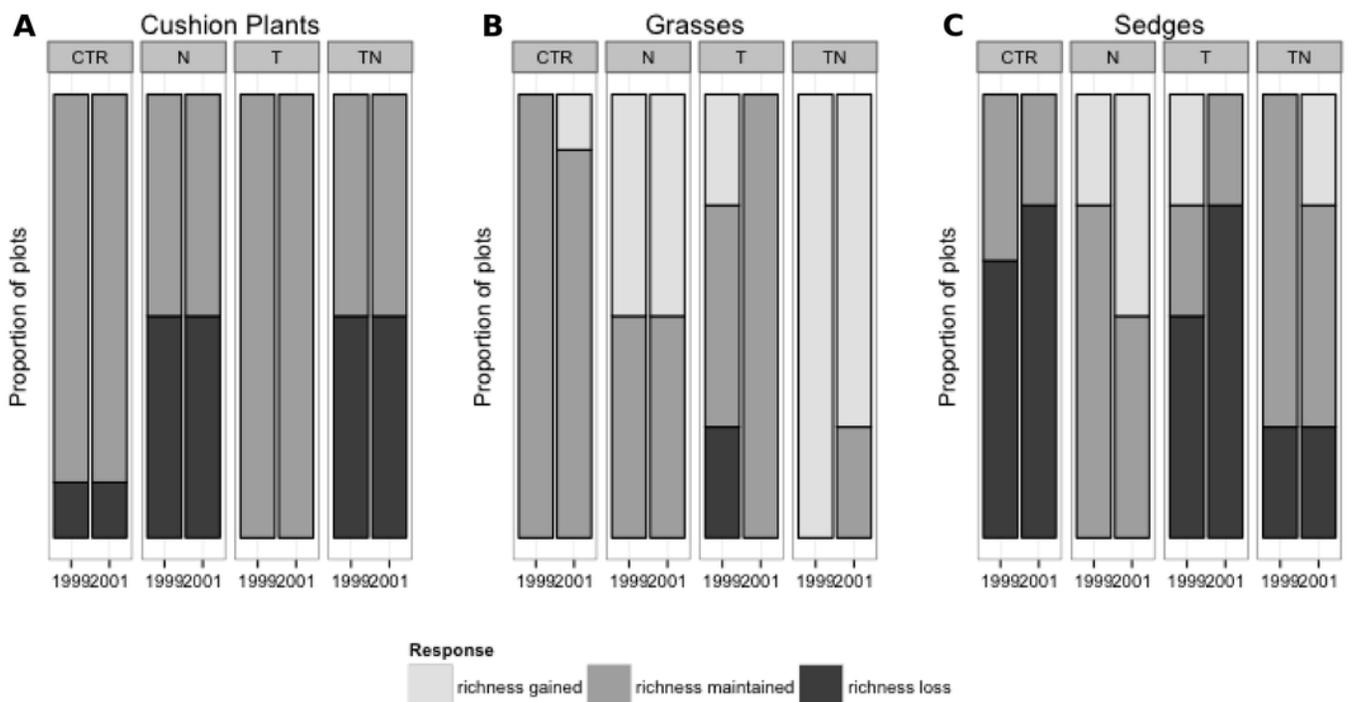


Table 1 (on next page)

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