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.

1   **Trait profiles and functional diversity following disturbance in a mixed grassland**

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23   **Abstract**

24   **Background.** Localized disturbances within established grasslands alter a suite of biological and

25   chemical properties, leading to shifts in species composition. For example, relatively rare

26   species in established communities may become dominant in successional communities if they

27   exhibit traits that are suited to disturbance conditions. Although the idea that plant species

28   exhibit different trait 'strategies' is well established, it is unclear how ecological selection for

29   specific traits may change as a function of disturbance. Further, there is little data available

30   testing whether disturbances select for single trait-characters within communities

31   (homogenization), or allow multiple trait-types to persist (diversification). We investigated how

32   (a) traits and (b) functional diversity of post-disturbance communities compared to those in

33   adjacent undisturbed grasslands, and (c) if changes in functional diversity resulted in the

34   homogenization or diversification of functional traits within local communities.

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36   measured plant community composition of twelve paired plots in a native grassland within the

37   central parkland of Alberta, Canada. Each pair consisted of one undisturbed plot and one which

38   had all plants terminated two years prior. We used species abundances in conjunction with a

39   local trait database to calculate community weighted means for maximum height, specific leaf

40   area, specific root length, leaf nitrogen percent, and root nitrogen percent. To test the impacts of

41   disturbance on community functional traits, we calculated functional diversity measures and

42   compared them between disturbed and undisturbed local communities.

43   **Results.** Within two years, species richness and evenness in disturbed communities had

44   recovered and was equivalent to undisturbed communities. However, disturbed and undisturbed

45   communities had distinct community compositions that differed in functional diversity.

46   Functional divergence was significantly lower in the disturbed plots. Further, disturbance was

47 also linked to increases in community-weighted mean trait values associated with resource-

48 acquisitive traits, such as specific leaf area, and leaf and root nitrogen.

49 **Discussion.** Disturbance had lasting effects on the functional traits and diversity of communities,

50 despite traditional measures of biodiversity such as richness and evenness recovering within two

51 years. There was a discrete shift in the trait space of post-disturbance communities compared to

52 undisturbed communities such that post-disturbance communities were dominated by traits that

53 enhance resource uptake and growth rates. Overall, these results show that disturbance

54 fundamentally changes the functional character of communities, even if they superficially appear

55 recovered.

56 **Introduction**

57   Habitat heterogeneity in grasslands is maintained in part by small-scale mortality

58 inducing disturbances, such fossorial mammal activity (Davidson and Lightfoot, 2008;

59 Davidson, Detling, and Brown, 2012), drought (Godfree et al., 2011), overgrazing (di Virgilio

60 and Morales, 2016), pathogens (Mursinoff and Tack, 2017), and even herbicide drift (Fried,

61 Villers, and Porcher, 2018). In extreme instances, disturbance can result in the total mortality of

62 mature vegetation (e.g. Cahill 2003). Though each of these disturbances have unique

63 characteristics, they all result in the localized death of established vegetation, creating vegetation

64 "gaps" (Suding, 2001). Gaps result in changes to competitive hierarchies and abiotic soil

65 conditions and competitive hierarchies (Suding and Goldberg, 2001; Suding, 2001), leading to

66 changes in species diversity and community composition.

67   Examining traits can shed light on the specific impacts of disturbance on plant

68 communities. Traits are measurable individual morphological, physiological, or phenological

69 characteristics that provide insight into life history strategies and influence plant ranges and

70   species interactions (Viole et al., 2007; Cadotte, Carscadden, & Mirotchnick, 2011). "Functional

71   traits" specifically impact growth, reproduction and survival (Viole et al., 2007). At small scales,

72   trait differences can influence local diversity patterns by determining competitive outcomes (Liu

73   et al., 2015). Traits can also provide insight as to species resource acquisition strategies by

74   indicating species location on the fast-slow plant economics spectrum, where "fast" strategies

75   prioritize resource acquisition and growth while "slow" strategies favour stress tolerance and

76   longevity (Reich et al., 2014). Measuring functional traits after a disturbance (such as those

77   which create gaps) can reveal how a community has changed in functional strategies and can be

78   used to examine the resulting community's functional diversity. Cadotte (2007) describes gap

79   species as prioritizing rapid resource uptake, whereas non-gap species take a slower, tolerance-

80   based approach. For example, specific leaf area (SLA) values are likely to be larger in post-

81   disturbance successional communities as high SLA is correlated to fast growth and low

82   competitive ability (Kunstler et al., 2016). Additionally, Loughnan and Gilbert (2017) found that

83   SLA may be involved with shifts in competitive ability as greater SLA is associated with more

84   sunlight acquisition and thus increased energy acquisition. Thus, changes in communities post-

85   disturbance are likely due to differences in the trait profiles of successional species.

