

# Trait profiles and functional diversity following disturbance in a mixed grassland

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**Background.** Localized disturbances within established grasslands alter a suite of biological and chemical properties, leading to shifts in species composition. For example, relatively rare species in established communities may become dominant in successional communities if they exhibit traits that are suited to disturbance conditions. Although the idea that plant species exhibit different trait ‘strategies’ is well established, it is unclear how ecological selection for specific traits may change as a function of disturbance. Further, there is little data available testing whether disturbances select for single trait-characters within communities (homogenization), or allow multiple trait-types to persist (diversification). We investigated how (a) traits and (b) functional diversity of post-disturbance communities compared to those in adjacent undisturbed grasslands, and (c) if changes in functional diversity resulted in the homogenization or diversification of functional traits within local communities.

**Methods.** Here we emulate the impacts of an extreme disturbance in a mixed grassland site. We measured plant community composition of twelve paired plots in a native grassland within the central parkland of Alberta, Canada. Each pair consisted of one undisturbed plot and one which had all plants terminated two years prior. We used species abundances in conjunction with a local trait database to calculate community weighted means for maximum height, specific leaf area, specific root length, leaf nitrogen percent, and root nitrogen percent. To test the impacts of disturbance on community functional traits, we calculated functional diversity measures and compared them between disturbed and undisturbed local communities.

**Results.** Within two years, species richness and evenness in disturbed communities had recovered and was equivalent to undisturbed communities. However, disturbed and undisturbed communities had distinct community compositions that differed in functional diversity. Functional divergence was significantly lower in the disturbed plots. Further, disturbance was also linked to increases in community-weighted mean trait values associated with resource-acquisitive traits, such as specific leaf area, and leaf and root nitrogen.

**Discussion.** Disturbance had lasting effects on the functional traits and diversity of communities, despite traditional measures of biodiversity such as richness and evenness recovering within two years. There was a discrete shift in the trait space of post-disturbance communities compared to undisturbed communities such that post-disturbance communities were dominated by traits that enhance resource uptake and growth rates. Overall, these results show that disturbance fundamentally changes the functional character of communities, even if they superficially appear recovered.

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56 recovered.

## 57 **Introduction**

58 Habitat heterogeneity in grasslands is maintained in part by small-scale mortality  
59 inducing disturbances, such as fossorial mammal activity (Davidson and Lightfoot, 2008;  
60 Davidson, Detling, and Brown, 2012), drought (Godfree et al., 2011), overgrazing (di Virgilio  
61 and Morales, 2016), pathogens (Mursinoff and Tack, 2017), and even herbicide drift (Fried,  
62 Villers, and Porcher, 2018). In extreme instances, disturbance can result in the total mortality of  
63 mature vegetation (e.g. Cahill 2003). Though each of these disturbances have unique  
64 characteristics, they all result in the localized death of established vegetation, creating vegetation  
65 “gaps” (Suding, 2001). Gaps result in changes to competitive hierarchies and abiotic soil  
66 conditions and competitive hierarchies (Suding and Goldberg, 2001; Suding, 2001), leading to  
67 changes in species diversity and community composition.

68 Examining traits can shed light on the specific impacts of disturbance on plant  
69 communities. Traits are measurable individual morphological, physiological, or phenological

70 characteristics that provide insight into life history strategies and influence plant ranges and  
71 species interactions (Viole et al., 2007; Cadotte, Carscadden, & Mirotnick, 2011). “Functional  
72 traits” specifically impact growth, reproduction and survival (Viole et al., 2007). At small scales,  
73 trait differences can influence local diversity patterns by determining competitive outcomes (Liu  
74 et al., 2015). Traits can also provide insight as to species resource acquisition strategies by  
75 indicating species location on the fast-slow plant economics spectrum, where “fast” strategies  
76 prioritize resource acquisition and growth while “slow” strategies favour stress tolerance and  
77 longevity (Reich et al., 2014). Measuring functional traits after a disturbance (such as those  
78 which create gaps) can reveal how a community has changed in functional strategies and can be  
79 used to examine the resulting community’s functional diversity. Cadotte (2007) describes gap  
80 species as prioritizing rapid resource uptake, whereas non-gap species take a slower, tolerance-  
81 based approach. For example, specific leaf area (SLA) values are likely to be larger in post-  
82 disturbance successional communities as high SLA is correlated to fast growth and low  
83 competitive ability (Kunstler et al., 2016). Additionally, Loughnan and Gilbert (2017) found that  
84 SLA may be involved with shifts in competitive ability as greater SLA is associated with more  
85 sunlight acquisition and thus increased energy acquisition. Thus, changes in communities post-  
86 disturbance are likely due to differences in the trait profiles of successional species.

87       It is important to note that these changes in species composition and community-level  
88 traits changes may not be reflected in the total number of species in the community (i.e. species  
89 richness). Disturbance may change the nature of community assembly in successional  
90 communities by altering the process by which species from the regional pool are able to colonize  
91 local communities (HilleRisLambers et al., 2012, Escobedo et al., 2021). Disturbance changes  
92 the environmental filters which constrain species dispersal and recruitment to communities

93 (Myers et al., 2015; Brown & Cahill, 2020); in this case we would expect the resulting  
94 community to contain species that possess functional traits better suited to the new set of  
95 environmental filters, changing the community-level traits and functional diversity of the  
96 disturbed community. Thus, if taxonomic measures like species richness or evenness remain  
97 unchanged after disturbance, they may mask functional differences and result in a mirage of  
98 stability when, in fact, the community has undergone great change. This emphasizes the  
99 importance of studying functional traits and quantifying functional diversity to understand  
100 community drivers.

101         Functional diversity is a subset of biological diversity which measures the traits present  
102 in an ecosystem (Tillman, 2001). It is distinct from taxonomic diversity as it reflects the breadth  
103 of the functional space occupied by species in a community (Rosenfeld, 2002; Villéger et al.,  
104 2008), whereas taxonomic diversity indicates the number of species in a given community  
105 separate from any measure of community function (Laliberté and Legendre, 2010). Some  
106 functional diversity measures are not greatly influenced by taxonomic measures such as species  
107 richness (Laliberté and Legendre, 2010) and can offer a more nuanced approach to understanding  
108 community characteristics. Disturbance affects functional diversity (Parreira de Castro, Dolédec,  
109 & Callisto, 2018) and can potentially result in functional homogenization, or selection for similar  
110 trait-characters in species colonizing in disturbed communities (Olden et al., 2004). However,  
111 resource fluxes associated with disturbance (Davis, Grime, & Thompson, 2000) may lead to trait  
112 diversification within colonizing species to allow for more efficient utilization of the increased  
113 resources available in disturbed communities (Chapman, Childers, & Vallino, 2016; Jentsch &  
114 White, 2019). As functional diversity is associated with the provisioning of ecosystem services

115 (Díaz et al., 2007; Roscher et al., 2012; Pakeman, 2014), the homogenizing or diversifying  
116 effects of disturbance on functional diversity must be better understood.

