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Functional diversity is a passenger but not driver of drought-related plant diversity losses in annual grasslands

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Abstract

1. Effects of climate change on plant community functional diversity are of interest since experiments have found functional diversity to predict ecosystem function. Functional diversity has been hypothesized to confer resilience to plant communities (as a "driver" of community change), but in unmanipulated natural communities, it might alternatively (or additionally) act as a "passenger" by responding to changes in plant diversity caused by extrinsic factors such as climate.

2. We examined trends in plant functional diversity in annual grasslands in Northern California over a 19-year period, during which a trend towards drier winters had previously been associated with the losses of drought-intolerant species. We tested whether functional diversity decreased over the period of the study (acting as a passenger), and also whether initial site functional diversity influenced the degree of community change over the study period (acting as a driver).

3. Initial community functional diversity was not related to species richness loss or community variability. We found that functional diversity declined as plant species richness and community mean specific leaf area declined over the course of the study, and all of these trends were associated with declining precipitation, indicating that functional diversity acted as a passenger of community change.

4. *Synthesis*. This study is among the first to demonstrate that recent climatic trends may drive loss of functional diversity. Our findings highlight that functional diversity does not necessarily confer community resilience when its variation is shaped by the environment rather than by experimental treatments.

KEYWORDS
annual grasslands, climate change, functional diversity, functional traits, plant communities

1 | INTRODUCTION

Although the effects of climate change vary geographically, many terrestrial regions have become significantly warmer and drier, and these changes are expected to intensify over coming decades (Cook, Ault, & Smerdon, 2015; Huang, Yu, Guan, Wang, & Guo, 2016; Schlaepfer et al., 2017). For plant communities, such environmental changes may lead to substantial community shifts that could include significant losses of plant diversity, particularly in ecosystems where

plant growth is limited primarily by water availability (Breshears et al., 2005; Harrison, Gornish, & Copeland, 2015; Pauli et al., 2012; Sommer et al., 2010). Within plant communities, the responses of individual species to warmer and drier conditions caused by climate change are likely to vary. Functional traits can provide insight into mechanisms linking fitness to environmental conditions (Reich et al., 2003). For example, plant species with functional traits conferring less efficient water use should be more likely to decline under warmer, drier conditions (Dorji et al., 2015; Greenwood et al., 2017).

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Since functional diversity, or the degree of variation in community functional traits, can be a strong correlate of ecosystem function (Cadotte, Carscadden, & Mirotchnick, 2011; Diaz & Cabido, 2001), understanding how functional diversity will shift with changes in community composition is particularly important. Rapid climatic change may deplete functional diversity through the selective losses of vulnerable trait combinations, a possibility that is supported by analyses of post-Pleistocene plant community change (Ordonez & Svenning, 2017).

At the community level, plant assemblages with greater functional diversity have been hypothesized to have greater constancy of biomass and/or composition—properties we refer to here as "resilience"—as the result of their fuller resource utilization, consequent greater resistance to invasions, and/or the potential for compensatory growth that arises from their greater diversity in species' responses to perturbations (e.g. Diaz & Cabido, 2001; Folke et al., 2004; Standish et al., 2014). These positive relationships between functional diversity and various metrics of resilience have been demonstrated by conceptual and mathematical models (e.g. Mori, Furukawa, & Sasaki, 2013; Sakschewski et al., 2016). Experiments manipulating functional diversity at the level of discrete functional groups (e.g. grasses/forbs, N-fixers/non-fixers) have sometimes found positive effects on biomass, invasion resistance and temporal constancy of composition (Diaz & Cabido, 2001). Evidence for the positive effects of continuous trait-based functional diversity on stability and resilience of communities remains somewhat scarcer, however. A recent meta-analysis of experimental studies found positive effects of species diversity and phylogenetic diversity but not of trait-based functional diversity on the stability of community biomass (Craven et al., 2018). Evidence from unmanipulated natural systems also remains inconclusive. For example, droughts in the Mediterranean region were found to cause less reduction in growth of a focal tree species when it was growing in functionally more-diverse stands (Gazol & Camarero, 2016), but also to have greater effects on the composition of shrublands that were initially more functionally diverse (Riva et al., 2017).