86   It is important to note that these changes in species composition and community-level

87   traits changes may not be reflected in the total number of species in the community (i.e. species

88   richness). Disturbance may change the nature of community assembly in successional

89   communities by altering the process by which species from the regional pool are able to colonize

90   local communities (HilleRisLambers et al., 2012, Escobedo et al., 2021). Disturbance changes

91   the environmental filters which constrain species dispersal and recruitment to communities

92   (Myers et al., 2015; Brown & Cahill, 2020); in this case we would expect the resulting

93   community to contain species that possess functional traits better suited to the new set of

94   environmental filters, changing the community-level traits and functional diversity of the

95   disturbed community. Thus, if taxonomic measures like species richness or evenness remain

96   unchanged after disturbance, they may mask functional differences and result in a mirage of

97   stability when, in fact, the community has undergone great change. This emphasizes the

98   importance of studying functional traits and quantifying functional diversity to understand

99   community drivers.

100   Functional diversity is a subset of biological diversity which measures the traits present

101   in an ecosystem (Tillman, 2001). It is distinct from taxonomic diversity as it reflects the breadth

102   of the functional space occupied by species in a community (Rosenfeld, 2002; Villéger et al.,

103   2008), whereas taxonomic diversity indicates the number of species in a given community

104   separate from any measure of community function (Laliberté and Legendre, 2010). Some

105   functional diversity measures are not greatly influenced by taxonomic measures such as species

106   richness (Laliberté and Legendre, 2010) and can offer a more nuanced approach to understanding

107   community characteristics. Disturbance affects functional diversity (Parreira de Castro, Dolédec,

108   & Callisto, 2018) and can potentially result in functional homogenization, or selection for similar

109   trait-characters in species colonizing in disturbed communities (Olden et al., 2004). However,

110   resource fluxes associated with disturbance (Davis, Grime, & Thompson, 2000) may lead to trait

111   diversification within colonizing species to allow for more efficient utilization of the increased

112   resources available in disturbed communities (Chapman, Childers, & Vallino, 2016; Jentsch &

113   White, 2019). As functional diversity is associated with the provisioning of ecosystem services

114   (Díaz et al., 2007; Roscher et al., 2012; Pakeman, 2014), the homogenizing or diversifying

115   effects of disturbance on functional diversity must be better understood.

116   If species in post-disturbance areas are more likely to possess traits which support faster

117   resource acquisition (e.g. Cadotte, 2007; Kunstler et al., 2016), then shifts in trait distributions

118   after disturbance may alter functional diversity by changing the success of different trait suites to

119   favor "fast" traits prioritizing resource acquisition.at the local scale. However, it is unclear which

120   traits differ between plants in disturbed and undisturbed areas, and how these different strategies

121   are reflected in functional diversity. To resolve these outstanding questions, we ask:

122   1. How do functional traits of a grassland community change after disturbance?

123   2. How does functional diversity change after disturbance?

124   3. If functional distributions do change, will it result in the homogenization or

125   diversification of community-level traits?

126   If disturbance causes shifts in habitat filters, then we expect to observe shifts in the functional

127   trait space of the resulting community. If disturbance constrains the competitive strategies that

128   succeed in successional communities (for instance, favouring plants with resource-acquisitive

129   traits), we would expect changes in trait values (i.e. community-weighted means) and potentially

130   the homogenization of community-level traits. Alternatively, if species turnover after disturbance

131   drives shifts in community traits, we then expect to observe both taxonomic and functional trait

132   shifts, which could in turn diversify community-level traits.

133   **Methods**

134   **Study site**

135   Our study site was located in the Roy Berg Kinsella Research Ranch in Kinsella, AB,

136   Canada (53°5′ N, 111°33′ W). Data collection took place in a native grassland dominated by

137   *Hesperostipa curtiseta* (Hitchc.) Barkworth, *Festuca hallii* (Vasey) Piper and *Poa pratensis* (L.)

