Disturbance has lasting effects on functional traits and diversity of grassland plant communities

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ABSTRACT

Background: Localized disturbances within grasslands alter biological properties and may shift species composition. For example, rare species in established communities may become dominant in successional communities if they exhibit traits well-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 gap communities compared to those in adjacent undisturbed grasslands, and (c) if altered functional diversity resulted in the homogenization or diversification of functional traits.

Methods: Here we emulate the impacts of an extreme disturbance in a native grassland site. We measured plant community composition of twelve paired 50 × 50 cm plots (24 total) in Alberta, Canada. Each pair consisted of one undisturbed plot and one which had all plants terminated 2 years prior. We used species abundances and 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 communities.

Results: Within 2 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, resulting in lower functional divergence in disturbed plots. Further, disturbance was linked to increases in community-weighted mean trait values for 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 biodiversity measures such as richness and evenness recovering within 2 years. The trait space of gap communities shifted compared to undisturbed communities such that gap communities were dominated by traits enhancing resource uptake and growth rates. Overall, these results show that

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short-term disturbance fundamentally changes the functional character of early-successional communities, even if they superficially appear recovered.

Subjects Ecology, Plant Science
Keywords Functional diversity, Functional traits, Successional communities, Disturbance, Grasslands, Plant strategies

INTRODUCTION

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

Examining traits can shed light on the specific impacts of disturbance on plant communities. Traits are measurable individual morphological, physiological, or phenological characteristics that provide insight into life history strategies and influence plant ranges and species interactions (*Voille et al., 2007*; *Cadotte, Carscadden & Mirotchnick, 2011*). "Functional traits" specifically impact growth, reproduction and survival (*Voille et al., 2007*). At small scales, trait differences can influence local diversity patterns by determining competitive outcomes (*Liu et al., 2015*). Traits can also provide insight as to species resource acquisition strategies by indicating species location on the fast-slow plant economics spectrum, where "fast" strategies prioritize resource acquisition and growth while "slow" strategies favour stress tolerance and longevity (*Reich, 2014*). Measuring functional traits after a disturbance (such as those which create gaps) can reveal how a community has changed in functional strategies and can be used to examine the resulting community's functional diversity. *Cadotte (2007)* describes gap species as prioritizing rapid resource uptake, whereas non-gap species take a slower, tolerance-based approach. For example, specific leaf area (SLA) values are likely to be larger in post-disturbance successional communities as high SLA is correlated to fast growth and low competitive ability (*Kunstler et al., 2016*). Additionally, *Loughnan & Gilbert (2017)* found that SLA may be involved with shifts in competitive ability as greater SLA is associated with more sunlight acquisition and thus increased energy acquisition. Thus, changes in communities after mortality are likely due to differences in the trait profiles of successional species.

It is important to note that these changes in species composition and community-level traits changes may not be reflected in the total number of species in the community (*i.e.* species richness). Disturbance may change the nature of community assembly in successional communities by altering the process by which species from the regional pool are able to colonize local communities (*HilleRisLambers et al., 2012*; *Escobedo et al., 2021*). Disturbance changes the environmental filters which constrain species dispersal and recruitment to communities (*Myers et al., 2015*; *Brown & Cahill, 2020*); in this case we would expect the resulting community to contain species that possess functional traits better suited to the new set of environmental filters, changing the community-level traits and functional diversity of the disturbed community. Thus, if taxonomic measures like species richness or evenness remain unchanged after disturbance, they may mask functional differences and result in a mirage of stability when, in fact, the community has undergone great change. This emphasizes the importance of studying functional traits and quantifying functional diversity to understand community drivers.

Functional diversity is a subset of biological diversity which measures the traits present in an ecosystem (*Tilman, 2001*). It is distinct from taxonomic diversity as it reflects the breadth of the functional space occupied by species in a community (*Rosenfeld, 2002*; *Villéger, Mason & Mouillot, 2008*), whereas taxonomic diversity indicates the number of species in a given community separate from any measure of community function (*Laliberté & Legendre, 2010*). Some functional diversity measures are not greatly influenced by taxonomic measures such as species richness (*Laliberté & Legendre, 2010*) and can offer a more nuanced approach to understanding community characteristics. Disturbance affects functional diversity (*Parreira de Castro, Dolédec & Callisto, 2018*) and can potentially result in functional homogenization, or selection for similar trait-characters in species colonizing in disturbed communities (*Olden et al., 2004*). However, resource fluxes associated with disturbance (*Davis, Grime & Thompson, 2000*) may lead to trait diversification within colonizing species to allow for more efficient utilization of the increased resources available in disturbed communities (*Chapman, Childers & Vallino, 2016*; *Jentsch & White, 2019*). As functional diversity is associated with the provisioning of ecosystem services (*Díaz et al., 2007*; *Roscher et al., 2012*; *Pakeman, 2014*), the homogenizing or diversifying effects of disturbance on functional diversity must be better understood.

