

Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse

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Long-term and persistent human disturbances have simultaneously altered the stability and diversity of ecological systems, with disturbances directly reducing functional attributes such as invasion resistance, while eliminating the buffering effects of high species diversity^{1–4}. Theory predicts that this combination of environmental change and diversity loss increases the risk of abrupt and potentially irreversible ecosystem collapse^{1–3,5–7}, but long-term empirical evidence from natural systems is lacking. Here we demonstrate this relationship in a degraded but species-rich pyrogenic grassland in which the combined effects of fire suppression, invasion and trophic collapse have created a species-poor grassland that is highly productive, resilient to yearly climatic fluctuations, and resistant to invasion, but vulnerable to rapid collapse after the re-introduction of fire. We initially show how human disturbance has created a negative relationship between diversity and function, contrary to theoretical predictions^{3,4}. Fire prevention since the mid-nineteenth century is associated with the loss of plant species but it has stabilized high-yield annual production and invasion resistance, comparable to a managed high-yield low-diversity agricultural system. In managing for fire suppression, however, a hidden vulnerability to sudden environmental change emerges that is explained by the elimination of the buffering effects of high species diversity. With the re-introduction of fire, grasslands only persist in areas with remnant concentrations of native species, in which a range of rare and mostly functionally redundant plants proliferate after burning and prevent extensive invasion including a rapid conversion towards woodland. This research shows how biodiversity can be crucial for ecosystem stability despite appearing functionally insignificant beforehand, a relationship probably applicable to many ecosystems given the globally prevalent combination of intensive long-term land management and species loss.

Biodiversity can stabilize ecological systems by functional complementarity, with different species thriving under different conditions thereby buffering the effects of environmental change^{1–5}. Despite an often demonstrated positive correlation between diversity and stability, however, the generality of this relationship remains unclear in natural systems, especially in those under persistent anthropogenic influences^{1,8,9}. Human land management is often persistent, by intentional (for example, fire suppression and overfishing) or inadvertent (for example, nitrogen pollution) disturbances that homogenize both resident diversity and environmental conditions. Persistent disturbances obscure diversity–stability relationships because they can affect ecosystem function independently of diversity^{1–3}, as when overgrazing directly decreases production and provides opportunities for invasion^{1,2}. Because persistent disturbances can also drive species loss, false positives may arise between diversity and ecosystem function, in which reductions in diversity and function are correlated but have weak mechanistic connections.

The homogenizing effect of human activity on environmental conditions and diversity may also increase the risk of abrupt and potentially irreversible changes after disturbance pulses, even when systems appear stable beforehand^{5–7}. The question of whether simpler systems

are more or less resistant to disturbance has characterized diversity–stability research for decades^{4,10–13}. Recent research typically supports the latter model, but data are often derived from shorter-term studies in constructed experimental communities⁴. It is unclear, however, whether these stability-regulating mechanisms operate in a similar manner in environmentally heterogeneous natural systems^{2,3}, and whether all measures of stability respond similarly in different environmental contexts (for example, the presence or absence of disturbance)¹. The stabilization of functional attributes after abrupt disturbances is assumed to derive from the asynchronous population-level responses of disturbance-resistant species, which maintain function at the aggregate community level as disturbance-sensitive species falter³. Yet in persistently managed systems characterized by the loss of environmental variability and diversity, species that are well-adapted to previous environmental conditions have often become rare or extinct¹³. These declines may have little functional significance as long as the existing conditions of persistent management are maintained¹⁴. However, this may create a hidden vulnerability to abrupt environmental change, analogous to reduced genetic diversity limiting the capacity for adaptive responses in populations.

Here we demonstrate this vulnerability to collapse in a degraded grassland system in western North America, where responses to abrupt disturbance were mediated by the levels of remnant diversity. As with most grasslands globally, long-term anthropogenic management has homogenized diversity and function (Supplementary Fig. 1). After approximately 150 years of fire suppression, most areas are dominated by high-biomass, low-diversity mixtures of exotic pasture grasses. Over a ten-year period along a naturally occurring diversity gradient, we experimentally re-introduced burning at two intervals: a ten-year press, and a five-year pulse with five years of recovery. The diversity gradient is associated with interactions among grass dominance, dispersal limitation and soil depth, with higher grass production on deeper soils, in the absence of fire, eventually displacing dispersal-limited native populations to areas with shallower soils that are also grass-dominated but with 24% less cover and 22% less production per plot (see Methods). We monitored four measures of stability in response to the immediate and longer term effects of re-introducing fire: resistance to species invasion, resilience of microhabitat conditions, resistance to plot-level extinction, and constancy of biomass production including grass litter (the major fuel source for fire). We quantified the direct effects of fire on stability (for example, the potential extinction of precariously rare native species after burning), versus those mediated by diversity (that is, whether species-rich areas were more resilient to the disturbance). We also contrasted relative abundance and biomass in the press and pulse treatments, to determine the stability of the responses to five years of burning when fire was once again suppressed.