Functional diversity could also act as a "passenger" of community change, either instead of or in addition to acting as a driver of change. For example, if altered environmental conditions primarily affect species with certain traits, the abundance of species with susceptible traits in a given community may provide stronger predictive power for community shifts than functional diversity per se (Barkaoui, Roumet, & Volaire, 2016; Riva et al., 2017). In such a scenario, the loss of susceptible species (e.g. species with lower water-use efficiency in a drying climate) could lead to reduced functional diversity, casting functional diversity as a community property that changes passively in response to extrinsically driven community change. For example, grassland functional diversity may be enhanced where grazing by livestock reduces the dominance of faster-growing species, whereas it may be undermined by wet periods that increase this dominance (Hallett, Stein, & Suding, 2017). With regard to individual functional traits, considerable effort has been devoted to distinguishing those that act as drivers of

community and ecosystem-level effects from those that are best described as responses to (or passengers of) environmental change (Suding et al., 2008). With regard to multivariate functional diversity, in striking contrast, very little previous research has attempted to distinguish whether it is a driver or passenger of community change.

We examined 19-year trends in functional diversity in an annual-dominated grassland community in which long-term changes in species richness and functional trait means had already been observed, and had been associated with decreasing winter precipitation (Harrison et al., 2015; Harrison, LaForgia, & Latimer, 2018). We asked whether any observed trends in functional diversity could be considered passengers in the sense that they followed directly from the climatically induced losses of species with stress-intolerant functional traits. We also asked whether functional diversity could be considered a driver in the sense that communities with high initial values of this form of diversity were more resistant to changes over time.

2 | MATERIALS AND METHODS

2.1 | Study system & previous findings

Our study took place at the University of California McLaughlin Reserve, a 2,776 ha facility at 366–914 m elevation in the Inner North Coast Range (38°52′N, 122°26′W). The climate is Mediterranean with mean temperatures of 8°C in January and 25°C in July, and mean annual rainfall (=all precipitation) of 62 cm. Substrates include fertile soils derived from volcanic and sedimentary rocks, and infertile, Mg-rich and nutrient-poor soils derived from serpentine rock. Grasslands consist mainly of annuals that germinate in fall (September–November) shortly after rains begin, are present as seedlings during winter (December–February) and flower in spring (March–May) except for a few that flower in summer. The most abundant species on fertile soils are approximately 10 species of exotic (Eurasian) annual grasses, and the majority of other species are native and exotic annual forbs (non-grasses), with natives being most prevalent on the infertile serpentine soils where exotic grasses are sparse.

Grassland community composition was measured beginning in 2000 at 80 heterogeneous sites widely dispersed around the reserve, with 38 sites on serpentine and 42 on non-serpentine soils (Harrison et al., 2015; 2018). Each site consisted of five permanently marked 1-m² quadrats evenly spaced on a 40-m transect. Sites were ≥50 m apart and were well interspersed. Species composition was sampled annually in April and June; presence (2000–2005) and visually estimated maximum cover (2006–2018) were recorded for each species.

Species richness and diversity declined over the study period on serpentine and non-serpentine soils, with native annual forbs declining the most and no functional group increasing substantially in its richness or cover (Harrison et al., 2015, 2018). Native forbs with high specific leaf area (leaf area/ dry mass), a trait associated with drought intolerance, declined fastest as they "blinked

out" (i.e. disappeared from the community) more and "blinked in" (i.e. reappeared from the seedbank) less often over time than other species. These community changes were statistically associated with a decline in winter (December–February) rainfall, which was the only significant quarterly climatic trend except for parallel declines in winter humidity and cloud cover (Harrison et al., 2015). An extremely wet winter in 2016–2017 produced no recovery in grassland diversity, and severe winter drought returned in 2017–2018. In a hierarchical model, there was an initially strong positive effect of winter rainfall on species richness that weakened with time over the period 2000–2017 (Harrison et al., 2018). A field experiment in 2015–2017 showed that on serpentine soils, winter drought-induced high seedling mortality and that water addition only restored native forb diversity when coupled with seed addition. This combined evidence supported the interpretation that prolonged winter drought led to elevated seedling mortality, which depleted the seedbank and prevented a rebound of diversity in the wet year (Harrison et al., 2018).