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

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

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

METHODS

Study site

Our study site was located in the Roy Berg Kinsella Research Ranch in Kinsella, AB, Canada (53°5′N, 111°33′W). Data collection took place in a native grassland dominated by *Hesperostipa curtiseta* (Hitchc.) Barkworth, *Festuca hallii* (Vasey) Piper and *Poa pratensis* (L.) (*Brown, Oppon & Cahill, 2019*). The site is part of the Aspen Parkland ecoregion, a savanna-type habitat characterized by a mosaic of mixed-grass prairie and trembling aspen (*Populus tremuloides* Michx.). The field site is periodically grazed by cattle with a heavy grazing event in October 2019 and a light grazing event occurring in May 2020.

Study design

We sampled 24 plots (50 cm × 50 cm), arranged in 12 blocks of paired plots, which were originally established in 2016 (*Brown & Cahill, 2020*). Each block contained an undisturbed plot, where no standing vegetation was terminated, and a disturbed plot, where all standing vegetation was terminated. Disturbed plots were created in May 2016, by having all biomass trimmed to the soil surface and an undiluted glyphosate herbicide (Roundup©, Bayer, Leverkusen, Germany) liberally applied to the remaining stems to ensure death of the resident vegetation. This treatment was maintained through August 2018 with any regenerating plant materials or newly germinated recruits trimmed and painted with herbicide during the growing seasons. This treatment does not represent any specific natural event, and instead is testing the extreme event of complete removal of the resident vegetation, without a soil disturbance. Additionally, this treatment does not remove the seed bank present at the site (*Brown & Cahill, 2020*) and thus does not affect new plant recruitment from seed after the treatment window (see *Grubb, 1977*).

Plant community composition was measured in July 2018 by visually estimating percent cover of all species present within each plot. Two years post-treatment, in July 2020, plot pairs were revisited, by which time vegetation had regrown in the disturbed plots. Communities were colonized through enhanced germination of seed from the existing seed bank and seed dispersal from surrounding areas (*Brown & Cahill, 2020*), Community composition was measured using percent cover estimation of each species. Sedges were unable to be identified to species and were recorded as “*Carex* spp.”.

Plant traits

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

Trait profiles and functional diversity

To characterize communities by their traits, we first calculated community weighted means (CWMs) for five traits: SLA, maximum height, leaf N %, root N %, and SRL. CWMs are the average value of a given trait in a community weighted by the abundance of all species possessing said trait (*Lavorel et al., 2008*), and are useful for understanding community properties and dynamics, as well as quantifying community change (*Garnier et al., 2004*, *2007*; *Louault et al., 2005*). CWMs were calculated at the species-level. While disturbance is likely to result in intraspecific variability in functional traits, here we focus on species-level values as a first-level test to detect if disturbance does result in persistent change to community functional traits. We encourage future studies to collect trait data from individual plants across species to quantify how intraspecific trait variation changes with disturbance regimes. Outlier trait values (values more than three standard deviations away from the species' mean) were removed prior to calculating CWM.

We then quantified the functional diversity of communities using functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and Rao's quadratic entropy (Q) (*Villéger, Mason & Mouillot, 2008*; *Mouchet et al., 2010*; Table 1). These metrics allow us to characterize the volume (*via* FRic), evenness (*via* FEve), and spread (*via* FDiv and Q) of the communities' functional traits in multidimensional space. By using these multivariate descriptors of communities, we are able to compare communities' character before and after disturbance, as well as to determine if community traits become more or less homogenous as a result of disturbance. We used package vegan (*Oksanen et al., 2017*) in program R (v 4.0.0; *R Development Core Team, 2020*) to compute species richness and evenness, using methods from *Oksanen (2020)*. We used package FD (*Laliberté, Legendre & Shipley, 2014*) to compute CWMs. We also computed FRic, FDiv, FEve, and Rao's Q using package FD.

Table 1 Functional diversity metric definitions.

Functional diversity metric definitions	
Functional diversity (FD)	The functional space occupied by species, where axes are functional features (*Rosenfeld, 2002*; *Villéger, Mason & Mouillot, 2008*). The functional differences between a group of species (*Tilman, 2001*)
Functional richness (FRic)	The breadth of functional space filled by a communities (*Villéger, Mason & Mouillot, 2008*)
Functional evenness (FEve)	The evenness of the distribution of abundances and functional features of species (*Villéger, Mason & Mouillot, 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*).