138   (Brown and Cahill, 2019). The site is part of the Aspen Parkland ecoregion, a savanna-type

139   habitat characterized by a mosaic of mixed-grass prairie and trembling aspen (*Populus*

140   *tremuloides* Michx.). The field site is periodically grazed by cattle with a heavy grazing event in

141   October 2019 and a light grazing event occurring in May 2020.

142   **Study design**

143   We sampled twenty-four plots (50 cm x 50 cm), arranged in twelve pairs, which were

144   originally established in 2016 (Brown & Cahill, 2020). Each pair contained an undisturbed plot,

145   where no standing vegetation was terminated, and a disturbed plot, where all standing vegetation

146   was terminated. Disturbed plots were created in May 2016, by having all biomass trimmed to the

147   soil surface and a glyphosate herbicide (Roundup©) applied to the remaining stems to ensure

148   death of the resident vegetation. This treatment was maintained through August 2018 with any

149   regenerating plant materials trimmed and painted with herbicide during the growing seasons.

150   This treatment does not represent any specific natural event, and instead is testing the extreme

151   event of complete removal of the resident vegetation. Additionally, this treatment does not

152   remove the seed bank present at the site (Brown and Cahill, 2020) and thus does not affect

153   community regeneration from seed (see Grubb, 1977).

154   Plant community composition was measured in July 2018 by visually estimating percent

155   cover of all species present within each plot. Two years post-treatment, in July 2020, plot pairs

156   were revisited, by which time vegetation had regenerated in the disturbed plots. Community

157   composition was measured using percent cover estimation of each species. Sedges were unable

158   to be identified to species and were recorded as "*Carex* spp.".

159   *Plant traits*

160   Disturbance can alter abiotic conditions (Suding and Goldberg 2001); however, here we

161   focus on its impacts on vegetative traits. Plant trait data came from a database developed

162 principally at this field site (Cahill, 2020), thus representing local trait data. Details of trait

163 measures are found in Cahill (2020), but largely follow the methods outlined in Cornelissen et al.

164 (2003) and Pérez-Harguindeguy et al. (2013). Here we focused on five traits which encompass

165 aspects of plant structure and above- and belowground resource acquisition: maximum height,

166 specific leaf area (SLA), specific root length (SRL), leaf nitrogen percentage (N %), and root N

167 %. See Cahill (2020) for trait definitions. These traits were chosen to provide a holistic scope of

168 above and below ground functional strategies with reference to trait groups described by Cadotte

169 (2017). Site-specific trait data was available in the database for all species except for *Cirsium*

170 *vulgare* (Savi) Tenore, *Collomia linearis* Nuttall, *Gentianella amarella* (Linnaeus) Börner,

171 *Sonchus arvensis* Linnaeus, and two unidentified forbs. Trait data was obtained for species that

172 represent at least 93% of total composition, which exceeds the 80% threshold standard for trait

173 studies (Pakeman & Quested 2007).

174 *Trait profiles and functional diversity*

175   To characterize communities by their traits, we first calculated community weighted

176 means (CWMs) for five traits: SLA, maximum height, leaf N %, root N %, and SRL. CWMs are

177 the average value of a given trait in a community weighted by the abundance of all species

178 possessing said trait (Lavorel et al., 2008), and are useful for understanding community

179 properties and dynamics, as well as quantifying community change (Garnier et al., 2004, 2007;

180 Louault et al., 2005). CWMs were calculated at the species-level. While disturbance is likely to

181 result in intraspecific variability in functional traits, here we focus on species-level values as a

182 first-level test to detect if disturbance does result in persistent change to community functional

183 traits. We encourage future studies to collect trait data from individual plants across species to

184 quantify how intraspecific trait variation changes with disturbance regimes. Outlier trait values

185   (values more than three standard deviations away from the species' mean) were removed prior to

186   calculating CWM. We then quantified the functional diversity of communities using functional

187   richness (FRic), functional evenness (FEve), functional divergence (FDiv), and Rao's quadratic

188   entropy (Q) (Villéger, Mason, & Mouillot, 2008; Mouchet et al., 2010; Table 1). These metrics

189   allow us to characterize the volume (via FRic), evenness (via FEve), and spread (via FDiv and

190   Q) of the communities' functional traits in multidimensional space. By using these multivariate

191   descriptors of communities, we are able to compare communities' character before and after

192   disturbance, as well as to determine if community traits become more or less homogenous as a

193   result of disturbance. We used package vegan (Oksanen et al., 2017) in program R (v 4.0.0; R

194   Core Team, 2020) to compute species richness and evenness, using methods from Oksanen

195   (2020). We used package FD (Laliberté, Legendre, & Shipley, 2014) to compute CWMs. We

196   also computed FRic, FDiv, FEve, and Rao's Q using package FD.

