Climate-driven diversity loss in a grassland community

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Local ecological communities represent the scale at which species coexist and share resources, and at which diversity has been experimentally shown to underlie stability, productivity, invasion resistance, and other desirable community properties. Globally, community diversity shows a mixture of increases and decreases over recent decades, and these changes have relatively seldom been linked to climatic trends. In a heterogeneous California grassland, we documented declining plant diversity from 2000 to 2014 at both the local community (5 m^2) and landscape (27 km^2) scales, across multiple functional groups and soil environments. Communities became particularly poorer in native annual forbs, which are present as small seedlings in midwinter; within native annual forbs, community composition changed toward lower representation of species with a trait indicating drought intolerance (high specific leaf area). Time series models linked diversity decline to the significant decrease in midwinter precipitation. Livestock grazing history, fire, succession, N deposition, and increases in exotic species could be ruled out as contributing causes. This finding is among the first demonstrations to our knowledge of climate-driven directional loss of species diversity in ecological communities in a natural (nonexperimental) setting. Such diversity losses, which may also foreshadow larger-scale extinctions, may be especially likely in semiarid regions that are undergoing climatic trends toward higher aridity and lower productivity.

climate change | aridification | drought | grasslands | biodiversity

Large-scale elevational and latitudinal range shifts, altered seasonal timing, and disrupted interactions among interdependent species are well-known consequences of recent global warming, all of which are predicted to intensify in coming decades and to be accompanied by increasing rates of global extinction (1–4). Consequences of rapid climate change for the diversity of local ecological communities are far less clear; diversity might increase or decrease at any given location, depending on the particular nature of climatic changes and the potential for dispersal (5–8). For two decades, gains in plant species richness have been observed on European mountain summits in boreal-temperate regions, where climatic warming has led to longer growing seasons and higher productivity (5), and where steep topography may have facilitated upward dispersal from lower elevations (6, 7). However, in one of the first documentations of the opposite trend, declines in species richness were reported on 10 European mountain summits, mostly in the Mediterranean region where warming has led to more severe climatic water deficits (8). Globally, the species diversity of ecological communities has shown neither consistent increases nor decreases in recent decades (9, 10). It remains unknown how widely across biomes, and at what spatial scales, climatically driven losses of plant community diversity may be expected in the near future. Diversity at relatively local spatial scales has been linked experimentally to resource use efficiency, productivity, temporal stability, resistance to invasion, and other desirable functional properties (11–13). To the extent that climate is causing declining diversity at local scales, there is increased support for concerns about ecosystem service loss, and reasons to expect larger-scale extinctions in the not too distant future.

Climatic drying (aridification), arising from both increases in temperature and declines in precipitation during the growing season, is a major facet of contemporary and anticipated climate

change throughout the world's arid and semiarid climates (14–19). Aridification in the western United States has already been linked to large-scale tree dieoffs and other vegetation changes (20–23). In California, where overall aridity has increased in recent decades (18) and coastal and inland fog have declined dramatically (24, 25), aridification is predicted to dominate the effects of climate change on natural vegetation over the coming century (18, 19, 26). Although directional declines in species richness in western US grasslands in response to long-term drying trends are not yet documented, they may be expected based on evidence that grassland species richness is higher in wetter than drier years, geographical locations, and experimental treatments (27–29). Seed dormancy, especially by annuals, is likely an important facet of short-term fluctuations in grassland species richness in response to water availability (e.g., ref. 28); however, dormancy during dry years is clearly not a strategy by which species can survive longer-term, directional drying of the climate.