117 If species in post-disturbance areas are more likely to possess traits which support faster  
118 resource acquisition (e.g. Cadotte, 2007; Kunstler et al., 2016), then shifts in trait distributions  
119 after disturbance may alter functional diversity by changing the success of different trait suites to  
120 favor “fast” traits prioritizing resource acquisition at the local scale. However, it is unclear which  
121 traits differ between plants in disturbed and undisturbed areas, and how these different strategies  
122 are reflected in functional diversity. To resolve these outstanding questions, we ask:

- 123 1. How do functional traits of a grassland community change after disturbance?
- 124 2. How does functional diversity change after disturbance?
- 125 3. If functional distributions do change, will it result in the homogenization or  
126 diversification of community-level traits?

127 If disturbance causes shifts in habitat filters, then we expect to observe shifts in the functional  
128 trait space of the resulting community. If disturbance constrains the competitive strategies that  
129 succeed in successional communities (for instance, favouring plants with resource-acquisitive  
130 traits), we would expect changes in trait values (i.e. community-weighted means) and potentially  
131 the homogenization of community-level traits. Alternatively, if species turnover after disturbance  
132 drives shifts in community traits, we then expect to observe both taxonomic and functional trait  
133 shifts, which could in turn diversify community-level traits.

## 134 **Methods**

### 135 **Study site**

136 Our study site was located in the Roy Berg Kinsella Research Ranch in Kinsella, AB,  
137 Canada (53°5' N, 111°33' W). Data collection took place in a native grassland dominated by

138 *Hesperostipa curtiseta* (Hitcch.) Barkworth, *Festuca hallii* (Vasey) Piper and *Poa pratensis* (L.)  
139 (Brown and Cahill, 2019). The site is part of the Aspen Parkland ecoregion, a savanna-type  
140 habitat characterized by a mosaic of mixed-grass prairie and trembling aspen (*Populus*  
141 *tremuloides* Michx.). The field site is periodically grazed by cattle with a heavy grazing event in  
142 October 2019 and a light grazing event occurring in May 2020.

### 143 **Study design**

144 We sampled twelve plots (50 cm x 50 cm), arranged in six pairs, which were originally  
145 established in 2016 (Brown & Cahill, 2020). Each pair contained an undisturbed plot, where no  
146 standing vegetation was terminated, and a disturbed plot, where all standing vegetation was  
147 terminated. Disturbed plots were created in May 2016, by having all biomass trimmed to the soil  
148 surface and a glyphosate herbicide (Roundup©) applied to the remaining stems to ensure death  
149 of the resident vegetation. This treatment was maintained through August 2018 with any  
150 regenerating plant materials trimmed and painted with herbicide during the growing seasons.  
151 This treatment does not represent any specific natural event, and instead is testing the extreme  
152 event of complete removal of the resident vegetation. Additionally, this treatment does not  
153 remove the seed bank present at the site (Brown and Cahill, 2020) and thus does not affect  
154 community regeneration from seed (see Grubb, 1977).

155 Plant community composition was measured in July 2018 by visually estimating percent  
156 cover of all species present within each plot. Two years post-treatment, in July 2020, plots were  
157 revisited, by which time vegetation had regenerated in the disturbed plots. Community  
158 composition was measured using percent cover estimation of each species. Sedges were unable  
159 to be identified to species and were recorded as “*Carex* spp.”.

### 160 *Plant traits*

161 Disturbance can alter abiotic conditions (Suding and Goldberg 2001); however, here we  
162 focus on its impacts on vegetative traits. Plant trait data came from a database developed  
163 principally at this field site (Cahill, 2020), thus representing local trait data. Details of trait  
164 measures are found in Cahill (2020), but largely follow the methods outlined in Cornelissen et al.  
165 (2003) and Pérez-Harguindeguy et al. (2013). Here we focused on five traits which encompass  
166 aspects of plant structure and above- and belowground resource acquisition: maximum height,  
167 specific leaf area (SLA), specific root length (SRL), leaf nitrogen percentage (N %), and root N  
168 %. See Cahill (2020) for trait definitions. These traits were chosen to provide a holistic scope of  
169 above and below ground functional strategies with reference to trait groups described by Cadotte  
170 (2017). Site-specific trait data was available in the database for all species except for *Cirsium*  
171 *vulgare* (Savi) Tenore, *Collomia linearis* Nuttall, *Gentianella amarella* (Linnaeus) Börner,  
172 *Sonchus arvensis* Linnaeus, and two unidentified forbs. Trait data was obtained for species that  
173 represent at least 93% of total composition, which exceeds the 80% threshold standard for trait  
174 studies (Pakeman & Quested 2007).

#### 175 *Trait profiles and functional diversity*

176 To characterize communities by their traits, we first calculated community weighted  
177 means (CWMs) for five traits: SLA, maximum height, leaf N %, root N %, and SRL. CWMs are  
178 the average value of a given trait in a community weighted by the abundance of all species  
179 possessing said trait (Lavorel et al., 2008), and are useful for understanding community  
180 properties and dynamics, as well as quantifying community change (Garnier et al., 2004, 2007;  
181 Louault et al., 2005). CWMs were calculated at the species-level. While disturbance is likely to  
182 result in intraspecific variability in functional traits, here we focus on species-level values as a  
183 first-level test to detect if disturbance does result in persistent change to community functional

184 traits. Outlier trait values (values more than three standard deviations away from the species'  
185 mean) were removed prior to calculating CWM. We then quantified the functional diversity of  
186 communities using functional richness (FRic), functional evenness (FEve), functional divergence  
187 (FDiv), and Rao's quadratic entropy (Q) (Villéger, Mason, & Mouillot, 2008; Mouchet et al.,  
188 2010; Table 1). These metrics allow us to characterize the volume (via FRic), evenness (via  
189 FEve), and spread (via FDiv and Q) of the communities' functional traits in multidimensional  
190 space. By using these multivariate descriptors of communities, we are able to compare  
191 communities' character before and after disturbance, as well as to determine if community traits  
192 become more or less homogenous as a result of disturbance. We used package vegan (Oksanen et  
193 al., 2017) in program R (v 4.0.0; R Core Team, 2020) to compute species richness and evenness,  
194 using methods from Oksanen (2020). We used package FD (Laliberté, Legendre, & Shipley,  
195 2014) to compute CWMs. We also computed FRic, FDiv, FEve, and Rao's Q using package FD.

## 196 **Statistical analysis**

197 To determine if community traits differed between control and disturbed treatments after  
198 recovery, we used five separate linear models (LMs). The CWM's for SLA, height, leaf N %,  
199 root N %, and SRL were used as response variables, plot type (disturbed or undisturbed) was a  
200 fixed effect and plot pair (i.e., disturbed and undisturbed plot location) was a random effect. All  
201 LMMs were run using an underlying normal distribution with the lme4 (Bates et al., 2015) and  
202 lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017) packages. We also used four separate  
203 LMMs to quantify how functional diversity measures, namely FRic, FDiv, FEve, and Rao's Q,  
204 differed between disturbance types. FRic, FDiv, FEve, and Rao's Q were used as response  
205 variables, plot pair was included as a random effect and plot type (disturbed or undisturbed) was  
206 a fixed effect in all models. Functional richness was log-transformed to fit assumptions of

207 normality. To determine whether disturbed and undisturbed communities had different  
208 community compositions, we conducted a permutational multivariate analysis of variance  
209 (PERMANOVA), with plot as a strata, using packages *vegan* and *RVAideMemoire* (Hervé,  
210 2021).