In the absence of fire, based on decade-long data from control plots, we detected a negative association between stability and diversity by the persistent maintenance of low-diversity communities of introduced grasses (Fig. 1a, b). High-density near-monoculture populations can be unstable in nature owing to the intensification of density-dependent

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factors such as intraspecific competition and enemy attack³. Here, these limitations were weakened by anthropogenic management beginning in the mid-nineteenth century (Supplementary Fig. 1). Similar to an agricultural system in which a few species account for most production, the introduced grasses are more productive (Supplementary Table 1), maintain more environmentally homogeneous understory conditions (such as ground level light; Supplementary Fig. 2), and are less affected by climate variability than plots with high remnant diversity (Fig. 1a). Previous studies have shown how compensatory dynamics in species-rich systems buffer the effects of climatic variability¹⁵. We observed the opposite response, indicating that diversity–stability relationships can sometimes be more system-specific than universal¹. Stability was mechanistically explained by the dense canopy that was more than twice the height of native species (exotic canopy height: 157.3 ± 13.6 cm (mean \pm s.e.m.); native canopy height: 67.63 ± 9.1 cm) and a deep litter layer. Together, they significantly reduced variability in yearly biomass production (Fig. 1b) and ground level light availability (Supplementary Fig. 2), suppressed native plant diversity (Supplementary Table 1), and resisted invasion by woody plants (Supplementary Table 1). When combined with vegetative sprouting that maintains grass recruitment

despite low ground-level light, the net outcome is a species-poor but productive and temporally resilient grassland community that persists despite both the absence of burning and high regional rainfall levels typically associated with woodland ($\sim 1,000$ mm per annum).

The re-introduction of fire, however, caused this system to collapse within one growing season, with immediate dominance by invasive species, especially woody plants. Elton predicted simpler systems to be more prone to invasion¹¹; here, this was only true when the species-poor grassland suffered a sudden disturbance. Experimental burning transformed each stability measure, with significant shifts in species composition, biomass and light levels (Supplementary Table 1 and Supplementary Fig. 2), plus increased plot-level extinctions (Supplementary Table 1) and invasion by both woody plants and pernicious non-native herbaceous species including thistle and annual brome-grasses (Fig. 2 and Supplementary Table 1). These changes were explained by the acute sensitivity of the dominant grasses to burning, resulting in cover reductions to $<5\%$ m⁻² per species or their plot-level eradication (Supplementary Table 1). The most significant change was the rapid invasion by woody plants including late-successional tree species (for example, Douglas-fir (*Pseudotsuga menziesii*)). Typically, tree invasion of grassland is restricted by fire mortality and biotic interactions, which can maintain tree–grassland boundaries for decades^{16,17}. Here, grass elimination led to a significant influx of woody plants within one growing season, with this conversion representing a potentially irreversible state-change given that obligate grassland flora are rapidly extirpated under woodland canopies^{16,17}.

By contrast, woody plant invasion was inhibited in areas with high remnant diversity of native flora (Fig. 2). The underlying mechanisms