2.2 | Data preparation

We used data collected in 2012 on five plant functional traits: specific leaf area (SLA), carbon to nitrogen ratio (C:N), leaf dry matter content (LDC), plant height and seed mass. These traits span the leaf-height-seed set of plant ecological strategies (Westoby, Leishman, & Lord, 1996). SLA, C:N and LDC all represent the leaf economic spectrum, capturing the trade-off between "fast" (rapidly growing species with low stress tolerance) and "slow" species (slower-growing species with greater stress tolerance); species with low SLA, high LDC and high C:N are typically considered "slow" species while those with the opposite are considered "fast" species (Reich, 2014; Wright et al., 2004). Plant height may also represent a trade-off between competitive ability and stress tolerance to some extent (Kunstler et al., 2015). Seed mass relates to both dispersal ability as well as resource-acquisition life-history trade-offs (Westoby et al., 1996).

Seed weight data came from Kew Royal Botanic Gardens (2015). All other trait data came from a previous study at our site (Spasojevic et al., 2014), and were collected in 2012 from 10 individuals of each species using standardized protocols (Cornelissen et al., 2003). For species that occurred on both serpentine and non-serpentine soils, soil-specific trait values from 10 individuals per soil were measured and used in analyses. To improve variable normality and better meet model assumptions, we log-transformed seed mass, plant height and C:N; square root transformed SLA; and raised LDC to the 3.5 power.

We defined functional diversity as the degree of community-level variation in multiple plant functional traits. We focused on functional dispersion, defined as the mean distance of each coexisting species from the community's centroid in multivariate trait space, because it is robust, commonly used and structurally independent from species richness (Laliberté & Legendre, 2010). Focusing on a single functional diversity metric also allowed us to avoid issues with multiple comparisons. We calculated functional dispersion (referred as FD hereafter) for each site using R package FD v1.0-12 (Laliberté,

Legendre, & Shipley, 2014) after converting the species by traits matrix as a Gower distance matrix.

2.3 | Statistical analyses

2.3.1 | Functional diversity as a passenger

Because drought-induced diversity losses in this ecosystem have been previously shown to be driven primarily by losses of native annual forbs (Harrison et al., 2015, 2018), we examined functional diversity patterns for both the entire plant community and for native annual forbs only. Because a few species of exotic annual grasses make up most of the plant cover but only a small share of the plant diversity in this system, and because we have five more years of data for species presence–absence than cover, we used metrics based on presence/absence rather than abundance.

To test whether FD changed over the 19-year period, we used linear mixed models (LMMs) with FD of all species (FD_{all}) or FD of native annual forbs (FD_{naf}) as the response variable, year as the predictor and site as a random effect. For all models that included year, we coded year 2000 as the 0th year so that their intercepts have clear interpretations. To test whether winter precipitation affected FD, we used linear mixed models with FD_{all} or FD_{naf} as the response variable, winter precipitation as the predictor variable and site as a random effect. We also ran a version of these models that included an autocorrelation structure of order 1 (AR1) to account for temporal autocorrelations, which did not qualitatively change the relationships (results not shown).

To test whether changes in FD were related to changes in community mean SLA, the main trait found to predict the decline in native annual forb richness (Harrison et al., 2015), we used a linear mixed model with FD as the response variable, community mean SLA as the predictor and site as a random effect. To provide insight into whether FD responses were driven by trends in SLA (which was correlated with functional dispersion), we also calculated FD using the other four traits (LDC, C:N, plant height and seed mass) but not SLA, and used this "reduced" functional diversity variable as the response variable in a linear mixed model with year as the predictor variable, and site as a random effect.