## 211 **Results**

212       Between 2018 and 2020, total species richness in undisturbed plots decreased from 55 to  
213 52 while average species richness in disturbed plots increased from 0 in 2018 to 53 in 2020  
214 (Table S1). Six species were found only in disturbed communities (*Androsace septentrionalis*,  
215 *Cirsium arvense*, *Mulgedium pulchellum*, *Thalictrum venulosum*, an unidentified *Brassicaceae*  
216 plant, and an unidentified herbaceous dicot; Table S1). *Androsace septentrionalis*, *Cirsium*  
217 *arvense*, and *Mulgedium pulchellum* are commonly found in disturbed areas (Tannas, 2004). In  
218 particular, *Cirsium arvense* is associated high rates of reproduction and dispersal. 15 species  
219 were found only in undisturbed communities (Table S1). These species, except *Fallopia*  
220 *convolvulus*, are all native to Alberta (Desmet and Brouilet, 2013).

221       Despite persistent effects on local diversity, and although disturbed plots began with zero  
222 species present in 2018, within two years there was no significant difference between plot-level  
223 (alpha) richness and evenness between disturbed and undisturbed plots (richness = 17, evenness  
224 = 0.82; Fig.1). However, underlying this similarity are differences in species composition ( $R^2 =$   
225 0.24,  $F = 7.06$ ,  $p = 0.001$ ; Fig. 2), with one third of plant species unique to either treatment type  
226 (Fig. 1, Table S1). Post-disturbance communities were segregated from undisturbed communities  
227 in multivariate space, with the exception of one disturbed/undisturbed pair (pair #12) (Fig. 2).

228       Community weighted means of SLA, leaf N %, and root N % differed between disturbed  
229 and undisturbed plots, with disturbed plots typically having trait values more consistent with the

230 ‘fast’ end of the leaf economics spectrum. Specifically, disturbed plots had significantly larger  
231 CWM for SLA, leaf %N, root %N, and there was a trend towards larger root SRL (Fig.3; Table  
232 2). There was no difference in CWM of maximum height, indicating a more rapid recovery to  
233 overall physiognomy relative to other functional characteristics of the communities.

234 Post-disturbance communities were functionally distinct from undisturbed communities  
235 after two years of recovery. Undisturbed communities showed higher FDiv values (FDiv =  $0.08 \pm$   
236  $0.02$ ,  $p = 0.0020$ ; Fig.4). FEve (FEve =  $0.07 \pm 0.02$ ,  $p = 0.0129$ ; Fig.4), FRic (difference =  $1.07 \pm$   
237  $1.16$ ,  $p = 0.376$ ; Fig.4), and Rao’s Q (difference =  $0.004 \pm 0.002$ ,  $p = 0.0733$ ; Fig.4) were not  
238 significantly different among the two treatments (Table 3).

## 239 Discussion

240 Although local communities recovered in species richness after only two years, there  
241 were a number of legacies of disturbance found in functional traits. There are persistent effects of  
242 disturbance on local diversity, suggesting successional communities are shaped by a combination  
243 of local dispersal and niche conditions. However, given competition can be reduced by  
244 disturbance (Wilson & Tilman, 1993), dispersal most likely limits recruitment in post-  
245 disturbance communities. At the same time, at the plot level we find there is great stability in  
246 species richness and evenness, suggesting the local structure of communities in this system is  
247 highly stable but the species who fill each “role” are variable. Thus, the functional differences  
248 we observe are not due to fundamental changes in the dominance structure (i.e. evenness) of  
249 successional communities, but rather due to species filtering.

## 250 Traits after disturbance

251 Consistent with *a priori* expectations, we show disturbance leads to functional shifts  
252 favouring species with higher SLA, leaf N %, and root N %, which are important for the rapid

253 acquisition of resources. SLA and leaf nitrogen content are widely viewed as indicative of a fast-  
254 growing, rapid nutrient acquisition strategy (Wright et al., 2004; Liu et al., 2017). Greater leaf  
255 nitrogen content works in concert with high SLA to increase energy exploitation through  
256 improved photosynthetic capacity, as high leaf N content is necessary for photosynthetic protein  
257 functioning (Wright et al., 2004). High root N is also indicative of quick resource acquisition as  
258 it is related to high root respiration, high foraging ability, and low root longevity (Craine et al.,  
259 2002; Reich, 2014; Roumet et al., 2016; McCormack et al., 2017). SRL, while higher in post-  
260 disturbance communities, was not significantly different between plot types. Typically SRL  
261 indicates potential resource uptake per root mass investment (Reich, 2014), and high SRL is  
262 associated with quick growth, high foraging capacity, and lower root longevity (Comas and  
263 Eissenstat, 2004; Roumet et al., 2016); as such, that disturbed communities did not show  
264 significantly higher SRL is contrary to our expectations. Overall, the higher levels of SLA, leaf  
265 N %, and root N % among the post-disturbance plots signal disturbed conditions permit the  
266 success of quick-growing plants that can quickly access resources. Thus, it is likely that the  
267 spatial variability of disturbances in this system are an important means to create functional  
268 variation across the landscape.

269         Height variation in grasslands is a significant predictor of species richness and  
270 community productivity (Brown and Cahill, 2019), yet we found that maximum height recovers  
271 quickly (within two years) after disturbance and is not significantly different among successional  
272 and undisturbed communities. This is surprising as greater height is thought to be indicative of  
273 greater competitive ability (Givnish, 1995; Cornelissen et al., 2003; Falster and Westoby, 2003).

#### 274 **Functional diversity after disturbance**

275 Disturbance causes a number of changes to functional diversity, with functional diversity  
276 typically increasing in post-disturbance communities (Purschke et al., 2013; Eler et al., 2018).  
277 However, we observed that disturbance either decreased or did not affect functional diversity  
278 measures. There was no difference in FRic values between the disturbed and undisturbed plots,  
279 indicating both treatments filled the same amount of functional niche space (Schleuter et al.,  
280 2010). Similarly, FEve did not differ between treatments, denoting that species abundances  
281 and/or the functional distances between species were equally even in disturbed and undisturbed  
282 plots. However, FDiv values were significantly higher in undisturbed communities. Lower FDiv  
283 values in the disturbed plots signify that the most abundant species in disturbed plots had more  
284 homogenous trait ranges. Thus, while disturbance does not affect the breadth or evenness of  
285 community functional traits, it does lower FDiv, promoting homogenization of functional  
286 diversity.