197   **Statistical analysis**

198   To determine if community traits differed between control and disturbed treatments after

199   recovery, we used five separate linear mixed models (LMMs). The CWM's for SLA, height, leaf

200   N %, root N %, and SRL were used as response variables, plot type (disturbed or undisturbed)

201   was a fixed effect and plot pair (i.e., disturbed and undisturbed plot location) was a random

202   effect. "Pair" was included as a random effect in models to account for spatial autocorrelation in

203   community data as disturbed and undisturbed plots were adjacent. All LMMs were run using an

204   underlying normal distribution with the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova,

205   Brockhoff, & Christensen, 2017) packages. We also used four separate LMMs to quantify how

206   functional diversity measures, namely FRic, FDiv, FEve, and Rao's Q, differed between

207   disturbance types. FRic, FDiv, FEve, and Roa's Q were used as response variables, plot pair was

208   included as a random effect and plot type (disturbed or undisturbed) was a fixed effect in all

209   models. Functional richness was log-transformed to fit assumptions of normality. To determine

210   whether disturbed and undisturbed communities had different community compositions, we

211   conducted a permutational multivariate analysis of variance (PERMANOVA), with plot as a

212   strata, using packages vegan and RVAideMemoire (Hervé, 2021).

213   **Results**

214   Between 2018 and 2020, total species richness in undisturbed plots decreased from 55 to

215   52 while average species richness in disturbed plots increased from 0 in 2018 to 53 in 2020

216   (Table S1). Six species were found only in disturbed communities (*Androsace septentrionalis*,

217   *Cirsium arvense*, *Mulgedium pulchellum*, *Thalictrum venulosum*, an unidentified *Brassicaceae*

218   plant, and an unidentified herbaceous dicot; Table S1). *Androsace septentrionalis*, *Cirsium*

219   *arvense*, and *Mulgedium pulchellum* are commonly found in disturbed areas (Tannas, 2004). In

220   particular, *Cirsium arvense* is associated high rates of reproduction and dispersal. 15 species

221   were found only in undisturbed communities (Table S1). These species, except *Fallopia*

222   *convolvulus*, are all native to Alberta (Desmet and Brouilet, 2013).

223   Despite persistent effects on local diversity, and although disturbed plots began with zero

224   species present in 2018, within two years there was no significant difference between plot-level

225   (alpha) richness and evenness between disturbed and undisturbed plots (richness = 17, evenness

226   = 0.82; Fig.1). However, underlying this similarity are differences in species composition (R^2 =

227   0.24, F = 7.06, p = 0.001; Fig. 2), with one third of plant species unique to either treatment type

228   (Fig. 1, Table S1). Post-disturbance communities were segregated from undisturbed communities

229   in multivariate space, with the exception of one disturbed/undisturbed pair (pair #12) (Fig. 2).

230   Community weighted means of SLA, leaf N %, and root N % differed between disturbed

231   and undisturbed plots, with disturbed plots typically having trait values more consistent with the

232   'fast' end of the leaf economics spectrum. Specifically, disturbed plots had significantly larger

233   CWM for SLA, leaf %N, root %N, and there was a trend towards larger root SRL (Fig.3; Table

234   2). There was no difference in CWM of maximum height, indicating a more rapid recovery to

235   overall physiognomy relative to other functional characteristics of the communities.

236   Post-disturbance communities were functionally distinct from undisturbed communities

237   after two years of recovery. Undisturbed communities showed higher FDiv values (FDiv = 0.08±

238   0.02, p = 0.0020; Fig.4). FEve (FEve = 0.07± 0.02, p = 0.0129; Fig.4), FRic (difference = 1.07±

239   1.16, p = 0.376; Fig.4), and Rao's Q (difference = 0.004± 0.002, p = 0.0733; Fig.4) were not

240   significantly different among the two treatments (Table 3).