Statistical analysis

To determine if community traits differed between control and disturbed treatments after recovery, we used five separate linear mixed models (LMMs). The CWM's for SLA, height, leaf N %, root N %, and SRL were used as response variables, plot type (disturbed or undisturbed) was a fixed effect and block (*i.e*., disturbed and undisturbed plot location) was a random effect. "Block" was included as a random effect in models to account for spatial autocorrelation in community data as disturbed and undisturbed plots were adjacent. All LMMs were run using an underlying normal distribution with the lme4 (*Bates et al., 2015*) and lmerTest (*Kuznetsova, Brockhoff & Christensen, 2017*) packages. We also used four separate LMMs to quantify how functional diversity measures, namely FRic, FDiv, FEve, and Rao's Q, differed between disturbance types. FRic, FDiv, FEve, and Roa's Q were used as response variables, block was included as a random effect and plot type (disturbed or undisturbed) was a fixed effect in all models. Functional richness was log-transformed to fit assumptions of normality. To determine whether disturbed and undisturbed communities had different community compositions, we conducted a permutational multivariate analysis of variance (PERMANOVA), with plot as a strata, using packages vegan and RVAideMemoire (*Herve, 2021*).

RESULTS

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

Despite persistent effects on local diversity, and although disturbed plots began with zero species present in 2018, within 2 years there was no significant difference between plot-level (alpha) richness and evenness between disturbed and undisturbed plots (richness = 17, evenness = 0.82; Fig. 1). However, underlying this similarity are differences

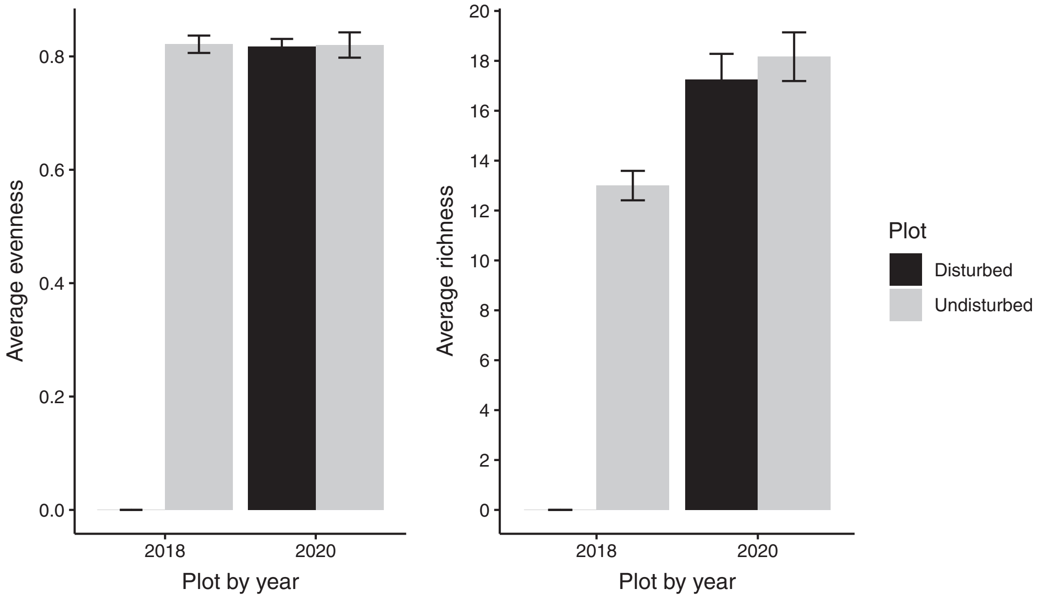

Figure 1 **Average species evenness and richness of disturbed and undisturbed plots in 2018 and 2020.** In disturbed plots, all biomass was trimmed to the soil surface and a glyphosate herbicide (Roundup©) applied to the remaining stems to ensure death of the resident vegetation from 2016–2018. Plots 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. Full-size DOI: 10.7717/peerj.13179/fig-1

in species composition ($R^2 = 0.24$, $F = 7.06$, $p = 0.001$; Fig. 2), with one third of plant species unique to either treatment type (Fig. 1; Table S1). Gap communities were segregated from undisturbed communities in multivariate space, with the exception of one disturbed/undisturbed pair (pair #12) (Fig. 2).

Community weighted means of SLA, leaf N %, and root N % differed between disturbed and undisturbed plots, with disturbed plots typically having trait values more consistent with the 'fast' end of the leaf economics spectrum. Specifically, disturbed plots had significantly larger CWM for SLA, leaf N %, root N %, and there was a trend towards larger root SRL (Fig. 3; Table 2). There was no difference in CWM of maximum height, indicating a more rapid recovery to overall physiognomy relative to other functional characteristics of the communities.