We monitored grassland species richness for 15 y (2000–2014) at 80 sites in a heterogeneous California landscape. Thirty-eight sites were on infertile serpentine soils, considered an important refuge for native species, and 42 sites were on fertile soils dominated by exotic grasses. Each site consisted of five, 1 m^2 quadrats at which species presence or absence (2000–2014) and visual estimates of species cover (2006–2014) were recorded in April and June annually (see Dataset S1 for a complete species list). Native annual forbs were the most numerous group (110 of 237 species) although they were individually uncommon (median cover 2%, median occupancy five sites). These species germinate in late fall to early winter and most of them flower in April–May, although a few flower earlier or later. Local richness of native annual forbs was higher on serpentine soils (mean 17 native annual forbs of 29 total species) than on more fertile soils (mean 9 native annual forbs of 24 total species). Livestock grazing on half the sites slightly enhanced local

Significance

Whereas a dominant conservation paradigm proposes that species are being lost from ecological communities with a consequent loss of ecosystem function, recent analyses have concluded there is no globally consistent trend toward lower community diversity. In a study of Californian grassland communities, we show that 15 years of climatic drying—consistent with the forecasts for this and other semiarid regions under climate change—have led to directional losses of plant species richness, especially of native annual forb ("wildflower") species with traits indicative of low drought tolerance. Although many anthropogenic impacts may increase or not affect community diversity, our result underlines that declining plant community diversity may be especially likely in climates that are becoming more arid and less productive.

species richness before ceasing in 2001, and a fire affecting some sites in 1999 had a modest positive effect on local species richness in 2000 (ref. 30; *Methods*). Local species richness was higher in years of higher rainfall (31, 32), as has been seen in other studies in similar grasslands (e.g., ref. 28). The study area lies within a region that has warmed and dried in recent decades (18, 19).

We analyzed trends in grassland species richness at the local (5 m^2) and landscape scales (27 km^2, all 80 sites). We compared trends among native and exotic species, sites on fertile (non-serpentine) and infertile (serpentine) soils, and sites with and without histories of livestock grazing. We similarly analyzed time trends in climatic variables recorded at the site, focusing on precipitation because of its well-documented effects on grassland diversity, but also including temperature, solar radiation (an inverse measure of cloudiness), and humidity, because of the potential of these variables to either ameliorate or exacerbate the effects of declining precipitation. We examined trends in these climatic variables for the whole rainy season (Sep–Jun) and its early (Sep–Nov), middle (Dec–Feb), and late (Mar–Jun) thirds; the middle period (Dec–Feb) is especially critical for native annual forbs, which are then present as small seedlings dependent on shallow soil moisture. Upon identifying significant time trends in species richness and in precipitation, we used time-series models (as in ref. 27) to test for a direct link between richness and precipitation.

To further explore the community consequences of aridification, we examined plant functional traits (33). Variation among species in mean specific leaf area (SLA; leaf area/dry mass; or its inverse, termed leaf mass per unit area) has been found to correlate well with among-species variation in key physiological attributes such as leaf longevity (LL), water use efficiency (WUE), and relative growth rate (RGR). Species with high SLA and RGR, and low LL and WUE, are more prevalent in wetter climates (34) and in wetter years (35) and tend to increase disproportionately in response to experimental watering (36) and natural precipitation increase (37). Several previous studies have found that high-SLA species are especially vulnerable to decline or loss under aridification (38, 39).

We hypothesized that aridification would lead to grassland communities poorer in overall species diversity. We also hypothesized that community functional composition would change, such that the native annual forb component would show a lower community mean value of SLA, consistent with the disproportionate local disappearance of drought-intolerant species. Because high SLA is linked to rapid litter decomposition and nutrient cycling (40), such a shift in community mean trait values could affect community function. We tested for time trends in community mean SLA, and for a direct link between precipitation and community mean SLA, using the same models as for species richness.

Results

From 2000 to 2014, species richness declined at both the local community scale (5 m^2; estimate = −0.02, $z = −8.40$, $P < 0.001$; Fig. 1) and the landscape scale (27 km^2, all 80 sites; estimate = −0.02, $z = −2.89$, $P = 0.003$; Fig. 2). Native annual forbs dominated this decline, although it was shared to lesser extents by other functional groups (Fig. 1 and Table S1). Rather than large decreases in a few common species, declining species richness at the local scale was attributable to small net changes in site occupancy by a large number of species (Fig. 3). From 2006 to 2014, when cover data were available, there were also declining trends in the Shannon–Weiner index of community diversity, which weights species by their relative abundances (serpentine soils, estimate = −0.01, $t = −1.74$, $P = 0.08$; nonserpentine soils, estimate = −0.02, $t = −2.48$, $P = 0.01$).