241   **Discussion**

242   Although local communities recovered in species richness after only two years, there

243   were a number of legacies of disturbance found in functional traits. There are persistent effects of

244   disturbance on local diversity, suggesting successional communities are shaped by a combination

245   of local dispersal and niche conditions. However, given competition can be reduced by

246   disturbance (Wilson & Tilman, 1993), dispersal most likely limits recruitment in post-

247   disturbance communities. At the same time, at the plot level we find there is great stability in

248   species richness and evenness, suggesting the local structure of communities in this system is

249   highly stable but the species who fill each "role" are variable. Thus, the functional differences

250   we observe are not due to fundamental changes in the dominance structure (i.e. evenness) of

251   successional communities, but rather due to species filtering.

252   **Traits after disturbance**

253   Consistent with *a priori* expectations, we show disturbance leads to functional shifts

254   favouring species with higher SLA, leaf N %, and root N %, which are important for the rapid

255   acquisition of resources. SLA and leaf nitrogen content are widely viewed as indicative of a fast-

256   growing, rapid nutrient acquisition strategy (Wright et al., 2004; Liu et al., 2017). Greater leaf

257   nitrogen content works in concert with high SLA to increase energy exploitation through

258   improved photosynthetic capacity, as high leaf N content is necessary for photosynthetic protein

259   functioning (Wright et al., 2004). High root N is also indicative of quick resource acquisition as

260   it is related to high root respiration, high foraging ability, and low root longevity (Craine et al.,

261   2002; Reich, 2014; Roumet et al., 2016; McCormack et al., 2017). SRL, while higher in post-

262   disturbance communities, was not significantly different between plot types. Typically SRL

263   indicates potential resource uptake per root mass investment (Reich, 2014), and high SRL is

264   associated with quick growth, high foraging capacity, and lower root longevity (Comas and

265   Eissenstat, 2004; Roumet et al., 2016); as such, that disturbed communities did not show

266   significantly higher SRL is contrary to our expectations. Overall, the higher levels of SLA, leaf

267   N %, and root N % among the disturbed plots signal post-disturbance conditions permit the

268   success of quick-growing plants that can quickly access resources. Thus, it is likely that the

269   spatial variability of disturbances in this system are an important means to create functional

270   variation across the landscape.

271   Height variation in grasslands is a significant predictor of species richness and

272   community productivity (Brown and Cahill, 2019), yet we found that maximum height recovers

273   quickly (within two years) after disturbance and is not significantly different among successional

274   and undisturbed communities. This is surprising as greater height is thought to be indicative of

275   greater competitive ability (Givnish, 1995; Cornelissen et al., 2003; Falster and Westoby, 2003).

276 **Functional diversity after disturbance**

277   Disturbance causes a number of changes to functional diversity, with functional diversity

278 typically increasing in post-disturbance communities (Purschke et al., 2013; Eler et al., 2018).

279 However, we observed that disturbance either decreased or did not affect functional diversity

280 measures. There was no difference in FRic values between the disturbed and undisturbed plots,

281 indicating both treatments filled the same amount of functional niche space (Schleuter et al.,

282 2010). Similarly, FEve did not differ between treatments, denoting that species abundances

283 and/or the functional distances between species were equally even in disturbed and undisturbed

284 plots. However, FDiv values were significantly higher in undisturbed communities. Lower FDiv

285 values in the disturbed plots signify that the most abundant species in disturbed plots had more

286 homogenous trait ranges. Thus, while disturbance does not affect the breadth or evenness of

287 community functional traits, it does lower FDiv, promoting homogenization of functional

288 diversity.

289 **Conclusions**

290   Overall, we found while traditional metrics of community composition such as species

291 richness and evenness recovered within two years of disturbance, there were persistent impacts

292 of disturbance on community-level traits and functional diversity. SLA, leaf N %, and root N %

293 values were significantly larger in the disturbed condition, supporting the conclusion that species

294 in post-disturbance areas are more likely to possess traits that support faster resource acquisition.

295 The prevalence of individuals possessing these "fast" traits was reflected in distinct differences

296 in community membership among undisturbed and post-disturbance communities. Disturbance

297 also impacted functional diversity by promoting homogenization of community's functional

298 traits. In all, this work suggests functional trait shifts from small disturbances are a critical

299   mechanism for maintaining spatial heterogeneity in grassland systems, even as species richness

300   and evenness recover.

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Functional diversity metric definitions.