## 287 **Conclusions**

288 Overall, we found while traditional metrics of community composition such as species  
289 richness and evenness recovered within two years of disturbance, there were persistent impacts  
290 of disturbance on community-level traits and functional diversity. SLA, leaf N %, and root N %  
291 values were significantly larger in the disturbed condition, supporting the conclusion that species  
292 in post-disturbance areas are more likely to possess traits that support faster resource acquisition.  
293 The prevalence of individuals possessing these “fast” traits was reflected in distinct differences  
294 in community membership among undisturbed and post-disturbance communities. Disturbance  
295 also impacted functional diversity by promoting homogenization of community’s functional  
296 traits. In all, this work suggests functional trait shifts from small disturbances are a critical

297 mechanism for maintaining spatial heterogeneity in grassland systems, even as species richness  
298 and evenness recover.

299

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**References**

306 Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015) Fitting linear mixed-effects models  
307 using lme4. *Journal of Statistical Software*, 67, 1-48.

308 <https://doi.org/doi:10.18637/jss.v067.i01>

309 Brown, C., and Cahill, J.F. Jr. (2020) Replication Data for: Standing vegetation as a coarse biotic  
310 filter for seed bank dynamics: effects of gap creation on seed inputs and outputs in a  
311 native grassland. <https://doi.org/10.7939/DVN/IGVVFZ>, UAL Dataverse.

312 Brown, C., and Cahill, J.F. Jr. (2020) Standing vegetation as a coarse biotic filter for seed bank  
313 dynamics: Effects of gap creation on seed inputs and outputs in a native grassland.  
314 *Journal of Vegetation Science*, 31, 1006–1016. <https://doi.org/10.1111/jvs.12890>

315 Cadotte, M.W. (2007) Competition-colonization trade-offs and disturbance effects at multiple  
316 scales. *Ecology*, 88(4), 823-829. <https://doi.org/10.1890/06-1117>

317 Cadotte, M.W. (2017) Functional traits explain ecosystem function through opposing  
318 mechanisms. *Ecology Letters*, 20(8), 989-996. <https://doi.org/10.1111/ele.12796>

319 Cadotte, M.W., Carscadden, K. and Mirotchnick, N. (2011) Beyond species: functional diversity  
320 and the maintenance of ecological processes and services. *Journal of Applied Ecology*,  
321 48, 1079-1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>

322 Cahill, J. F. Jr. (2003) Lack of relationship between below-ground competition and allocation to  
323 roots in 10 grassland species. *Journal of Ecology*, 91, 532-540.

324 <https://doi.org/10.1046/j.1365-2745.2003.00792.x>

325 Cahill, J. F. Jr. (2020) Alberta grassland plant trait data. <https://doi.org/10.7939/r3-wszy-4x39>

- 326 Chapman, E.J., Childers, D.L., and Vallino, J.J. (2016) How the second law of thermodynamics  
327 has informed ecosystem ecology throughout its history. *BioScience*, 66(1), 27-39.  
328 <https://doi.org/10.1093/biosci/biv166>
- 329 Comas, L. H., and Eissenstat, D. M. (2004) Linking fine root traits to maximum potential growth  
330 rate among 11 mature temperate tree species. *Functional Ecology*, 18(3), 388–397.  
331 <https://doi.org/10.1111/j.0269-8463.2004.00835.x>
- 332 Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B.,  
333 ter Steege, H., et al. (2003) A handbook of protocols for standardised and easy  
334 measurement of plant functional traits worldwide. *Australia Journal of Botany*, 51(4),  
335 335–380. <https://doi.org/10.1071/BT02124>
- 336 Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. and Knops, J. (2002) Functional  
337 traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional*  
338 *Ecology*, 16(5), 563-574. <https://doi.org/10.1046/j.1365-2435.2002.00660.x>
- 339 Davidson, A.D., Detling, J.K., and Brown, J.H. (2012). Ecological roles and conservation  
340 challenges of social, burrowing, herbivorous mammals in the world’s grasslands.  
341 *Frontiers in Ecology and the Environment*. 10(9), 477-486. <https://doi:10.1890/110054>
- 342 Davidson, A.D., and Lightfoot, D.C. (2008). Burrowing rodents increase habitat heterogeneity in  
343 a desert grassland. *Journal of Arid Environments*. 72(7), 1133-1145.  
344 <https://doi.org/10.1016/j.jaridenv.2007.12.015>
- 345 Davis, M.A., Grime, J.P, and Thompson, K. (2000) Fluctuating resources in plant communities:  
346 a general theory of invasibility. *Journal of Ecology*, 88(3), 528-534.  
347 <https://doi.org/10.1046/j.1365-2745.2000.00473.x>

- 348 Desmet, P., and Brouilet, L. (2013) Database of Vascular Plants of Canada (VASCAN): a  
349 community contributed taxonomic checklist of all vascular plants of Canada, Saint Pierre  
350 and Miquelon, and Greenland. *PhytoKeys*, **25**, 55-67.  
351 <http://dx.doi.org/10.3897/phytokeys.25.3100>
- 352  
353 di Virgilio A., and Morales J.M. 2016. Towards evenly distributed grazing patterns: including  
354 social context in sheep management strategies. *PeerJ*, 4:e2152.  
355 <https://doi.org/10.7717/peerj.2152>
- 356 Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., and Robson, T.M. (2007)  
357 Incorporating plant functional diversity effects in ecosystem service assessments.  
358 *Proceedings of the National Academy of Science*, 104(52), 20684-20689.  
359 <https://doi.org/10.1073/pnas.0704716104>
- 360 Eler, K., Kermavnar, J., Marinsek, A., and Kutnar, L. (2018) Short-term changes in plant  
361 functional traits and understory functional diversity after logging of different intensities:  
362 a temperate fir-beech forest experiment. *Annals of Forest Research*, 61(2), 223-241.
- 363 Escobedo, V.M., Rios, S.R., Alcayaga-Olivares, Y., and Gianoli, E. (2021) Disturbance  
364 reinforces assembly processes differentially across spatial scales. *Annals of Botany*,  
365 127(2), 175-189. <http://doi.org/10.1093/aob/mcaa162>
- 366 Falster, D. S., and Westoby, M. (2003) Plant height and evolutionary games. *Trends in Ecology*  
367 *and Evolution*, 18(7), 337-343. [https://doi.org/10.1016/S0169-5347\(03\)00061-2](https://doi.org/10.1016/S0169-5347(03)00061-2)
- 368 Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., *et al.* (2004) Plant  
369 functional markers capture ecosystem properties during secondary succession. *Ecology*,  
370 85(9), 2630-2637. <https://doi.org/10.1890/03-0799>