For total (native plus exotic) local species richness, the best model included terms for year, soil, grazing, year × soil, and soil × grazing. Declines in local richness were individually significant on nonserpentine (estimate = −0.02, $z = −9.02$, $P < 0.001$) and serpentine soils (estimate = −0.005, $z = −2.82$, $P = 0.005$) and in both formerly grazed (estimate = −0.01, $z = −6.95$, $P < 0.001$) and ungrazed sites (estimate = −0.008, $z = −5.01$, $P < 0.001$).

Native richness at the local scale showed similar declining trends; the best model included year, soil, and grazing, and native species declined on both nonserpentine (estimate = −0.02, $z = −8.46$,

Fig. 1. Mean (+SE) species richness at the local scale, 2000–2014, for the most common functional groups (note that "other exotics" includes perennial forbs and perennial grasses).
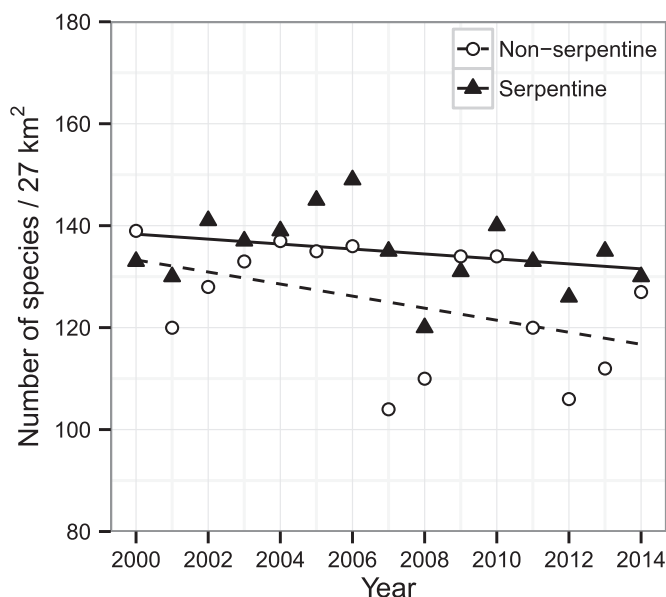
Fig. 2. Total species richness at the regional scale, 2000–2014.

$P < 0.001$) and serpentine soils (estimate $= -0.01$, $z = -4.03$, $P < 0.001$), and in both formerly grazed (estimate $= -0.02$, $z = -5.88$, $P < 0.001$) and ungrazed sites (estimate $= -0.01$, $z = -5.93$, $P < 0.001$). Exotic species richness did not increase in any habitat. The best model for exotic species richness included terms for year, soil, grazing, year × soil, and year × grazing, and soil × grazing; exotic species richness declined on nonserpentine soils (estimate $= -0.01$, $z = -4.34$, $P < 0.001$), and within nonserpentine soils it declined on both formerly grazed (estimate $= -0.02$, $z = -4.23$, $P < 0.001$) and ungrazed sites (estimate $= -0.01$, $z = -1.95$, $P = 0.05$).

Many causes of grassland diversity decline (e.g., N deposition, grazing cessation) would be expected to operate through an increase in exotic species cover; however, for the years with cover data (2006–2014), exotic species cover showed a declining trend (estimate $= -0.01$, $t = -0.11$, $P < 0.001$) that did not interact with soil type or grazing.

Precipitation declined significantly in the midwinter period (Dec–Feb), when annual forbs are present as shallow-rooted seedlings (estimate $= -1.90$ cm/yr, $P = 0.015$; Fig. 4). In a time-series model, midwinter precipitation was a significant direct predictor of local species richness (estimate $= 0.03$, $t = 8.25$, $P < 0.001$). Other climatic variables either did not change significantly, or changed in directions that were also consistent with greater aridity. In particular, there was an increase in solar radiation (i.e., decrease in cloudiness) in both fall (Sep–Nov) and midwinter, and a decrease in relative humidity in spring (Mar–Jun) (Table S2 and Figs. S1 and S2).