Functional diversity metric definitions	
Functional diversity (FD)	The functional space occupied by species, where axes are functional features (Rosenfeld, 2009; Villeger 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 (Villeger et al. 2008)
Functional evenness (FEve)	The evenness of the distribution of abundances and functional features of species (Villeger 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).

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.

	Disturbed plot mean ± SE	Undisturbed plot mean ± SE	df	p-value
Maximum height (cm)	35.78 (± 1.05)	36.30 (± 1.16)	11	0.66
Specific leaf area (cm^2/g)	139.96 (± 2.99)	119.34 (± 2.99)	11	**2.64 x 10^{-5}**
Specific root length (cm/g)	5612.82 (± 448.19)	4550.30 (± 570.50)	11	0.09
Leaf nitrogen (%)	1.92 (± 0.04)	1.74 (± 0.06)	11	**0.01**
Root nitrogen (%)	1.05 (± 0.03)	0.95 (± 0.04)	11	**0.02**

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.

	Disturbed plot mean ± SE	Undisturbed plot mean ± SE	df	*p*-value
FRic (log transformed)	-39.96 (± 0.92)	-38.75 (± 1.22)	11	0.345
FEve	0.66 (± 0.02)	0.69 (± 0.02)	11	0.218
FDiv	0.73 (± 0.02)	0.81 (± 0.02)	11	**0.003**
Rao's Q	0.02 (± 0.001)	0.02 (± 0.002)	11	0.078

Figure 1

Average species evenness and 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 evenness and richness was recorded in the summer of 2020. Error bars represent standard error.
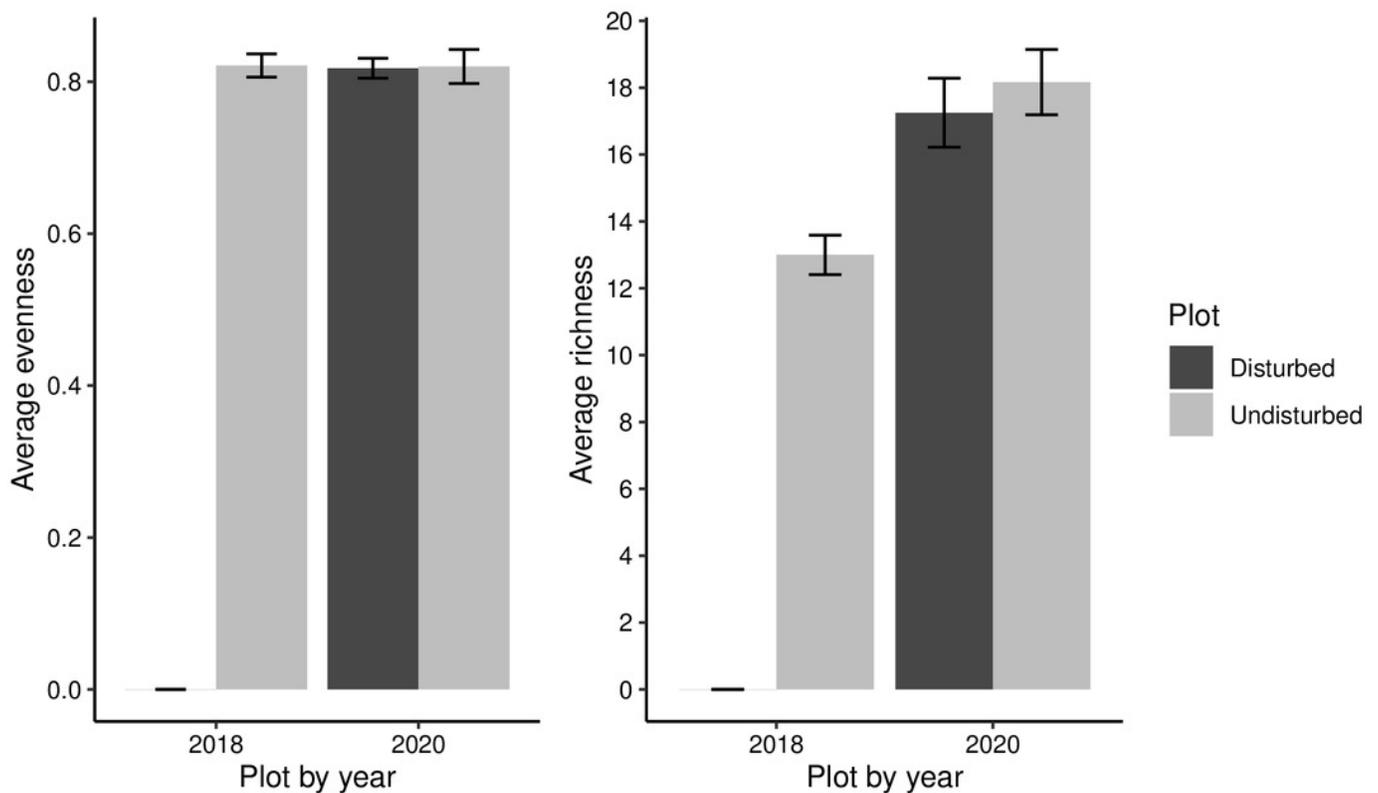
Figure 2