- 371 Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., *et al.* (2007) Assessing the  
372 effects of land-use change on plant traits, communities, and ecosystem functioning in  
373 grasslands: a standardized methodology and lessons from an application to 11 European  
374 sites. *Annals of Botany*, 5(1), 967-985. <https://doi.org/10.1093/aob/mcl215>
- 375 Givnish, T.J., (1995) Plant Stems: Biomechanical Adaptation for Energy Capture and Influence  
376 on Species Distributions, In: Gartner, B. L. (Eds), *Plant Stems: Physiology and*  
377 *Functional Morphology*. Cambridge: Academic Press, pp. 3-49.  
378 <https://doi.org/10.1016/B978-0-12-276460-8.X5000-0>
- 379 Godfree, R., Lepschi, B., Reside, A., Bolger, T., Robertson, B., Marshall, D. and Carnegie, M.  
380 (2011) Multiscale topographic heterogeneity increases resilience and resistance of a  
381 dominant grassland species to extreme drought and climate change. *Global Change*  
382 *Biology*, 17: 943-958. <https://doi-org/10.1111/j.1365-2486.2010.02292.x>
- 383  
384 Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of  
385 the regeneration niche. *Biological Reviews*, 52, 107-145. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-185X.1977.tb01347.x)  
386 [185X.1977.tb01347.x](https://doi.org/10.1111/j.1469-185X.1977.tb01347.x)
- 387 Fried, G., Villers, A., and Porcher, E. (2018) Assessing non-intended effects of farming practices  
388 on field margin vegetation with a functional approach. *Agriculture, Ecosystems &*  
389 *Environment*, 261, 33-44, <https://doi.org/10.1016/j.agee.2018.03.021>
- 390 Huang, M., Liu, X., Cadotte, M.W. and Zhou, S. (2020) Functional and phylogenetic diversity  
391 explain different components of diversity effects on biomass production. *Oikos*, 129(8),  
392 1185-1195. <https://doi.org/10.1111/oik.07032>
- 393 Jentsch, A. and White, P. (2019) A theory of pulse dynamics and disturbance in ecology.  
394 *Ecology*, 100(7), e02734. <https://doi.org/10.1002/ecy.2734>

- 395 Kunstler, G., Falster, D., Coomes, D., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L.,  
396 Vanderwel, M., *et al.* (2016) Plant functional traits have globally consistent effects on  
397 competition. *Nature*, 529, 204–207. <https://doi.org/10.1038/nature16476>
- 398 Kuznetsova, A., Brockhoff, P.B., and Christensen, R.H.B. (2017) lmerTest package: Tests in  
399 linear mixed effects models. *Journal of Statistical Software*, 82(13), 1-26.  
400 <https://doi.org/10.18637/jss.v082.i13>
- 401 Laliberté, E., and Legendre, P. (2010) A distance-based framework for measuring functional  
402 diversity from multiple traits. *Ecology*, 91, 299-305.
- 403 Laliberté, E., Legendre, P., and Shipley, B. (2014) *FD: measuring functional diversity from*  
404 *multiple traits, and other tools for functional ecology. R package version 1.0-12.*  
405 Available at <https://cran.r-project.org/web/packages/FD/index.html> [Accessed January  
406 2021]
- 407 Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S.,  
408 Quétier, F., Thébault, A., and Bonis, A. (2008) Assessing functional diversity in the field  
409 - methodology matters! *Functional Ecology*, 22, 134-147. [https://doi: 10.1111/j.1365-](https://doi:10.1111/j.1365-2435.2007.01339.x)  
410 [2435.2007.01339.x](https://doi:10.1111/j.1365-2435.2007.01339.x)
- 411 Laughlin, D.C. (2014) The intrinsic dimensionality of plant traits and its relevance to community  
412 assembly. *Journal of Ecology*, 102(1), 186-193. <https://doi.org/10.1111/1365-2745.12187>
- 413 Liu, J., Zhang, X., Song, F., Zhou, S., Cadotte, M.W. and Bradshaw, C.J.A. (2015). Explaining  
414 maximum variation in productivity requires phylogenetic diversity and single functional  
415 traits. *Ecology*, 96, 176-183. <https://doi.org/10.1890/14-1034.1>

- 416 Liu, M., Wang, Z., Li, S. Lü, X., Wang, X., and Han, X. (2017) Changes in specific leaf area of  
417 dominant plants in temperate grasslands along a 2500-km transect in northern China.  
418 *Scientific Reports*, 7. <https://doi.org/10.1038/s41598-017-11133-z>
- 419 Louault, F., Pillar, V.D., Aufrère, J., Garnier, E., and Soussana, J.-F. (2005) Plant traits and  
420 functional types in response to reduced disturbance in a semi-natural grassland. *Journal*  
421 *of Vegetation Science*, 16(2), 151-160. [https://doi.org/10.1111/j.1654-](https://doi.org/10.1111/j.1654-1103.2005.tb02350.x)  
422 [1103.2005.tb02350.x](https://doi.org/10.1111/j.1654-1103.2005.tb02350.x)
- 423 Loughnan, D. and Gilbert, B. (2017) Trait-mediated community assembly: distinguishing the  
424 signatures of biotic and abiotic filters. *Oikos*, 126(8), 1112-  
425 1122. <https://doi.org/10.1111/oik.03945>
- 426 McCormack, M.L., Guo, D., Iversen, C.M., Chen, W., Eissenstat, D.M., Fernandez, C.W., Li, *et*  
427 *al.* (2017) Building a better foundation: improving root-trait measurements to understand  
428 and model plant and ecosystem processes. *New Phytologist*, 215(1), 27-37.  
429 <https://doi.org/10.1111/nph.14459>
- 430 Mouchet, M.A., Villéger, S., Mason, N.W.H. and Moullot, D. (2010) Functional diversity  
431 measures: an overview of their redundancy and their ability to discriminate community  
432 assembly rules. *Functional Ecology*, 24(4), 867-876. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2435.2010.01695.x)  
433 [2435.2010.01695.x](https://doi.org/10.1111/j.1365-2435.2010.01695.x)
- 434 Moullot, D, Graham, N.A., Villéger, S., Mason, N.W., and Bellwood, D.R. (2013) A functional  
435 approach reveals community responses to disturbances. *Trends Ecology and Evolution*,  
436 28(3), 167-77. <https://doi.org/10.1016/j.tree.2012.10.004>
- 437 Mursinoff, S. and Tack, A.J.M. (2017) Spatial variation in soil biota mediates plant adaptation to  
438 a foliar pathogen. *New Phytologist*, 214, 644-654. <https://doi-org/10.1111/nph.14402>