For native annual forbs, which dominated the decline in species richness (estimate $= -0.019$, $z = -8.97$, $P < 0.001$; Fig. 1), precipitation was again a significant predictor of richness in an autoregressive time-series model (estimate $= 0.02$, $t = 11.26$, $P < 0.001$). Within this group there was a significant decline in unweighted community mean specific leaf area (SLA; estimate $= -1.07$, $t = -2.26$, $P = 0.02$; Fig. 5). Abundance-weighted community mean SLA showed an even steeper decline with time (Fig. 5), although this trend was not significant with only 10 y of data (estimate $= -12.03$, $t = -0.896$, $P = 0.37$). In a time-series model, midwinter precipitation was a significant direct predictor of the unweighted community mean SLA of native annual forbs (estimate $= 0.04$, $t = 2.17$, $P = 0.02$; Fig. 5), indicating that climatic drying was linked to the tendency for communities to

become disproportionately poorer in drought-intolerant, high-SLA native annual forbs.

Trajectories of individual species over time were highly stochastic; annual probabilities of local extirpation and reappearance for native annual forbs on a per-site basis were, respectively, 0.306 ± 0.123 (SE) and 0.274 ± 0.067 ($t = 2.081$, $P = 0.04$). However, native annual forbs with above-median SLA for a given site had higher mean annual probabilities of local extirpation than those with below-median SLA for a given site (0.354 ± 0.189 versus 0.259 ± 0.103; $t = 3.930$, $P < 0.001$); likewise, those with above-median SLA for a given site had lower mean annual probabilities of local reappearance than species with below-median SLA for a given site (0.209 ± 0.060 versus 0.241 ± 0.079; $t = 2.930$, $P = 0.004$). These relationships of SLA to annual rates of turnover were not evident when sites were pooled, indicating that the fate of any given native annual forb species varied depending on the ecological characteristics of the sites it occupied.

Discussion

We found a decline in diversity consistent with observed climatic trends, at a localized scale that has few precedents in the literature on effects of current climate change on natural communities. Diversity loss also transcended the local scale and was seen at the scale of the whole study area. The directional decline in species richness we observed is consistent with the known responses of grassland diversity to experimental alterations, interannual fluctuations, and geographic variation in moisture availability (27–29, 31, 32). The diversity trend was caused primarily by a loss of native annual forbs, which germinate in winter and are expected to be especially sensitive to shallow soil moisture at this time, although other groups of species also either decreased or did not increase in diversity. Like several other recent studies in aridifying climates (38, 39), we found that communities shifted toward lower prevalences of drought-intolerant, high-SLA species, consistent with general expectations based on plant physiology (33–37) and evidently driven by the declining midwinter precipitation at our site. Although some degree of recovery of diversity is possible under a future wetter climate, the directional component that we observed over 15 y clearly transcends "normal" interannual variation.

Our results are consistent with the recent finding that plant species richness has declined on European mountaintops in semiarid climates, in contrast to the species richness increases that have been seen on mountain summits in boreal-temperate
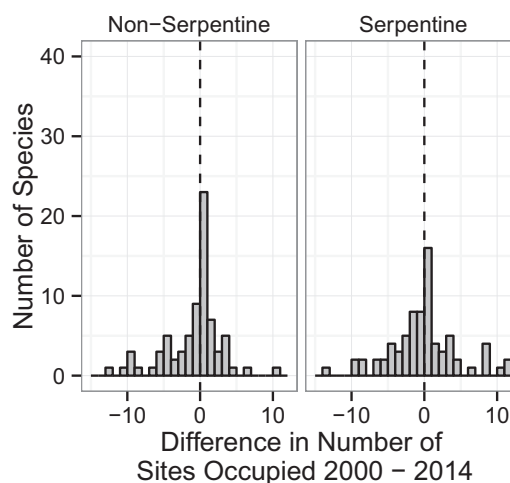

Fig. 3. Frequency distribution of changes in site occupancy by native annual forbs.

Fig. 4. Total midwinter (Dec–Feb) precipitation at the study site, 2000–2014.