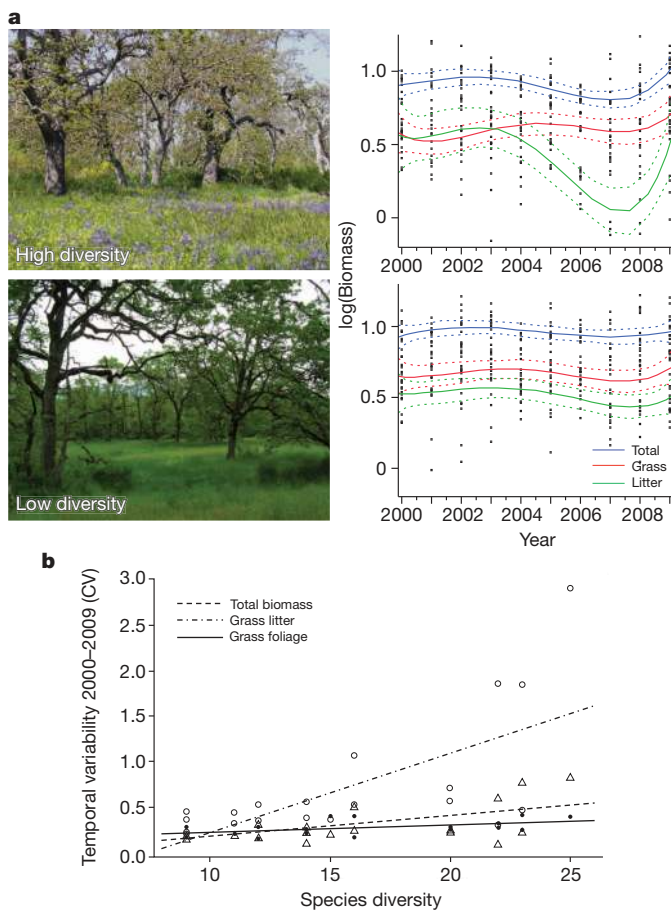


Figure 1 | Production responses to annual climatic variability. **a**, Annual biomass fluctuations in high (top) and low (bottom)-diversity plots. Trendlines are best-fit polynomials with 95% confidence intervals. All high-diversity measures fluctuate significantly with time (repeated-measures analysis of variance (ANOVA): grass $F_{1,9} = 2.2$, $P = 0.02$, litter $F_{1,9} = 4.0$, $P = 0.0002$, total $F_{1,9} = 5.8$, $P < 0.0001$). No biomass measure varies at low diversity (repeated-measures ANOVA: grass $F_{1,9} = 1.4$, $P = 0.2$, litter $F_{1,9} = 1.0$, $P = 0.4$, total $F_{1,9} = 1.49$, $P = 0.16$). **b**, Decadal variability in grass (filled circles), litter (open circles), and total production (triangles), by plot-level diversity. Variability is the coefficient of variation (CV) for the time series of each plot for 2000–2009. Variation increases as diversity increases (repeated-measures ANOVA: grass $F = 8.4$, $P = 0.009$, litter $F = 13.16$, $P = 0.002$, total biomass $F = 9.38$, $P = 0.007$).

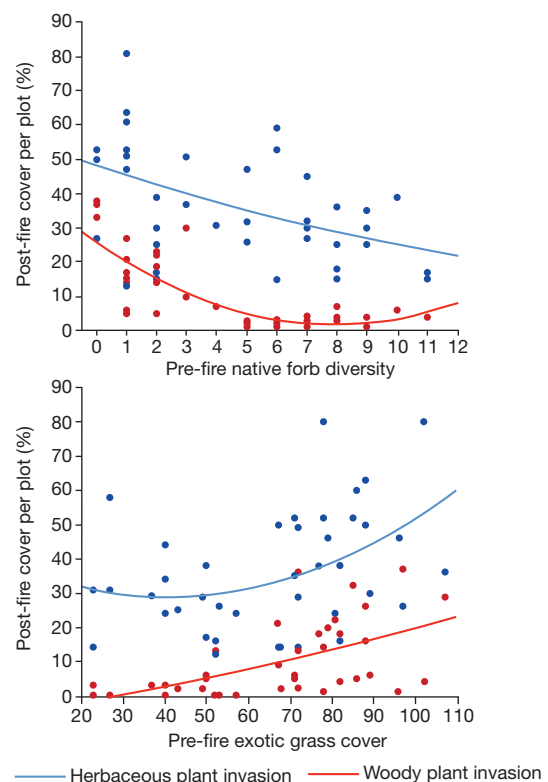


Figure 2 | Invasion by herbaceous exotics and woody plants after fire, in relation to pre-burn native forb diversity and exotic grass cover. All relationships were significant (best-fit trendlines for the relationship between pre-burn native forb cover versus woody plant invasion ($F_{2,39} = 28.2$; $P < 0.0001$) and non-woody plant invasion ($F_{2,39} = 4.9$; $P = 0.013$); for pre-burn exotic perennial grass cover versus woody plant invasion ($F_{2,39} = 8.6$; $P = 0.0008$) and non-woody plant invasion ($F_{2,39} = 4.1$; $P < 0.025$)). Control-plot data are pooled from the pulse- and press-burned treatments (see Methods).