2.3.2 | Functional diversity as a driver

To test whether FD was a driver of species richness loss, we calculated the coefficient of change in species richness of each site over the course of the study by regressing species richness against year. This coefficient was used as the response variable for a linear regression with initial (year 2000) functional diversity of the same site as the predictor variable. To test the alternate hypothesis that initial community mean trait values could be a stronger predictor of species richness loss than FD, we also ran a version of this model using initial (year 2000) community mean SLA as the predictor value in place of FD. To test whether initial functional diversity affected other metrics related to community stability, we also ran simple

linear models with the coefficients of variation for total species richness, exotic plant richness and total plant cover.
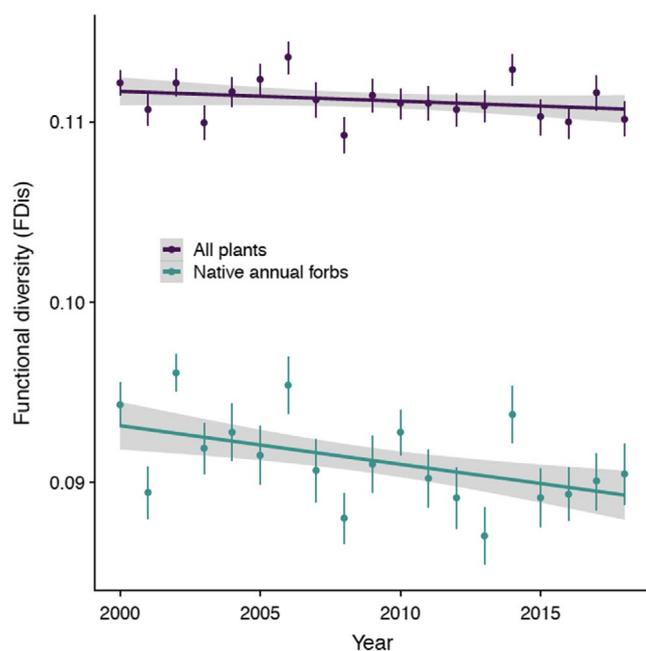
All analyses and data manipulations were conducted in R v3.5.0 (R Core Team, 2018). All LMMs were conducted with package nlme v3.1.137 (Pinheiro, Bates, DebRoy, & Sarkar, 2018).

3 | RESULTS

3.1 | Functional diversity as a passenger

Functional diversity (measured as functional dispersion) declined over the course of the study for both the entire community ($p = 0.037$, $R_C^2 = 0.510$; Figure 1) and for native annual forbs only ($p < 0.001$, $R_C^2 = 0.487$; Figure 1; Table S1), the functional group that has experienced the biggest diversity losses in this system (Harrison et al., 2015). These declines occurred both on serpentine (entire community $p = 0.01$; native annual forbs only, $p = 0.04$) and non-serpentine soils, though only for native annual forbs and not the entire community on non-serpentine (entire community $p = 0.591$; native annual forbs only, $p < 0.001$). There was a positive trend of increasing functional diversity in wetter years for all plants ($p = 0.068$, $R_C^2 = 0.572$; Figure 2a), and there was a positive relationship between winter precipitation and functional diversity of native forbs only ($p < 0.001$, $R_C^2 = 0.743$; Figure 2b; Table S2), indicating that drought was likely a cause of the functional diversity loss.