Gap communities were functionally distinct from undisturbed communities after 2 years of recovery. Undisturbed communities showed higher FDiv values (FDiv = 0.08 ± 0.02, $p = 0.0020$; Fig. 4). FEve (FEve = 0.07 ± 0.02, $p = 0.0129$; Fig. 4), FRic (difference = 1.07 ± 1.16, $p = 0.376$; Fig. 4), and Rao's Q (difference = 0.004 ± 0.002, $p = 0.0733$; Fig. 4) were not significantly different among the two treatments (Table 3).

DISCUSSION

Although local communities recovered in species richness after only 2 years, there were a number of legacies of disturbance found in functional traits. There are persistent effects of disturbance on local diversity, suggesting successional communities are shaped by a combination of local dispersal and niche conditions. However, given competition can be

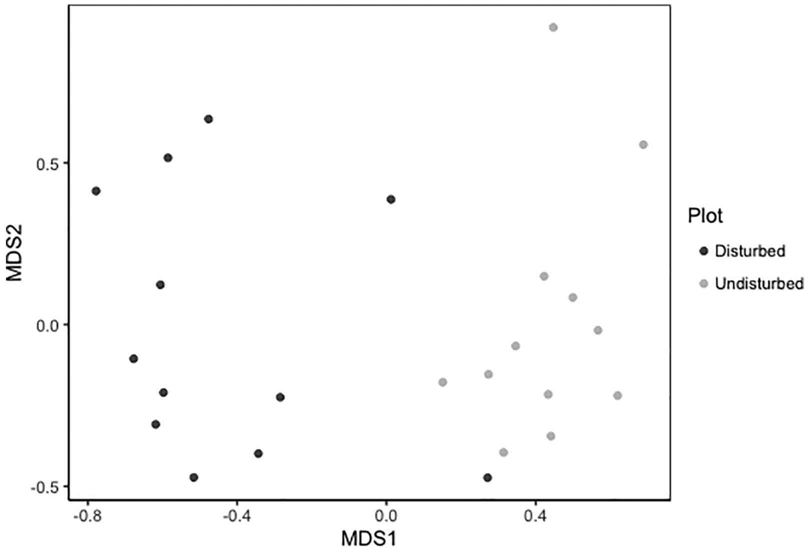

Figure 2 Metric multidimensional scaling (MDS) of disturbed and undisturbed community composition. Data points denote 2020 plant community composition in disturbed and undisturbed plots. In disturbed plots, all biomass was trimmed to the soil surface and a glyphosate herbicide (Roundup©) applied to the 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.