explaining sudden ecosystem collapse have been difficult to determine^{5,7,18}. Here, collapse was associated with local processes connected to plot-level species diversity. Resistance to woody plant invasion occurred by rapid increase in cover of 30 rare native plants representing a range of life-history strategies, with per-species cover increasing by 1.5–4 times compared with unburned plots (Supplementary Table 1). Sampling-effect models predict that one or several species will determine recovery, with more diverse communities more likely to have these species present¹⁹. Here, the diversity response was explained by the aggregate responses of the entire native ground flora community, suggesting functional redundancy despite their life-history differences. Redundancy is often crucial for stability in complex systems, with one species capable of substituting for another²⁰. This was the case here, because no species was distributed widely enough beforehand to compensate solely for the effects of fire. As diversity increased, ground level light returned in the range of pre-burn levels in the same growing season (Supplementary Fig. 2), and woody plant recruitment did not change significantly (Fig. 2 and Supplementary Table 1). Not all stability responses were positively correlated, as above-ground biomass production—a common stability metric—decreased by approximately 34% in the forb-dominated community compared with exotic grassland (Supplementary Table 1). This last observation supports the notion that diversity responses can vary by environmental context and the type of stability being measured¹. Here, low-diversity communities were more stable in the absence of fire, with greater resistance to invasion and greater resiliency in biomass production to yearly climatic variability. High-diversity communities were more stable with sudden perturbation, with greater resilience to microclimatic change and invasion resistance, but were also significantly less productive than the undisturbed low-diversity community.

Diversity influenced not only invasion after burning but also the dynamics of the fire regime itself, on the basis of trait differences between the two dominant functional groups: grasses and forbs. Classic fire models often predict burning to promote fire-tolerant species that maintain fire by producing high-fuel loads, thereby creating a stabilizing positive feedback²¹. We found that forbs in high-diversity areas proliferated with fire but produced little persistent litter, thereby making the reoccurrence of high-intensity fires less likely owing to fuel scarcity. The reduction of burning, in turn, leads to the rapid re-emergence of grasses, as observed in our pulse experiment in which the cessation of burning in 2005 was followed by the rapid recovery of grass biomass to pre-burn levels within two growing seasons (Supplementary Fig. 3). This would once again increase the likelihood of fire. These wide fluctuations in fuel availability over short periods suggest the potential for fine-scale non-equilibrium dynamics in the presence of fire, with local communities oscillating between grass and forb dominance depending on feedbacks between litter availability and fire frequency (see modelling simulations in Supplementary Fig. 4 and Supplementary Information). Historical accounts from southeastern Vancouver Island in the mid-nineteenth century support this exact interpretation, with local species composition and production fluctuating widely even within a single growing season depending on the timing and intensity of fire²². Today, this spatially heterogeneous dynamism has been eliminated, with fire suppression homogenizing species diversity at site and regional levels and changing how the system responds to fire.

Our work demonstrates how persistent human activity can homogenize the structure and function of ecological systems, while simultaneously weakening diversity-related compensatory mechanisms needed to respond to sudden disturbance. These findings are consistent with previously demonstrated connections between diversity and ecosystem function, in which a larger portfolio of functional strategies within a community provides insurance against sudden environmental change^{1–4,23}. Given that many terrestrial systems possess this signature of compositional homogenization owing to persistent human activity, there may be a similar vulnerability to sudden environmental change that will be only evident after the collapse occurs.

METHODS SUMMARY

In May 2000 at peak growing season, 80 1 m⁻² treatment plots were established along a natural diversity gradient in a 10.8-ha oak savanna on Vancouver Island, British Columbia, Canada (Nature Conservancy of Canada). This grassland is part of the California Floristic Province, associated with the Mediterranean climate of coastal western North America that includes pronounced yearly variability in temperature and precipitation including the influence of the Pacific decadal oscillation^{22,24,25}. The pre-European fire season was July–October before the winter rainy season²². The savanna has 115 plant species (75% native) including grasses, forbs and woody plants. Exotic grasses dominate all plots along the gradient, with their combined covers in 2000 ranging from 54 to 129%. Native species can persist at all points along the diversity gradient, with their present-day restriction to areas of lower grass cover associated with competition, acute dispersal limitation and soil depth²⁴ (see Methods). Total plot diversity ranged from 4 to 25 species m⁻². The percentage cover of plants and bare soil, ground level light, and soil moisture were measured in all plots in May–June 2000–2009. Biomass was measured in half of the 80 plots annually; soil nitrogen levels were measured in these same plots in 2000 and two years after burning. Biomass was separated into live grass, litter and forbs, dried for two days at 68 °C, and weighed.