- 439 Myers, J.A., Chase, J. M., Crandall, R. M., and Jiménez, I. (2015) Disturbance alters beta-  
440 diversity but not the relative importance of community assembly mechanisms. *Journal of*  
441 *Ecology*, 103(5), 1291-1299. <https://doi-org/10.1111/1365-2745.12436>
- 442  
443 Oksanen, J. (2020) Vegan: ecological diversity. Available at [https://cran.r-](https://cran.r-project.org/web/packages/vegan/vignettes/diversity-vegan.pdf)  
444 [project.org/web/packages/vegan/vignettes/diversity-vegan.pdf](https://cran.r-project.org/web/packages/vegan/vignettes/diversity-vegan.pdf) [Accessed January 2021]
- 445 Oksanen, J., Blanchet F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. *et al.* (2017)  
446 *Vegan: community ecology package. Version 2.4-5*. Available at [https://cran.r-](https://cran.r-project.org/web/packages/vegan/index.html)  
447 [project.org/web/packages/vegan/index.html](https://cran.r-project.org/web/packages/vegan/index.html) [Accessed 21 January 2018]
- 448 Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E., and Fausch, K.D. (2004) Ecological  
449 and evolutionary consequences of biotic homogenization. *Trends in Ecology and*  
450 *Evolution*, 19(1), 18-24. <http://dx.doi.org/10.1016/j.tree.2003.09.010>
- 451 Pakeman, R.J. (2014) Functional trait metrics are sensitive to the completeness of the species'  
452 trait data? *Methods in Ecology and Evolution*, 5(1), 9-15. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.12136)  
453 [210X.12136](https://doi.org/10.1111/2041-210X.12136)
- 454 Pakeman, R.J., and Quested, H.M. (2007) Sampling plant functional traits: What proportion of  
455 the species need to be measured? *Applied Vegetation Science*, 10(1), 91-96.  
456 <https://doi.org/10.1111/j.1654-109X.2007.tb00507.x>
- 457 Parreira de Castro, D.M., Dolédec, S., and Callisto, M. Land cover disturbance homogenizes  
458 aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators*,  
459 84, 573-582. <http://dx.doi.org/10.1016/j.ecolind.2017.09.030>
- 460 Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-  
461 Harte, M. S., Cornwell, W. K., *et al.* (2013) New handbook for standardised

- 462 measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3),  
463 167-234. <https://doi.org/10.1071/BT12225>
- 464 Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalksi, S.G., Durka, W., Kühn, I.,  
465 Winter, M., and Prentice, H.C. (2013) Contrasting changes in taxonomic, phylogenetic,  
466 and functional diversity during a long-term succession: insights into assembly processes.  
467 *Journal of Ecology*, 101, 857-866. <https://doi.org/10.1111/1365-2745.12098>
- 468 R Core Team (2020) R: A language and environment for statistical computing. R Foundation for  
469 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 470 Reich, P.B. (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto.  
471 *Journal of Ecology*, 102(2), 275-301. [https://doi-](https://doi.org.login.ezproxy.library.ualberta.ca/10.1111/1365-2745.12211)  
472 [org.login.ezproxy.library.ualberta.ca/10.1111/1365-2745.12211](https://doi.org/login.ezproxy.library.ualberta.ca/10.1111/1365-2745.12211)
- 473 Roscher, C., Schumacher, J., Gubsch, M., Lipowsky, A., Weigelt, A., Buchmann, N., Schmid,  
474 B., and Schulze, E.D. (2012) Using plant functional traits to explain diversity–  
475 productivity relationships. *PLoS ONE*, 7(5).  
476 <https://doi.org/10.1371/journal.pone.0036760>
- 477 Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, 98, 156–162.  
478 <https://doi.org/10.1034/j.1600-0706.2002.980116.x>
- 479 Roumet, C., Birouste, M., Picon-Cochard, C., Ghestem, M., Osman, N., Vriignon-Brenas, S.,  
480 Cao, K.-f. and Stokes, A. (2016) Root structure–function relationships in 74 species:  
481 evidence of a root economics spectrum related to carbon economy. *New Phytologist*,  
482 210(3), 815-826. <https://doi.org/10.1111/nph.13828>

- 483 Schleuter, D., Daufresne, M., Massol, F. and Argillier, C. (2010) A user's guide to functional  
484 diversity indices. *Ecological Monographs*, 80(3), 469-484. [https://doi.org/10.1890/08-](https://doi.org/10.1890/08-2225.1)  
485 [2225.1](https://doi.org/10.1890/08-2225.1)
- 486 Suding, K.N. (2001). The effects of gap creation on competitive interactions: Separating changes  
487 in overall intensity from relative rankings. *Oikos*. 94(2), 219-227.  
488 <https://doi.org/10.1034/j.1600-0706.2001.940202.x>
- 489 Suding, K.N., and Goldberg, D. (2001) Do Disturbances alter competitive hierarchies?  
490 Mechanisms of change following gap creation. *Ecology*, 82(8), 2133-  
491 2149. [https://doi.org/10.1890/0012-9658\(2001\)082\[2133:DDACHM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2133:DDACHM]2.0.CO;2)
- 492 Tannas, K.E. (2004) Common Plants of the Western Rangelands – Volume 3: Forbs. Alberta  
493 Agriculture and Rural Development, Edmonton, AB. ISBN 0-7732-6162-1
- 494 Valladares, F., Wright, S.J., Lasso, E., Kitajima, K. and Pearcy, R.W. (2000) plastic phenotypic  
495 response to light of 16 congeneric shrubs from a panamanian rainforest. *Ecology*, 81:  
496 1925-1936. [https://doi.org/10.1890/0012-9658\(2000\)081\[1925:PPRTLO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1925:PPRTLO]2.0.CO;2)
- 497
- 498 Villéger, S., Mason, N.W.H., and Mouillot, D. (2008) New multidimensional functional diversity  
499 indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290-2301.  
500 <https://doi.org/10.1890/07-1206.1>
- 501 Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D.,  
502 Watson, R.N. and Ghani, A. (1999) Plant removals in perennial grassland: Vegetation  
503 dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological*  
504 *Monographs*, 69(4), 535-568. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9615(1999)069[0535:PRIPGV]2.0.CO;2)  
505 [9615\(1999\)069\[0535:PRIPGV\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0535:PRIPGV]2.0.CO;2)

506 Wilson, S.D, and Tilman, D. (1993) Plant competition and resource availability in response to  
507 disturbance and fertilization. *Ecology*, 74(2), 599-611. <https://doi.org/10.2307/1939319>  
508 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al.* (2004) The  
509 worldwide leaf economics spectrum. *Nature*, 428, 821–827. <https://doi->  
510 [org.login.ezproxy.library.ualberta.ca/10.1038/nature02403](https://doi.org/login.ezproxy.library.ualberta.ca/10.1038/nature02403)

**Table 1** (on next page)

Functional diversity metric definitions.

Functional diversity metric definitions	
Functional diversity (FD)	The functional space occupied by species, where axes are functional features (Rosenfeld, 2009; Vileger et al. 2008). The functional differences between a group of species (Tillman, 2001)
Functional richness (FRic)	The breadth of functional space filled by a communities (Villegger et al. 2008)
Functional evenness (FEve)	The evenness of the distribution of abundances and functional features of species (Villegger et al. 2008)
Functional divergence (FDiv)	The average distance of species abundances from the centre of functional space (Mouchet et al. 2010)
Rao's quadratic entropy (Q)	The average functional distance between two randomly selected species in a group (Mouchet et al. 2010).

**Table 2** (on next page)

Results of the linear mixed models (LMM) for traits.

Community weighted means for specific leaf area (SLA), height, shoot percent nitrogen (shoot N %), root percent nitrogen (root N %), and specific root length (SRL) were used as response variables in separate models. Plot pair (i.e., disturbed and undisturbed plot location) was a random effect and plot type (disturbed or undisturbed) was used as the fixed effect. SE stands for standard error and df denotes degrees of freedom. Bold type indicates significant results.