Full-size DOI: 10.7717/peerj.13179/fig-2

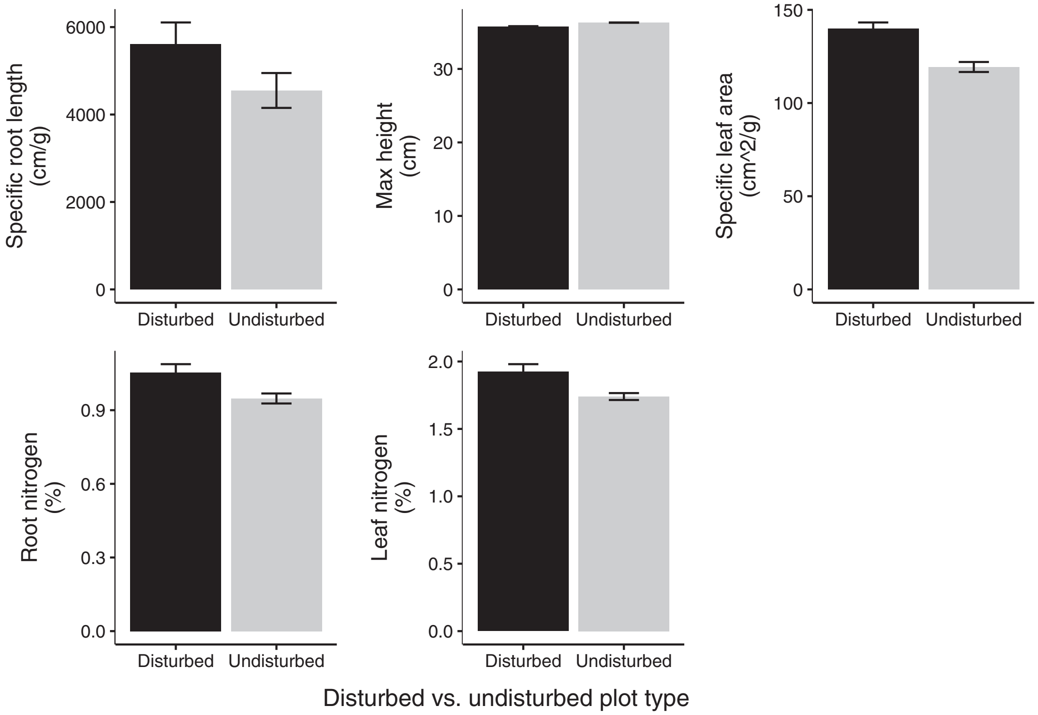

Figure 3 Mean trait values in 2020 disturbed and undisturbed communities. Comparisons of specific root length, maximum height, specific leaf area, root nitrogen, and leaf nitrogen between disturbed and undisturbed communities. Error bars represent standard error. Associated statistics are found in Table 2.

Full-size DOI: 10.7717/peerj.13179/fig-3

Table 2 **Results of the linear mixed models (LMM) for traits.**

	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	**2.64×10^{-5}**
Specific root length (cm/g)	5,612.82 (±448.19)	4,550.30 (±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**

Note:

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.

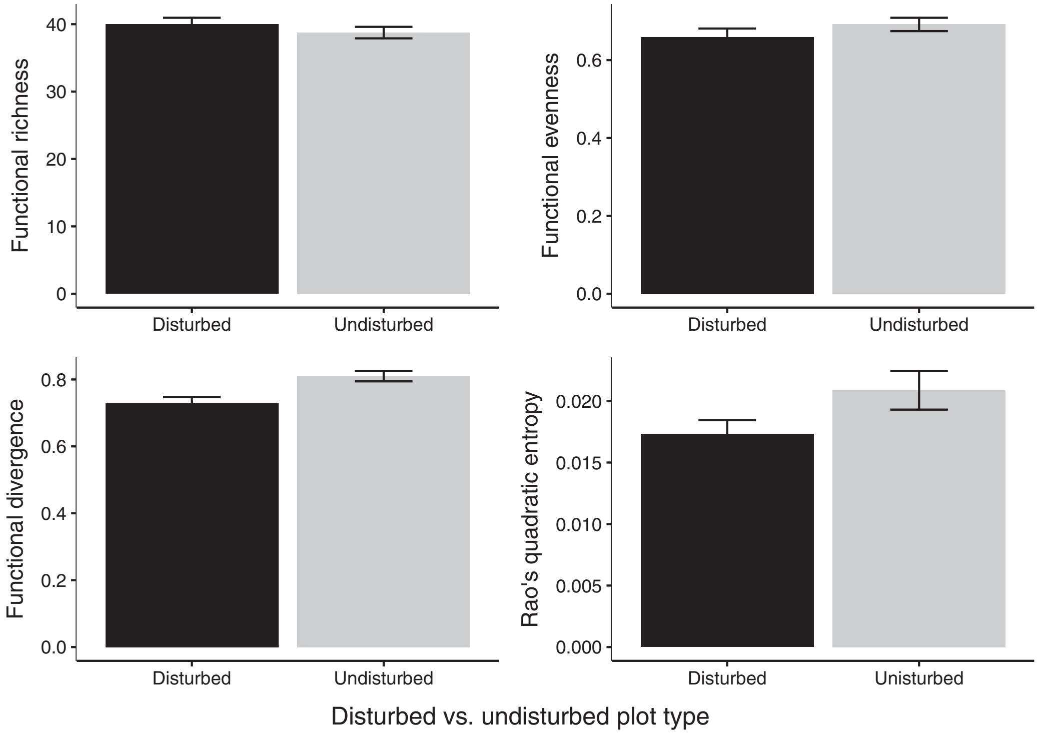

Figure 4 **Estimates of functional diversity values in 2020 disturbed and undisturbed communities.** Comparisons of functional richness, functional evenness, functional divergence, and Rao's quadratic entropy between disturbed and undisturbed communities. Functional richness was log-transformed to meet the assumption of normality and was multiplied by negative one. Error bars represent standard error. Associated statistics are found in Table 3. Full-size DOI: 10.7717/peerj.13179/fig-4

reduced by disturbance (*Wilson & Tilman, 1993*), dispersal most likely limits recruitment in gap communities. At the same time, at the plot level we find there is great stability in species richness and evenness, suggesting the local structure of communities in this system is highly stable but the species who fill each "role" are variable. Thus, the functional differences we observe are not due to fundamental changes in the dominance structure (*i.e.* evenness) of successional communities, but rather due to species filtering.

Table 3 Results of the linear mixed models (LMM) for functional diversity.

	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

Note:

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.