Burning was initiated in July 2000. Twenty plots were burned once each year from 2000–2009 during the summer fire period (July), in a press treatment to test the homogenizing effects of continuous burning on diversity, biomass and invasion. Twenty other plots were treated in the same way from 2000–2004, after which they were unburned for the next five years, in a pulse treatment to test the trajectory of vegetation recovery (see Methods for further details).

Full Methods and any associated references are available in the online version of the paper.

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Supplementary Information is available in the online version of the paper.

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METHODS

The study area was a species-rich remnant oak savanna, and supports communities of herbaceous ground flora in open areas surrounded by low-density patches of oak (*Quercus garryana*), Douglas-fir (*Pseudotsuga menziesii*) and shrubs (pictured in Fig. 1a). All experimental work occurred in open areas free from canopy cover. This system is part of the California Floristic Province, associated with the Mediterranean climate of coastal western North America that includes pronounced yearly variability in temperature and precipitation including the influence of the Pacific decadal oscillation^{22,24,25}.

The factorial field experiment was conducted along a natural diversity gradient, with all plots on the gradient dominated at the beginning of the experiment by two perennial agronomic grasses (*Poa pratensis* and *Dactylis glomerata*), with other exotic agronomic grasses occurring sporadically (*Alopecurus pratensis*, *Agrostis gigantea*, *Elymus repens* and *Phleum pratense*). Half of the 80 plots along the diversity gradient were randomly placed in areas with either deeper (range: 20 to >85 cm) or shallower (8 to 20 cm) soils, with depth of the glaciomarine clay-loam soils on the reserve varying owing to undulations in the underlying bedrock. The two areas do not differ in land-use history, although they are physically separated by an old cart-path (which we use for site access) that was avoided during plot placement in 2000. Soil depth in each plot was measured with an 85-cm rod driven to bedrock. Two burn and two control plots were paired in blocks (4 plots × 10 blocks × 2 soil depth zones = 80 plots), with blocking used to minimize the effects of fine-scale variability in soil depth and pre-burn cover of the dominant grasses on the analysis of burn responses. Plots were not selected based on diversity, which thus varied randomly. Plot diversity was surveyed each year starting in 2000, using a 20-cell 1-m² sampling frame laid over each plot. The percentage of cover was visually estimated to be 1% for each species, resulting in annual plot-level cover measures for the 115 species on the reserve from 2000–2009.

The natural diversity gradient on the site is correlated with exotic grass cover, grass litter cover and soil depth, with deeper soil plots having higher grass cover, more litter, and fewer native forb and native graminoid species²⁴. In the absence of long-term burning, the gradient is mechanistically influenced by the interaction between competition and dispersal limitation. All native species can establish, persist and reproduce along all parts of the diversity gradient, based on current distribution patterns plus experimental seed and seedling additions conducted on the reserve²⁴. Plant performance of most native species, however, is significantly constrained in areas of high exotic grass cover, with grass and litter cover reducing mean plant size, reproductive output, and seedling survival of most subordinate species^{24,26}. Although many native perennial forbs are long-lived bulb species that can persist for decades even among the dominant exotic grasses in areas of high production, their reduced fecundity combined with low establishment success increases the probability of their eventual displacement from areas with dense grass cover. They also demonstrate acute dispersal limitation^{24,26}, such that once species become displaced from deeper soil areas, the likelihood of re-colonization from remnant populations on areas with shallower soil is low.

There is no strong direct abiotic effect of soil depth on recruitment (that is, resistance to tree invasion on high diversity shallow-soil plots is not explained by moisture stress associated with shallower soils). Recruitment for all species, including woody plants and exotic herbaceous species, occurs during the winter–spring rainy season (November–March). When moisture becomes limiting in the summer drought period, seedlings in all areas have either matured sufficiently to avoid (senescence) or tolerate (rapidly-produced deep roots) the drought, or perish regardless of soil depth, because all areas along the diversity gradient become similarly moisture limited by early summer^{24,26}.