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.
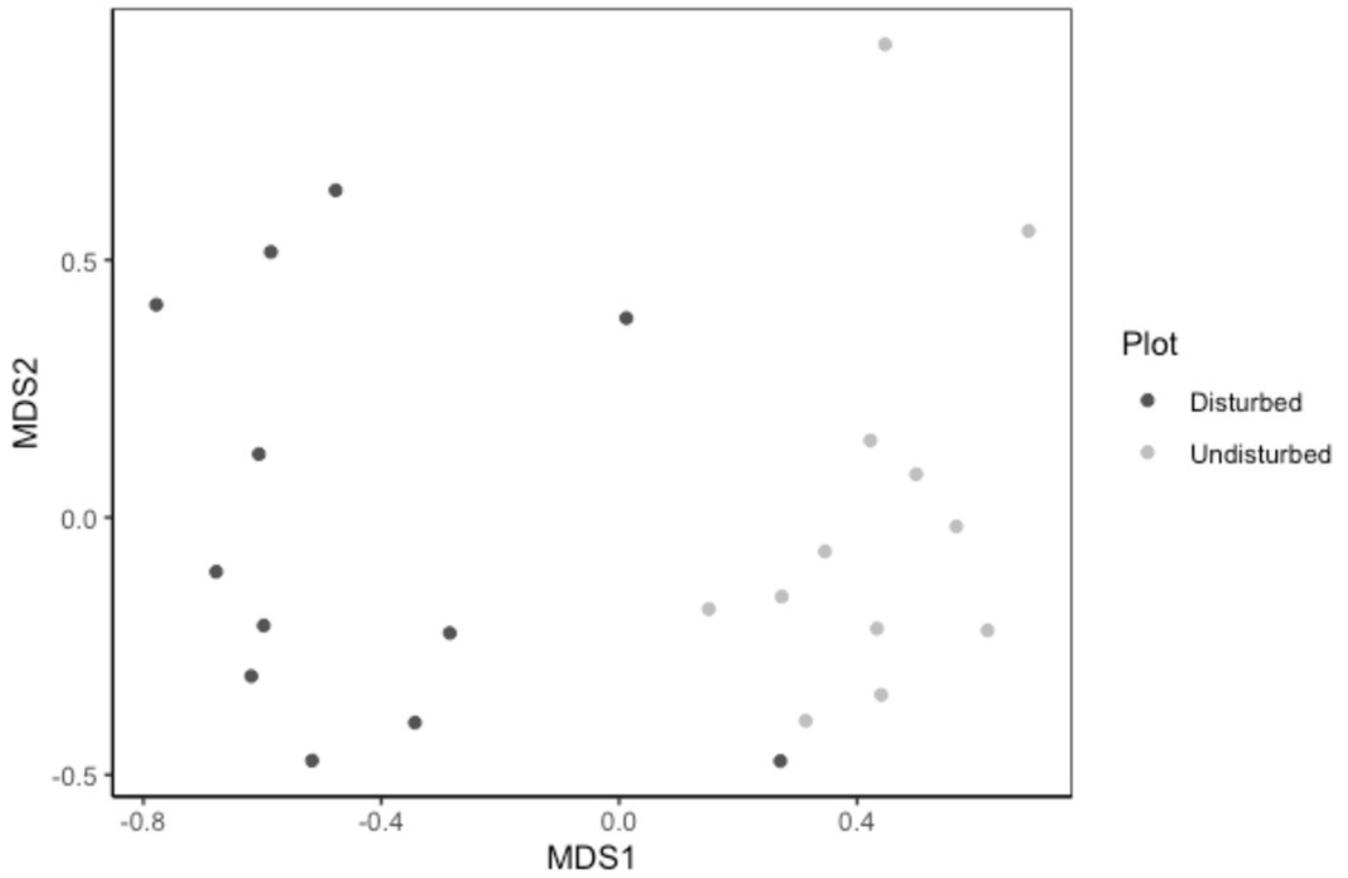
Figure 3