Traits after disturbance

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

Height variation in grasslands is a significant predictor of species richness and community productivity (Brown & Cahill, 2019), yet we found that maximum height recovers quickly (within 2 years) after disturbance and is not significantly different among successional and undisturbed communities. This is surprising as greater height is thought to be indicative of greater competitive ability (*Givnish, 1995*; *Cornelissen et al., 2003*; *Falster & Westoby, 2003*).

Functional diversity after disturbance

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

CONCLUSIONS

Overall, we found while traditional metrics of community composition such as species richness and evenness recovered within 2 years of disturbance, there were persistent impacts of disturbance on community-level traits and functional diversity. SLA, leaf N %, and root N % values were significantly larger in the disturbed condition, supporting the conclusion that species in gap areas are more likely to possess traits that support faster resource acquisition. The prevalence of individuals possessing these "fast" traits was reflected in distinct differences in community membership among undisturbed and gap communities. Disturbance also impacted functional diversity by promoting homogenization of community's functional traits. In all, this work suggests functional trait shifts from small disturbances are a critical mechanism for maintaining spatial heterogeneity in grassland systems, even as species richness and evenness recover.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Ellen A. Smith conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Emily M. Holden conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Charlotte Brown performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- James F. Cahill Jr conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The data is available at GitHub: https://github.com/emilmhold/Trait-profiles-and-functional-diversity-following-disturbance-in-a-mixed-grassland.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.13179#supplemental-information.

REFERENCES

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67(1)**:1–48 DOI 10.18637/jss.v067.i01.

Brown C, Oppon KJ, Cahill JF Jr. 2019. Species-specific size vulnerabilities in a competitive arena: nutrient heterogeneity and soil fertility alter plant competitive size asymmetries. *Functional Ecology* **33(8)**:1491–1503 DOI 10.1111/1365-2435.13340.

Brown C, Cahill JF Jr. 2020. Standing vegetation as a coarse biotic filter for seed bank dynamics: effects of gap creation on seed inputs and outputs in a native grassland. *Journal of Vegetation Science* **31(6)**:1006–1016 DOI 10.1111/jvs.12890.

Cadotte MW. 2007. Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* **88(4)**:823–829 DOI 10.1890/06-1117.

Cadotte MW. 2017. Functional traits explain ecosystem function through opposing mechanisms. *Ecology Letters* **20(8)**:989–996 DOI 10.1111/ele.12796.

Cadotte MW, Carscadden K, Mirotchnick N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* **48(5)**:1079–1087 DOI 10.1111/j.1365-2664.2011.02048.x.

Cahill JF Jr. 2003. Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. *Journal of Ecology* **91(4)**:532–540 DOI 10.1046/j.1365-2745.2003.00792.x.

Cahill JF Jr. 2020. Alberta grassland plant trait data. *Education & Research Archive* DOI 10.7939/r3-wszy-4x39.

Chapman EJ, Childers DL, Vallino JJ. 2016. How the second law of thermodynamics has informed ecosystem ecology throughout its history. *BioScience* **66(1)**:27–39 DOI 10.1093/biosci/biv166.

Comas LH, Eissenstat DM. 2004. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* **18(3)**:388–397 DOI 10.1111/j.0269-8463.2004.00835.x.

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australia Journal of Botany* **51(4)**:335–380 DOI 10.1071/BT02124.

Craine JM, Tilman D, Wedin D, Reich P, Tjoelker M, Knops J. 2002. Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology* **16(5)**:563–574 DOI 10.1046/j.1365-2435.2002.00660.x.

Davidson AD, Detling JK, Brown JH. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment* **10(9)**:477–486 DOI 10.1890/110054.

Davidson AD, Lightfoot DC. 2008. Burrowing rodents increase habitat heterogeneity in a desert grassland. *Journal of Arid Environments* **72(7)**:1133–1145 DOI 10.1016/j.jaridenv.2007.12.015.

Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88(3)**:528–534 DOI 10.1046/j.1365-2745.2000.00473.x.

Desmet P, Brouilet L. 2013. Database of vascular plants of Canada (VASCAN): a community contributed taxonomic checklist of all vascular plants of Canada, Saint Pierre and Miquelon, and Greenland. *PhytoKeys* **25**:55–67 DOI 10.3897/phytokeys.25.3100.

di Virgilio A, Morales JM. 2016. Towards evenly distributed grazing patterns: including social context in sheep management strategies. *PeerJ* **4**:e2152 DOI 10.7717/peerj.2152.

Díaz S, Lavorel S, de Bello F, Quétier F, Grigulis K, Robson TM. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Science* **104(52)**:20684–20689 DOI 10.1073/pnas.0704716104.

Eler K, Kermavnar J, Marinsek A, Kutnar L. 2018. Short-term changes in plant functional traits and understory functional diversity after logging of different intensities: a temperate fir-beech forest experiment. *Annals of Forest Research* **61(2)**:223–241 DOI 10.15287/afr.2018.1192.