Burning was conducted in late July each year at the height of summer drought, the time of year when fires most often occurred before the late-nineteenth century²². Most native forbs have set seed and senesced by this time. Most agronomic grasses, by contrast, are at their reproductive peak such that burning eliminates both foliage and seed. The two most abundant native perennial grasses on the reserve (*Bromus carinatus* and *Elymus glaucus*) are similarly sensitive to burning, suggesting that fire suppression would have favoured their abundance before the arrival of the agronomic invaders.

Fires were ignited using a roofing torch, and typically lasted less than 1 min in each plot. Previous fire work on the reserve using thermocouple sensors measured peak temperatures from 133–408 °C at 50 cm above ground level, with no change in temperature 5 cm below the soil surface²⁴. There is no effect of litter biomass on fire intensity (for example, fire does not burn hotter in deeper soil areas with higher litter biomass)²⁴. Burning in the press experiment was conducted annually up to (and including) 2009, even when litter biomass after 2004 had dropped beyond levels that might naturally support fire. Burning was continued to test the homogenizing effects of repeated burning on vegetation compared to the pulse experiment (see modelling details below). Burning in the pulse experiment was conducted annually for five years (July 2000–2004) in the same manner as the press experiment. All analyses on the effects of fire on stability emphasized the 2000 pre-burn data against the responses that unfolded up to and including 2004.

Burning responses were measured as described above, with the percentage cover of vegetation, bare soil, light level at ground level, and soil moisture measured annually at peak growing season (May–June) from 2000 to 2009. Light was measured at five locations within each plot, with measurements at ground level and above canopy (quantum sensor: LiCor). Soil moisture measurements were taken with a 12-cm TDR hydrosense probe (Campbell Scientific). Soil NO₃, NH₄ and total nitrogen were measured in 10-cm deep × 5-cm diameter soil cores before burning (2000) and after two years of burning (soil lab, University of British Columbia). Biomass data were not collected in 2005.

These data were used to calculate four measures of stability. ‘Resistance to species invasion’ was based on the establishment of woody plant species, and non-native herbaceous species that are known invaders elsewhere in North America. Establishing woody plants were both native (Douglas-fir, big-leaf maple (*Acer macrophyllum*), snowberry (*Symphoricarpos albus*)) and exotic species (scotch broom (*Cytisus scoparius*) and English hawthorn (*Crataegus laevigata*)). Herbaceous invaders were thistles (*Cirsium* spp.), annual brome grasses (*Bromus sterilis* and *Bromus hordeaceus*) and annual forbs (for example, *Trifolium dubium*, *Myosotis discolor* and *Valerianella locusta*). Because of the acute dispersal limitation by the native forbs, all diversity-mediated resistance to species invasion was determined by individuals present in plots at the beginning of the experiment (for example, burned plots with initial low native diversity in 2000 did not transition to plots with higher native diversity later during the experiment). ‘Resilience of microhabitat conditions’ was based on post-fire measures of ground level light, soil moisture, and soil nitrogen at the peak of the growing season. Neither soil nitrogen nor soil moisture was significantly affected by burning and is not discussed further²⁴. ‘Resistance to extinction’ was determined by comparing species composition in plots before and after burning, as well as comparing background levels of extinction in the control plots. ‘Constancy of biomass production’ was the yearly variation in biomass production of grasses, litter and forbs, and was tested in both control plots (Fig. 1) and burned plots.

To analyse our response data, we used repeated-measures ANOVA for multi-factorial analyses (for example, the interacting effects of forb diversity, grass cover, bare soil and light levels on post-fire tree invasion), generalized linear model Poisson regressions when testing the individual effects of plot-level diversity on various response measures (given that diversity was a count measure), and best-fit linear or polynomial regressions when testing the explanatory effects of continuous measures (for example, biomass). All data were log- or (log + 1)-transformed to improve normality. All analyses were done using JMP 8.0. For Fig. 1b, the population variability of each sample plot was calculated from biomass (log + 1) data using the coefficient of variation spanning the years 2000–2009. The community diversity of each plot was measured as the species richness from the first year (2000). Total biomass was calculated by summing the three community types (grass, forb and litter) for each year within each plot. Similarly, species richness for the total biomass measure was the sum of the species richness of all communities in the first year. Linear regression was used to find the relationship between species richness and population variability (coefficient of variation) across all plots. All these analyses were carried out using Wolfram Mathematica version 8.

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