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.
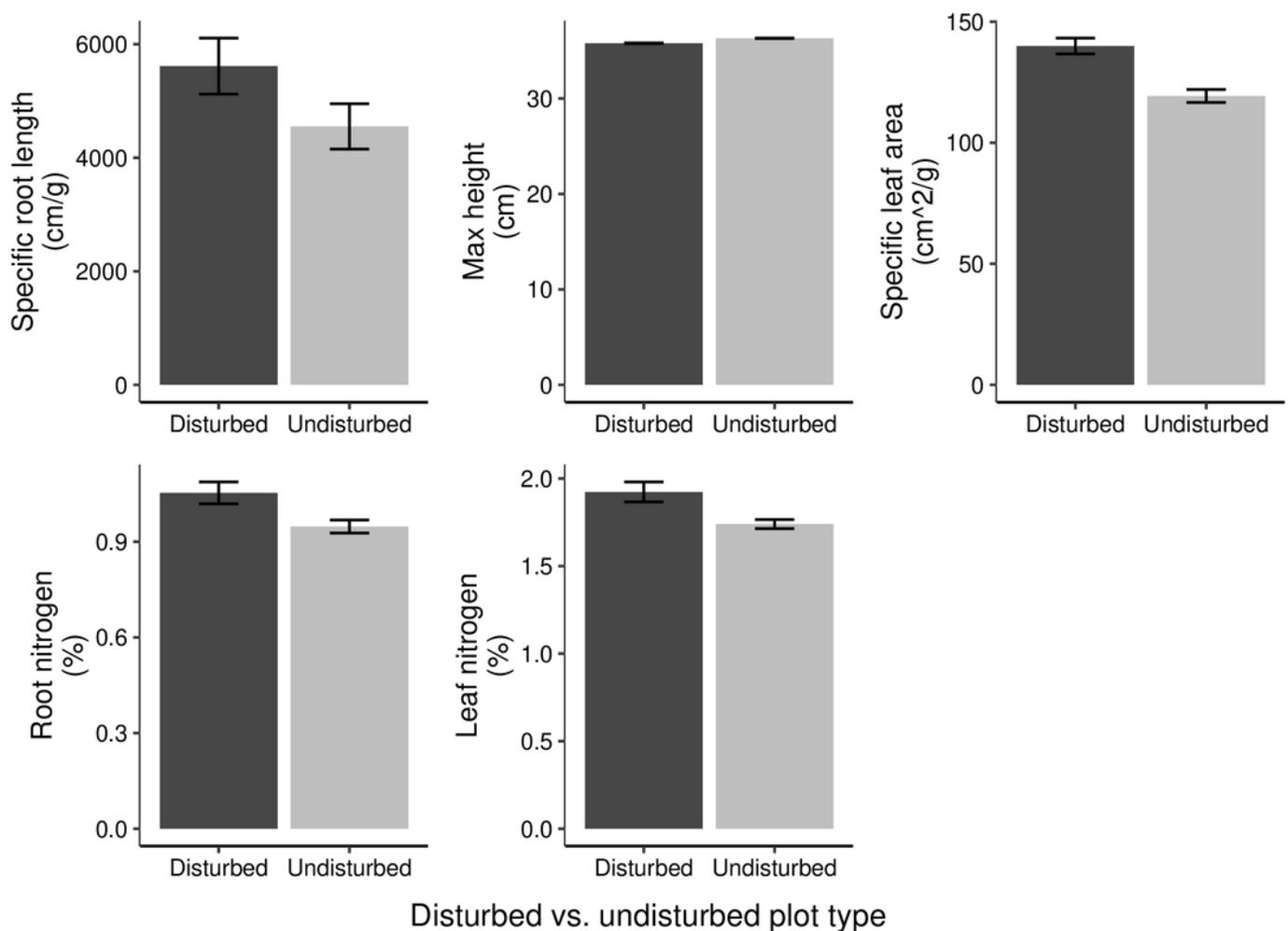
Figure 4

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.