Europe (8). Like the authors of that study, we attribute the observed decline in diversity to the deteriorating suitability of the drying environment for resident species, coupled with the unavailability of nearby species better adapted to the new climate to serve as immigrants. In addition to extending this finding beyond mountaintops and into to a semiarid grassland biome, our study also identifies the trend at a smaller spatial scale. The European study reported declines in plant species richness on entire mountaintops (i.e., the area within 10 vertical m of the summit). In our results, for example, the mean loss of roughly one-third of the native annual forbs from 5 m² of nonserpentine grassland, suggest that climate-driven diversity decline is occurring at a scale that is visible to the relatively casual observer. To the extent that the loss of diversity at small scales affects community function, as suggested by an extensive experimental literature (e.g.,

refs. 12 and 13), our result also suggests that future grassland communities may be less resilient, productive, invasion-resistant, or capable of retaining nutrients.

We considered but found no support for other causes of diversity loss. Major known causes of grassland change in northern California include grazing, fire, succession to shrublands following the removal of grazing, increased invasion of exotic grasses caused by N deposition, and unusual weather events (19). We found roughly equal diversity declines in formerly grazed and ungrazed sites, and the effects of fire in our system were already shown to be short-lived. Shrub encroachment occurs mainly in coastal grasslands (19) and is negligible in this arid interior region. Our study region is free of significant atmospheric N deposition (41, 42), and in any case, we found no increase in cover or richness of exotic species. Diversity declines were significant whether we included 2013–2014, a period of unprecedented drought. The disproportionate loss of native annual forbs with high mean SLA was both consistent with the climatic trends at the site and inconsistent with other known causes of grassland change. Our results suggest that climatic drying may be as significant as other, better-known sources of declining grassland diversity.

Climate change, like other impacts on community diversity, may exert indirect and direct effects. Previous studies in similar grasslands suggest that the indirect effects of an enhanced water supply may sometimes include increased competitive dominance by exotic annual grasses, which may suppress native annual forbs in the following year because of the germination-inhibiting effect of their dead biomass (43, 44). Aridification might thus be expected to cause positive indirect effects on grassland diversity, but our findings do not support this expectation. Our results are, however, consistent with studies concluding that the direct positive effects of water supply on annual grasslands tend to outweigh the indirect negative ones (29, 45).

The climatic changes we observed of decreasing midwinter precipitation, humidity, and cloud cover (i.e., increase in solar radiation), all during the fall-to-spring growing season, are broadly consistent with the scenario of aridification that has been observed over the past century and is forecast to intensify over the next century in our study region (18). The observed changes are not identical to the forecasts, in that we did not see significant

Fig. 5. Mean (+SE) SLA of native annual forbs versus year (*A*) and midwinter precipitation (*B*).

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temperature increases, the major driver of anticipated future increases in aridity. Declining precipitation, which we observed, is predicted in some but not all current climate forecasts for California (18). In any case, given that precipitation, cloud cover, humidity, and temperature all combine to determine the water stress experienced by plants, the community changes we observed should be a reasonable model for those to be expected in coming decades. Taken together, and combined with the large literature finding that plant and animal species richness are highest in productive climates (e.g., ref. 46), our study and other recent results (8) suggest that declining community diversity may be especially likely in water-limited climates as these become more arid and less productive.

Methods

Study System. 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 (N 38°52′, W 122°26′). The climate is Mediterranean with mean annual temperatures of 8 °C in January and 25 °C in July, and mean annual rainfall of 62 cm, falling mainly in Oct–Apr. Substrates include fertile soils derived from volcanic and sedimentary rocks, and infertile, Mg-rich, and nutrient-poor soils derived from serpentine rock. Grasslands are dominated by annual species, primarily native and exotic annual forbs (nongrasses) that flower in April–July, in addition to approximately 10 species of exotic (Eurasian) annual grasses that flower in May–Jun.

Community Data. Species composition was sampled annually in April and June. Each site consisted of five permanently marked 1 m^2 quadrats evenly spaced on a 40-m transect. Sites were ≥50 m apart and were well interspersed. To measure community composition, we annually recorded species presence or absence (2000–2014) and visual estimates of species cover (2006–2014). In previous analyses of these data, species diversity was higher in wetter years, and species present in drier years were subsets of those found in wetter years (31, 32).