Escobedo VM, Rios SR, Alcayaga-Olivares Y, Gianoli E. 2021. Disturbance reinforces assembly processes differentially across spatial scales. *Annals of Botany* **127(2)**:175–189 DOI 10.1093/aob/mcaa162.

Falster DS, Westoby M. 2003. Plant height and evolutionary games. *Trends in Ecology & Evolution* **18(7)**:337–343 DOI 10.1016/S0169-5347(03)00061-2.

Fried G, Villers A, Porcher E. 2018. Assessing non-intended effects of farming practices on field margin vegetation with a functional approach. *Agriculture, Ecosystems & Environment* **261**:33–44 DOI 10.1016/j.agee.2018.03.021.

Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint J-P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85(9)**:2630–2637 DOI 10.1890/03-0799.

Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Fortunel C, Freitas H, Golodets C, Grigulis K, Jouany C, Kazakou E, Kigel J, Kleyer M, Lehsten V, Leps J, Meier T, Pakeman R, Papadimitriou M, Papanastasis VP, Quested H, Quetier F, Robson M, Roumet C, Rusch G, Skarpe C, Sternberg M, Theau J-P, Thebault A, Vile D, Zarovali MP. 2007. Assessing the effects of land-use change on plant traits, communities, and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* **5(1)**:967–985 DOI 10.1093/aob/mcl215.

Givnish TJ. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In: Gartner BL, ed. *Plant Stems: Physiology and Functional Morphology*. Cambridge: Academic Press, 3–49.

Godfree R, Lepschi B, Reside A, Bolger T, Robertson B, Marshall D, Carnegie M. 2011. Multiscale topoedaphic heterogeneity increases resilience and resistance of a dominant grassland species to extreme drought and climate change. *Global Change Biology* **17(2)**:943–958 DOI 10.1111/j.1365-2486.2010.02292.x.

Grubb PJ. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* **52(1)**:107–145 DOI 10.1111/j.1469-185X.1977.tb01347.x.

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking community assembly through the lens of coexistence. *Annual Review of Ecology, Evolution, and Systematics* **43**:227–248 DOI 10.1146/annurev-ecolsys-110411-160411.

Herve M. 2021. *RVAideMemoire: Testing and Plotting Procedures for Biostatistics*. Version 09-81. *Available at https://cran.r-project.org/package=RVAideMemoire*.

Jentsch A, White P. 2019. A theory of pulse dynamics and disturbance in ecology. *Ecology* **100(7)**:e02734 DOI 10.1002/ecy.2734.

Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M, Vieilledent G, Wright SJ, Aiba M, Baraloto C, Caspersen J, Cornelissen JHC, Gourlet-Fleury S, Hanewinkel M, Herault B, Kattge J, Kurokawa H, Onoda Y, Peñuelas J, Poorter H, Uriarte M, Richardson S, Ruiz-Benito P, Sun I-F, Ståhl G, Swenson NG, Thompson J, Westerlund B, Wirth C, Zavala MA, Zeng H, Zimmerman JK, Zimmermann NE, Westoby M. 2016. Plant functional traits have globally consistent effects on competition. *Nature* **529**:204–207 DOI 10.1038/nature16476.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* **82(13)**:1–26 DOI 10.18637/jss.v082.i13.

Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91(1)**:299–305 DOI 10.1890/08-2244.1.

Laliberté E, Legendre P, Shipley B. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. *Available at https://cran.r-project.org/web/packages/FD/index.html*.

Lavorel S, Grigulis K, McIntyre S, Williams NSG, Garden D, Dorrough J, Berman S, Quétier F, Thébault A, Bonis A. 2008. Assessing functional diversity in the field—methodology matters!. *Functional Ecology* **22**:134–147 DOI 10.1111/j.1365-2435.2007.01339.x.

Liu M, Wang Z, Li S, Lü X, Wang X, Han X. 2017. Changes in specific leaf area of dominant plants in temperate grasslands along a 2500-km transect in northern China. *Scientific Reports* **7(1)**:365 DOI 10.1038/s41598-017-11133-z.

Liu J, Zhang X, Song F, Zhou S, Cadotte MW, Bradshaw CJA. 2015. Explaining maximum variation in productivity requires phylogenetic diversity and single functional traits. *Ecology* **96(1)**:176–183 DOI 10.1890/14-1034.1.

Louault F, Pillar VD, Aufrère J, Garnier E, Soussana J-F. 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science* **16(2)**:151–160 DOI 10.1111/j.1654-1103.2005.tb02350.x.