Functional diversity was positively related to community mean SLA for all plants ($p = 0.008$, $R_C^2 = 0.554$) as well as the community mean SLA of native annual forbs only ($p < 0.001$, $R_C^2 = 0.608$; Figure S1). Functional diversity calculated based on the other four traits
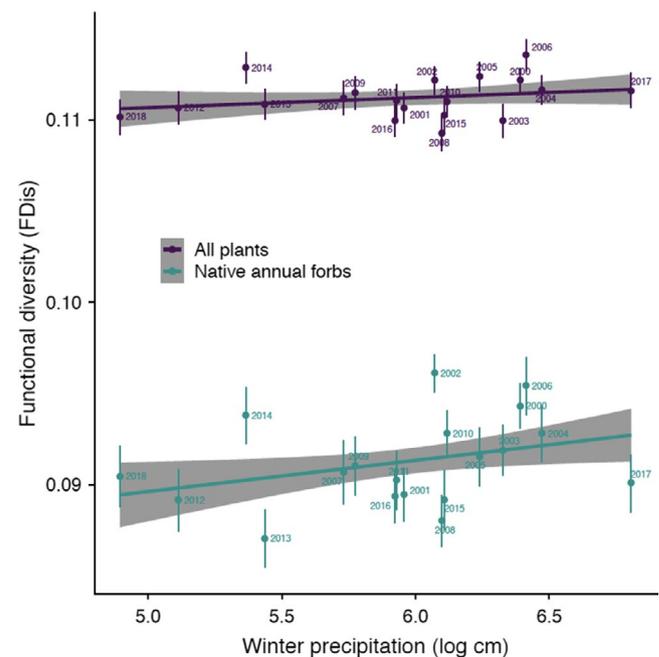
without SLA did not decline over the course of the study for the entire plant community ($p = 0.174$), though it did decline for native annual forbs ($p < 0.001$).

3.2 | Functional diversity as a driver

Initial (year 2000) functional diversity was not significantly related to change in species richness over the course of the study for either the entire plant community ($p = 0.496$, $R_C^2 = 0.006$) or for native annual forbs only ($p = 0.431$, $R_C^2 = 0.008$; Figure 3; Table S3). Sites with higher initial community mean SLA underwent greater losses of species richness both for all plants ($p < 0.001$, $R_C^2 = 0.186$) and for native annual forbs only ($p < 0.001$, $R_C^2 = 0.204$; Figure 3) over the course of the study. Initial functional diversity did not have a significant effect on the coefficient of variation of total species richness ($p = 0.867$, $R^2 < 0.001$) or exotic species richness ($p = 0.14$, $R^2 = 0.028$). There was a weak and marginally significant negative correlation of initial functional diversity with the coefficient of variation in total plant cover ($p = 0.053$, $R^2 = 0.047$). Initial functional diversity trended higher on serpentine than on non-serpentine soils (Scaled serpentine mean: 0.211, *SD*: 0.996; scaled non-serpentine mean: −0.191, *SD*: 0.975; $p = 0.07$).

4 | DISCUSSION

We found strong evidence that community functional diversity can be eroded during long-term community change. Our trait-based measures of functional diversity declined significantly as