Human Impacts. When first established, half of the sites on each soil type were grazed by livestock and the other half had been ungrazed for >20 y. Grazing followed regional practices, with one cow-calf pair per 25 ha in winter and spring. In 2001, the final year of grazing, grazed sites averaged 12.3% higher species richness per m^2 than ungrazed sites. Wildfire burned 35 sites in Oct 1999, and burned sites averaged 11.3% higher species richness per m^{-2} than unburned sites in 2000, but this difference had disappeared by 2001 (30).

The nearest National Atmospheric Deposition Program monitoring site is Hopland Field Station (N 39°00′, W 123°05′), 58 km WNW of our study location. Like our study location, it is >100 km N of the San Francisco Bay Area and not downwind of metropolitan areas. Mean N deposition rates from 1980 to 2012 were 0.2–1.8 kg·ha^{-1}·yr^{-1} with a mean of 0.7 and a downward time trend (40). These rates are well below the 6 kg·ha^{-1}·yr^{-1} considered a minimum threshold for triggering change in California grasslands (41).

Trait Data. We measured SLA (mm^{2}g^{-1} of dry mass) because of its widely documented links to water balance (33–37) and to the community-level consequences of aridification (38, 39). For clarity in interpretation, we focused this analysis on native annual forbs, the functional group largely responsible for the time trend in species richness. In 2010, we measured SLA by following standard protocols (33) on 10 individuals per species (Dataset S1). For each site and year, we then summed the SLA of each native annual forb

present and divided this sum by the number of species. Temporal changes in these mean SLA values reflect differential gains and losses of native annual forb species with high or low SLA. This approach allows us to ask whether communities became disproportionately impoverished in native annual forb species with relatively high SLA (similarly to refs. 38 and 39; note that this differs from the goal of studying all inter- and intraspecific sources of variation in SLA, as has been done in, e.g., ref. 37). We also repeated this analysis by using abundance-weighted community mean SLA (as in ref. 39), which was available only for 2006–2014.

Climate Data. Monthly data on climate came from the Knoxville Creek weather station of the Western Regional Climate Center (47), located near the center of our 2,776-ha (roughly 4 × 7 km) study landscape.

Analyses. To ask whether total species richness at the local (5 m^2) and landscape (80 sites, 27 km^2) scales declined over time, we used generalized linear models with time (year) as the predictor, site as a random factor, and a Poisson error structure because the data are counts (48). To next ask whether time trends in either total (native plus exotic) species richness, native or exotic species richness, exotic species cover (years 2006–2014 only), or community mean SLA differed between soils or depended on prior grazing, we used multivariate models with year, soil type (serpentine or nonserpentine), grazing history (formerly grazed or ungrazed), and their interactions as predictors, and an error term for site. For the multivariate analyses, we started with models that included all interaction terms and then used automated backward stepwise model selection to find the most parsimonious models. Variables were considered for the final models only if their significance level in the full model was <5%. The selection procedure used exact AIC values, and k = 2 degrees of freedom were used for the penalty (49, 50).

When the best models identified by this procedure included significant effects of year (i.e., significant time trends), and/or significant interactions between year and either soil type or grazing history (i.e., the time trends differed between soils or between formerly grazed and ungrazed sites), we used linear regressions to determine the sign of the time trends and their significance in each habitat type (serpentine or nonserpentine, formerly grazed or ungrazed).

For climate data, we used simple linear regressions with year as the predictor. We considered means, minima, and maxima of daily temperature and relative humidity, mean daily solar radiation, and total precipitation, for both the full water year and its early, middle, and late components (Sep–Nov, Dec–Feb, Mar–Jun).

Our time series model to test for a direct effect on species richness of midwinter precipitation (the climate variable expected to affect seedling mortality in this system, and found to be declining at our site) was a linear mixed effects model including midwinter precipitation (fixed factor) and site (random factor), with an autoregressive error structure for each plot to account for previous year effects on current year response (27). We used the same model to test for a direct effect of midwinter precipitation on the unweighted community mean of native annual forb SLA.

Analyses were conducted in R version 3.1.1 (51) by using the MASS and nlme packages (52).

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