Loughnan D, Gilbert B. 2017. Trait-mediated community assembly: distinguishing the signatures of biotic and abiotic filters. *Oikos* **126(8)**:1112–1122 DOI 10.1111/oik.03945.

McCormack ML, Guo D, Iversen CM, Chen W, Eissenstat DM, Fernandez CW, Li L, Ma C, Ma Z, Poorter H, Reich PB, Zadworny M, Zanne A. 2017. Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist* **215(1)**:27–37 DOI 10.1111/nph.14459.

Mouchet MA, Villéger S, Mason NWH, Mouillot D. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* **24(4)**:867–876 DOI 10.1111/j.1365-2435.2010.01695.x.

Mursinoff S, Tack AJM. 2017. Spatial variation in soil biota mediates plant adaptation to a foliar pathogen. *New Phytologist* **214(2)**:644–654 DOI 10.1111/nph.14402.

Myers JA, Chase JM, Crandall RM, Jiménez I. 2015. Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology* **103(5)**:1291–1299 DOI 10.1111/1365-2745.12436.

Oksanen J. 2020. Vegan: ecological diversity. *Available at https://cran.r-project.org/web/packages/vegan/vignettes/diversity-vegan.pdf*.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H. 2017. Vegan: community ecology package. Version 2.4-5. *Available at https://cran.r-project.org/web/packages/vegan/index.html* (accessed 21 January 2018).

Olden JD, LeRoy Poff N, Douglas MR, Douglas ME, Fausch KD. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* **19(1)**:18–24 DOI 10.1016/j.tree.2003.09.010.

Pakeman RJ. 2014. Functional trait metrics are sensitive to the completeness of the species' trait data? *Methods in Ecology and Evolution* **5(1)**:9–15 DOI 10.1111/2041-210X.12136.

Pakeman RJ, Quested HM. 2007. Sampling plant functional traits: what proportion of the species need to be measured? *Applied Vegetation Science* **10(1)**:91–96 DOI 10.1111/j.1654-109X.2007.tb00507.x.

Parreira de Castro DM, Dolédec S, Callisto M. 2018. Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators* **84**:573–582 DOI 10.1016/j.ecolind.2017.09.030.

Purschke O, Schmid BC, Sykes MT, Poschlod P, Michalksi SG, Durka W, Kühn I, Winter M, Prentice HC. 2013. Contrasting changes in taxonomic, phylogenetic, and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology* **101(4)**:857–866 DOI 10.1111/1365-2745.12098.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61(3)**:167–234 DOI 10.1071/BT12225.

R Development Core Team. 2020. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. *Available at https://www.R-project.org/*.

Reich PB. 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102(2)**:275–301 DOI 10.1111/1365-2745.12211.

Roscher C, Schumacher J, Gubsch M, Lipowsky A, Weigelt A, Buchmann N, Schmid B, Schulze ED. 2012. Using plant functional traits to explain diversity–productivity relationships. *PLOS ONE* **7(5)**:e36760 DOI 10.1371/journal.pone.0036760.

Rosenfeld JS. 2002. Functional redundancy in ecology and conservation. *Oikos* **98(1)**:156–162 DOI 10.1034/j.1600-0706.2002.980116.x.

Roumet C, Birouste M, Picon-Cochard C, Ghestem M, Osman N, Vrignon-Brenas S, Cao K-F, Stokes A. 2016. Root structure-function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist* **210(3)**:815–826 DOI 10.1111/nph.13828.

Schleuter D, Daufresne M, Massol F, Argillier C. 2010. A user's guide to functional diversity indices. *Ecological Monographs* **80(3)**:469–484 DOI 10.1890/08-2225.1.

Suding KN. 2001. The effects of gap creation on competitive interactions: separating changes in overall intensity from relative rankings. *Oikos* **94(2)**:219–227 DOI 10.1034/j.1600-0706.2001.940202.x.

Suding KN, Goldberg D. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology* **82(8)**:2133–2149 DOI 10.2307/2680221.

Tannas KE. 2004. *Common plants of the western rangelands—volume 3: Forbs*. Edmonton, AB: Alberta Agriculture and Rural Development.

Tilman D. 2001. Functional diversity. *Encyclopedia of Biodiversity* **3**:109–120 DOI 10.1006/rwbd.1999.0154.

Villéger S, Mason NWH, Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89(8)**:2290–2301 DOI 10.1890/07-1206.1.

Voille C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* **116(5)**:882–892 DOI 10.1111/j.0030-1299.2007.15559.x.

Wilson SD, Tilman D. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* **74(2)**:599–611 DOI 10.2307/1939319.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ülo, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R. 2004. The worldwide leaf economics spectrum. *Nature* **428**:821–827 DOI 10.1038/nature02403.