1

	Disturbed plot mean $\pm$ SE	Undisturbed plot mean $\pm$ SE	df	<i>p</i> -value
Maximum height (cm)	35.78 ( $\pm$ 0.03)	36.30 ( $\pm$ 0.02)	11	0.66
Specific leaf area (cm <sup>2</sup> /g)	139.96 ( $\pm$ 3.27)	119.34 ( $\pm$ 2.69)	11	<b>2.64 x 10<sup>-5</sup></b>
Specific root length (cm/g)	5612.82 ( $\pm$ 492.72)	4550.30 ( $\pm$ 398.71)	11	0.09
Leaf nitrogen (%)	1.92 ( $\pm$ 0.06)	1.74 ( $\pm$ 0.03)	11	<b>0.01</b>
Root nitrogen (%)	1.05 ( $\pm$ 0.03)	0.95 ( $\pm$ 0.02)	11	<b>0.02</b>

2

3

**Table 3**(on next page)

Results of the linear mixed models (LMM) for functional diversity.

Functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), and Rao's Q were used as response variables in separate models. Plot pair (i.e., disturbed and undisturbed plot location) was a random effect and plot type (disturbed or undisturbed) was a fixed effect. SE stands for standard error and df denotes degrees of freedom. Bold type indicates significant results.

1

	Disturbed plot mean $\pm$ SE	Undisturbed plot mean $\pm$ SE	df	<i>p</i> -value
FRic (log transformed)	-39.96 ( $\pm$ 0.99)	-38.75 ( $\pm$ 0.85)	11	0.345
FEve	0.66 ( $\pm$ 0.02)	0.69 ( $\pm$ 0.02)	11	0.218
FDiv	0.73 ( $\pm$ 0.02)	0.81 ( $\pm$ 0.02)	11	<b>0.003</b>
Rao's Q	0.02 ( $\pm$ 0.001)	0.02 ( $\pm$ 0.002)	11	0.078

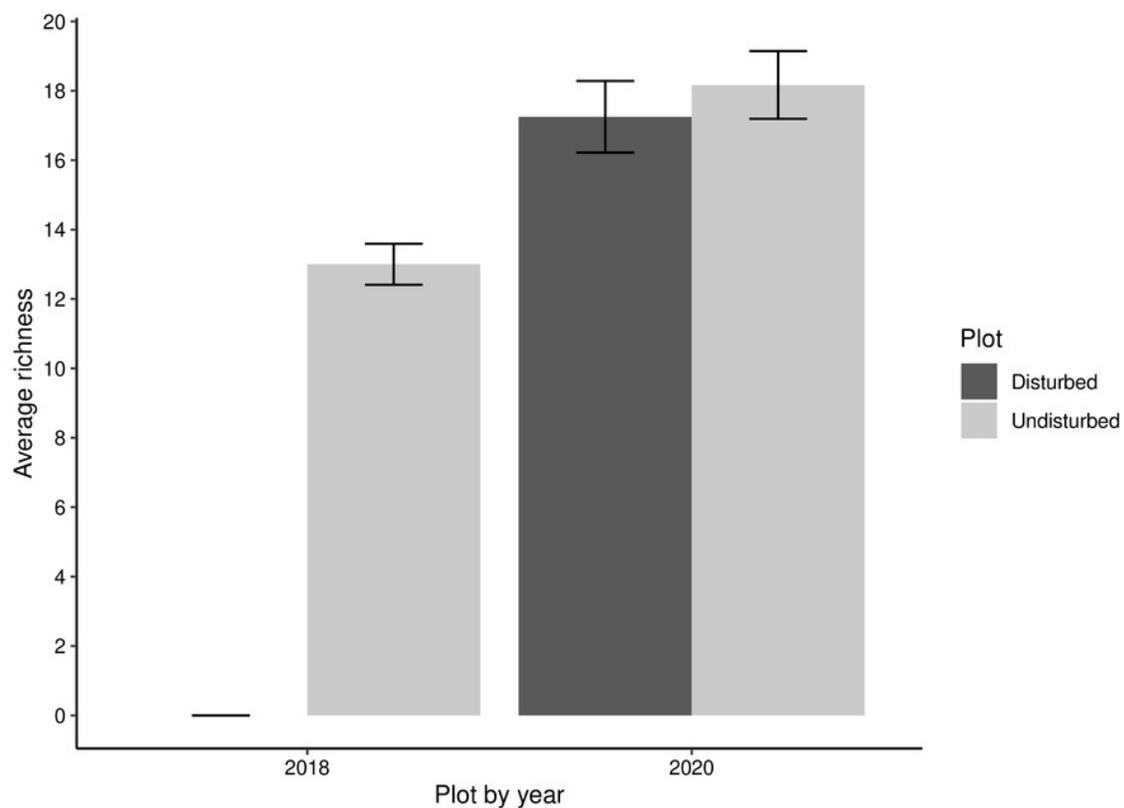
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## Figure 1

Average species richness of disturbed and undisturbed plots in 2018 and 2020.

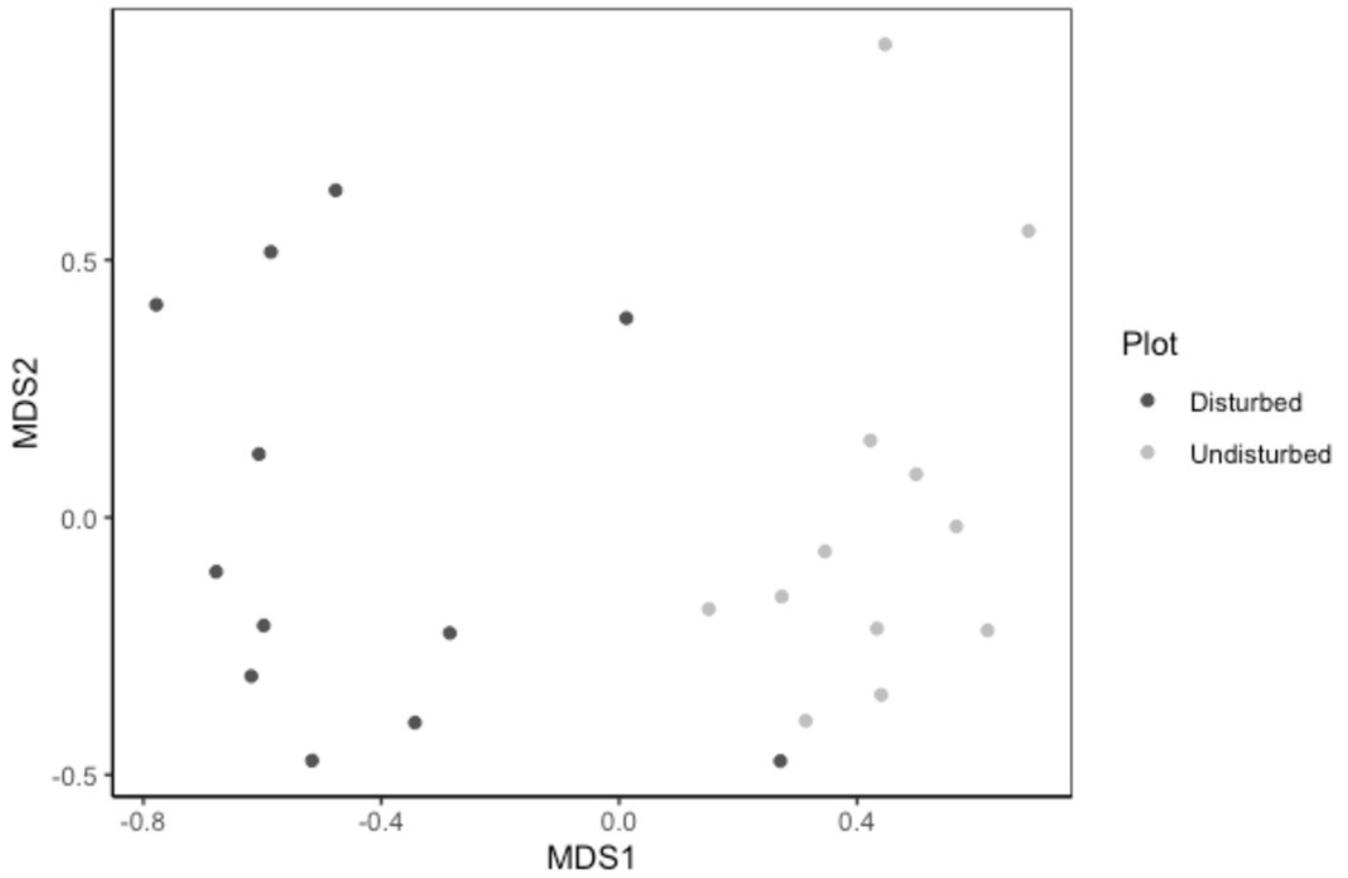
In disturbed plots, all biomass was trimmed to the soil surface and a glyphosate herbicide (Roundup©) applied to the remaining stems to ensure death of the resident vegetation from 2016 - 2018. Plots were allowed to regenerate from 2018 - 2020. Undisturbed plots had no standing vegetation removed. Species richness was recorded in the summer of 2020. Error bars represent standard error.