FIGURE 1 Functional diversity declined over the course of the study for both the entire plant community ($p < 0.037$, $R_C^2 = 0.510$) and for native annual forbs only ($p < 0.001$, $R_C^2 = 0.487$) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 Functional diversity for all plants showed a positive trend with winter precipitation ($p = 0.068$, $R_C^2 = 0.572$), and there was a significant and positive relationship between functional diversity of native annual forbs and winter precipitation ($p < 0.001$, $R_C^2 = 0.743$) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 There was no relationship between initial (year 2000) functional diversity and change in species richness over the course of the study for all plants ($p = 0.496$, $R^2_C = 0.006$, upper left) or for native annual forbs only ($p = 0.431$, $R^2_C = 0.008$, upper right). Sites with higher initial community mean SLA, however, experienced more negative changes in species richness for both all plants ($p < 0.001$, $R^2_C = 0.186$, lower left) and native annual forbs ($p < 0.001$, $R^2_C = 0.204$, lower right) than sites with lower initial community mean SLA [Colour figure can be viewed at wileyonlinelibrary.com]
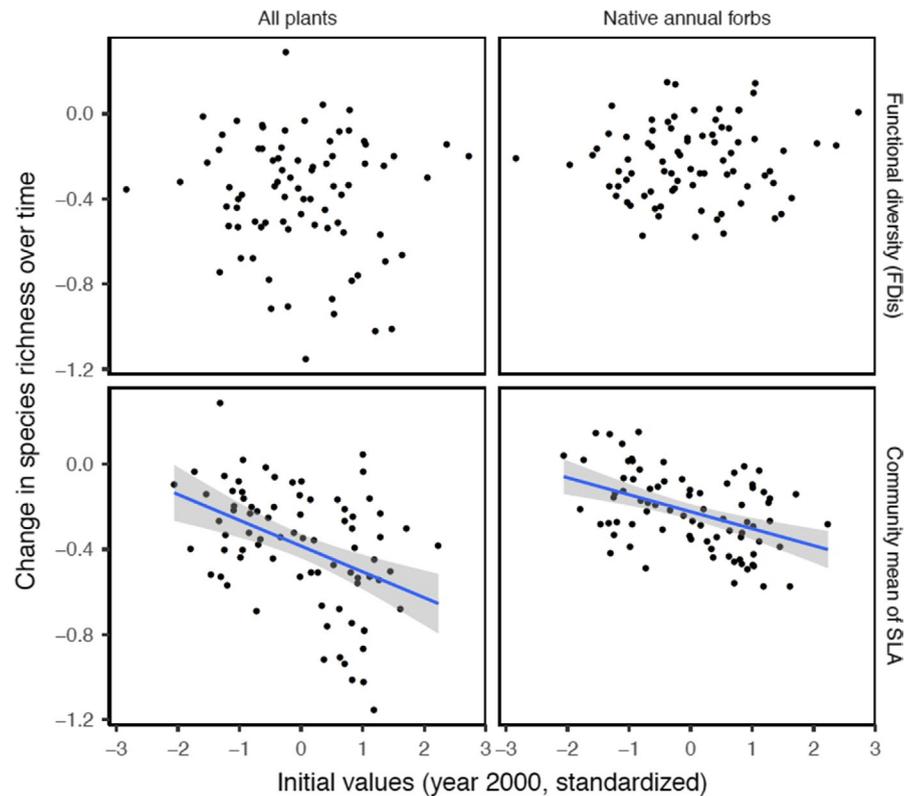
drought-intolerant native annual forbs were lost during a prolonged period of abnormally dry winters. Sequences of multiyear drought punctuated by extreme rainfall events, such as occurred during our study period, are an increasingly prevalent feature of forecasts for California and elsewhere (Swain, Langenbrunner, Neelin, & Hall, 2018; Wang, Yoon, Becker, & Gillies, 2017), and plant communities may not readily recover from drought-induced changes (Harrison et al., 2018). While previous analyses have hinted at the possibility that climatic change can erode functional diversity through trait-selective losses of taxonomic diversity (Ordonez & Svenning, 2017), our study presents some of the first evidence that modern-day climatic trends may have contributed to such an outcome. Given the longstanding paradigm linking functional diversity to ecosystem function (Cadotte et al., 2011; Diaz & Cabido, 2001), our result suggests the possibility that functional diversity losses associated with climate could have broader implications, potentially affecting multiple trophic levels.

We found little evidence for functional diversity as a driver of community change, in spite of considerable theory linking functional diversity to community resilience (Folke et al., 2004; Standish et al., 2014). Trait-based functional diversity at the beginning of our study did not predict the magnitude of change in species richness, year-to year variance in species richness, or year-to-year variance in exotic richness over the course of the study. Higher initial functional diversity did weakly (marginally significantly) correlate with less year-to-year variation in plant cover, however. One of the strongest proposed mechanisms linking functional diversity to stability is the portfolio effect, under which trait variation creates variation among species in their responses to disturbances, thus leading to lower variation in aggregate community properties such as biomass in response to disturbances

(reviewed by Schindler, Armstrong, & Reed, 2015). This paradigm may not have been very applicable to our study system, in which the community changed in a directional fashion through selective losses of species. Interestingly, much of the previous research linking functional diversity to community resilience has focused on functional groups or other categorical traits (e.g. growth from, reproductive mode, etc.; Diaz & Cabido, 2001; Spasojevic et al., 2016; Walker, Kinzig, & Langridge, 1999), and there is less evidence that functional diversity confers resilience when it is defined by continuous traits.