## Figure 2

Metric multidimensional scaling (MDS) of disturbed and undisturbed community composition.

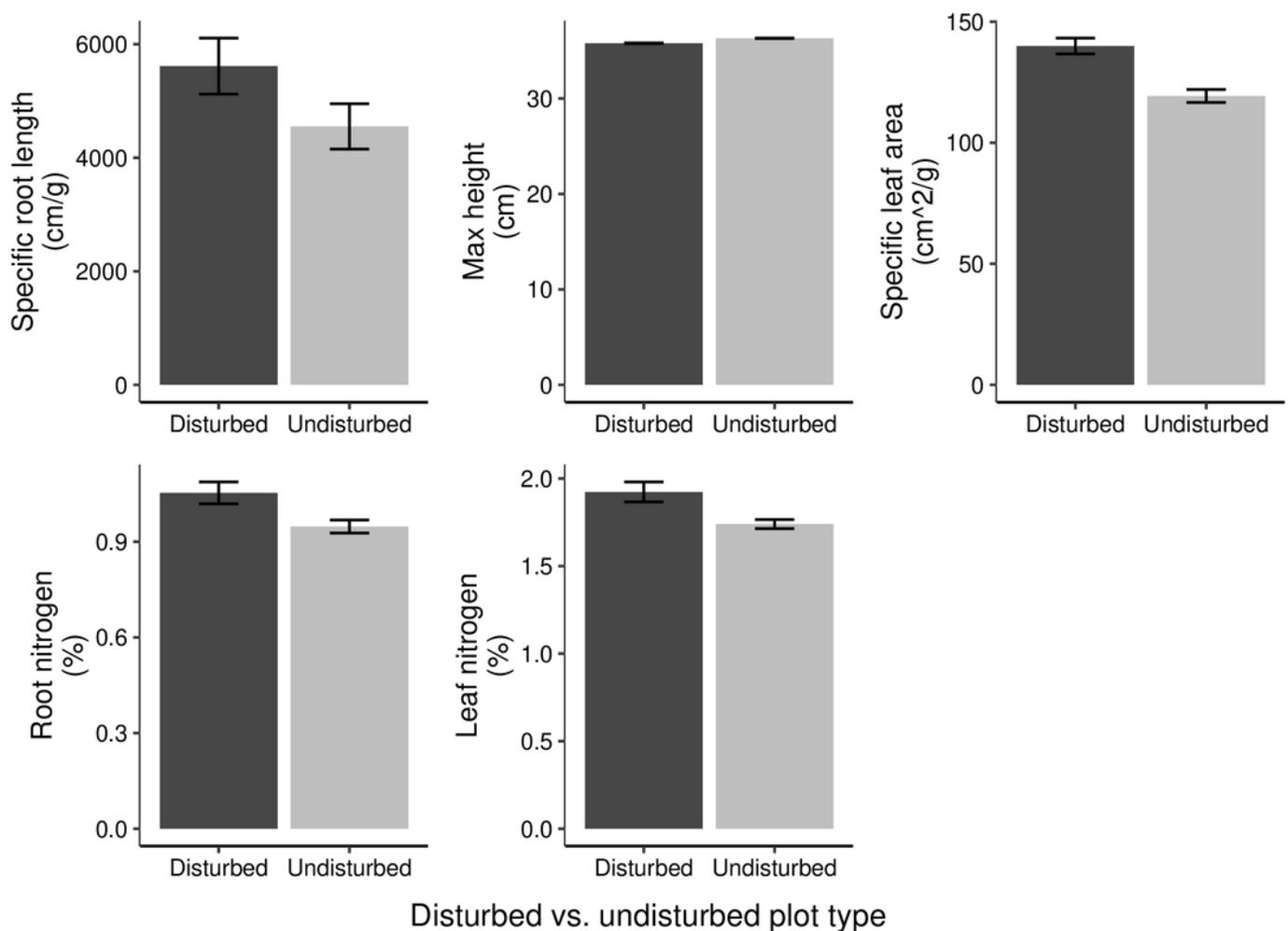
Data points denote 2020 plant community composition in disturbed and undisturbed plots. In disturbed plots, all biomass was trimmed to the soil surface and a glyphosate herbicide (Roundup©) applied to the remaining stems to ensure death of the resident vegetation from 2016 - 2018. Plots were allowed to regenerate from 2018 - 2020. Undisturbed plots had no standing vegetation removed. Community composition was assessed in the summer of 2020.



## Figure 3

Mean trait values in 2020 disturbed and undisturbed communities.

Comparisons of specific root length, maximum height, specific leaf area, root nitrogen, and leaf nitrogen between disturbed and undisturbed communities. Error bars represent standard error. Associated statistics are found in Table 2.



## Figure 4

Estimates of functional diversity values in 2020 disturbed and undisturbed communities.

Comparisons of functional richness, functional evenness, functional divergence, and Rao's quadratic entropy between disturbed and undisturbed communities. Functional richness was log-transformed to meet the assumption of normality and was multiplied by negative one. Error bars represent standard error. Associated statistics are found in Table 3.