Although initial functional diversity did not influence changes in species richness, we nonetheless found some evidence that initial composition predicted changes in species richness over the course of the study. Communities with higher initial mean SLA experienced greater losses of species richness, apparently because they contained more species with trait values conferring drought susceptibility. This suggests that the initial richness (or abundance) of species with stress-sensitive traits can be more important for determining community change than overall functional diversity. While mean trait values have been previously shown to be as important or more important than functional diversity for resilience (Barkaoui et al., 2016; Riva et al., 2017), documenting this pattern over a 19-year period provides some of the strongest evidence yet that mean trait values can be a stronger predictor of community shifts under climate change than functional diversity per se.

Functional diversity was correlated with community mean SLA in the grassland plant communities we observed, suggesting that responses of functional diversity are not necessarily independent of shifts in mean trait values. Furthermore, when functional diversity was calculated without SLA it did not change significantly

over the period of the study, at least when calculated for the entire plant community. These results suggest that drivers such as drought may alter communities via trait-specific effects on individual species that, in turn, give rise to patterns in community properties such as functional diversity. From this perspective, functional diversity could be viewed as an artefact of shifts in community mean trait values.

Our findings suggest that the relative importance of functional diversity per se for community resilience remains incompletely understood. Despite the widely expressed hypothesis that functional diversity may confer community resilience (Folke et al., 2004; Standish et al., 2014), there has been little consideration of the degree to which functional diversity is independent from shifts in mean trait values. Since correlations between mean trait values and functional diversity may be common, however (e.g. Gazol & Camarero, 2016), future research on unmanipulated systems should focus on statistically disentangling patterns in individual traits (e.g. shifts in community mean SLA) from multivariate properties such as functional diversity indices.

AUTHORS' CONTRIBUTIONS

S.H. designed the study and conducted field data collection. D.L., J.E.D.M. and M.L. conducted analyses. D.L. and M.L. made the figures. J.E.D.M. led writing the manuscript, and all authors contributed to writing and editing.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: http://doi.org/10.5061/dryad.17c6hj3 (Miller et al., 2019)

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REFERENCES

Barkaoui, K., Roumet, C., & Volaire, F. (2016). Mean root trait more than root trait diversity determines drought resilience in native and cultivated Mediterranean grass mixtures. *Agriculture, Ecosystems and Environment*, *231*, 122–132. https://doi.org/10.1016/j.agee.2016.06.035

Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., ... Meyer, C. W. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 15144–15148. https://doi.org/10.1073/pnas.0505734102

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*, 1079–1087.

Cook, B. I., Ault, T. R., & Smerdon, J. E. (2015). Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances*, *1*, e1400082. https://doi.org/10.1126/sciadv.1400082

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., ... Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*, 335.

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., ... Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology & Evolution*, *2*, 1579–1587.

Diaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*, 646–655. https://doi.org/10.1016/s0169-5347(01)02283-2

Dorji, T., Totland, Ø., Moe, S. R., Hopping, K. A., Pan, J., & Klein, J. A. (2015). Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Global Change Biology*, *19*, 459–472. https://doi.org/10.1111/gcb.12059

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., & Holling, C. S. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 557–581. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711

Gazol, A., & Camarero, J. J. (2016). Functional diversity enhances silver fir growth resilience to an extreme drought. *Journal of Ecology*, *104*, 1063–1075. https://doi.org/10.1111/1365-2745.12575

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., ... Jump, A. S. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, *20*, 539–553. https://doi.org/10.1111/ele.12748

Hallett, L. M., Stein, C., & Suding, K. N. (2017). Functional diversity increases ecological stability in a grazed grassland. *Oecologia*, *183*, 831–840. https://doi.org/10.1007/s00442-016-3802-3

Harrison, S. P., Gornish, E. S., & Copeland, S. (2015). Climate-driven diversity loss in a grassland community. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 8672–8677. https://doi.org/10.1073/pnas.1502074112

Harrison, S. P., LaForgia, M. L., & Latimer, A. M. (2018). Climate-driven diversity change in annual grasslands: Drought plus deluge does not equal normal. *Global Change Biology*, *24*, 1782–1792. https://doi.org/10.1111/gcb.14018

Huang, J., Yu, H., Guan, X., Wang, G., & Guo, R. (2016). Accelerated dryland expansion under climate change. *Nature Climate Change*, *6*, 166–171. https://doi.org/10.1038/nclimate2837

Kew Royal Botanic Gardens. (2015). *Seed information database*. Retrieved from https://data.kew.org/sid/

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., ... Ruiz-Benito, P. (2015). Plant functional traits have globally consistent effects on competition. *Nature*, *529*, 1–15.

Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.

Laliberté, É., Legendre, P., & Shipley, B. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology.

Miller, J. E. D., Li, D., Laforgia, M., & Harrison, S. (2019). Data from: Functional diversity is a passenger but not driver of drought-related plant diversity losses in annual grasslands. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.17c6hj3

Mori, A. S., Furukawa, T., & Sasaki, T. (2013). Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews*, *88*, 349–364.

Ordonez, A., & Svenning, J. C. (2017). Consistent role of Quaternary climate change in shaping current plant functional diversity patterns across European plant orders. *Scientific Reports*, *7*, 1–11. https://doi.org/10.1038/srep42988

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Luis, J., … Grabherr, G. (2012). Supplementary materials for recent plant diversity changes on Europe ' s mountain summits. *Science*, *353*, 353–356.

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D.; R Core Team. (2018). nlme: Linear and nonlinear mixed effects models. Vienna, Austria: R Core Team.

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Core Team.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., & Westoby, M.. (2003). The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*, *164*, S143–S164.

Reich, P. B. (2014). The world-wide "fast-slow" plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301.

Riva, E. G. D., Lloret, F., Pérez-Ramos, I. M., Marañón, T., Saura-Mas, S., & Díaz-Delgado, R. (2017). The importance of functional diversity in the stability of Mediterranean Shrubland Communities after the impact of extreme climatic events. *Journal of Plant Ecology*, *10*, 281–293.

Sakschewski, B., Von Bloh, W., Boit, A., Poorter, L., Peña-Claros, M., Heinke, J., … Thonicke, K. (2016). Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change*, *6*, 1032–1036.

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, *13*, 257–263. https://doi.org/10.1890/140275

Schlaepfer, D. R., Bradford, J. B., Lauenroth, W. K., Munson, S. M., Tietjen, B., Hall, S. A., … Jamiyansharav, K. (2017). Climate change reduces extent of temperate drylands and intensifies drought in deep soils. *Nature Communications*, *8*, 1–9. https://doi.org/10.1038/ncomms14196

Sommer, J. H., Kreft, H., Kier, G., Jetz, W., Mutke, J., & Barthlott, W. (2010). Projected impacts of Climate change on regional capacities for global plant species richness. *Proceedings of the National Academy of Sciences of the United States of America*, *277*, 2271–2280.

Spasojevic, M. J., Bahlai, C. A., Bradley, B. A., Butterfield, B. J., Tuanmu, M. N., Sistla, S., … Suding, K. N. (2016). Scaling up the diversity-resilience relationship with trait databases and remote sensing data: The recovery of productivity after wildfire. *Global Change Biology*, *22*, 1421–1432. https://doi.org/10.1111/gcb.13174

Standish, R. J., Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T., Suding, K. N., Battaglia, L. L., … Thomas, P. A. (2014). Resilience in ecology: Abstraction, distraction, or where the action is? *Biological Conservation*, *177*, 43–51. https://doi.org/10.1016/j.biocon.2014.06.008

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., … Navas, M. L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Swain, D. L., Langenbrunner, B., Neelin, J. D., & Hall, A. (2018). Increasing precipitation volatility in twenty-first-century California. *Nature Climate Change*, *8*, 427–433.

Walker, B., Kinzig, A., & Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: The nature and significance of dominant and minor species. *Ecosystems*, *2*, 95–113.

Wang, S.-Y.-S., Yoon, J.-H., Becker, E., & Gillies, R. (2017). California from drought to deluge. *Nature Climate Change*, *7*, 465–468. https://doi.org/10.1038/nclimate3330

Westoby, M., Leishman, M., & Lord, J. (1996). Comparitive ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *351*, 1309–1318. https://doi.org/10.1098/rstb.1996.0114

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. https://doi.org/10.1038/nature02403

SUPPORTING INFORMATION

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