



# Effects of Widespread Drought-Induced Aspen Mortality on Understory Plants

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**Abstract:** *Forest die-off around the world is expected to increase in coming decades as temperature increases due to climate change. Forest die-off will likely affect understory plant communities, which have substantial influence on regional biological diversity, ecosystem function, and land-atmosphere interactions, but how die-off alters these plant communities is largely unknown. We examined changes in understory plant communities following a widespread, drought-induced die-off of trembling aspen (*Populus tremuloides*) in the western United States. We assessed shrub and herbaceous cover and volume in quadrats in 55 plots located across a wide range of levels of aspen mortality. We measured species richness and composition of herbaceous plant communities by recording species presence and absence in 12 sets of paired (1 healthy, 1 dying) aspen plots. Although understory composition in healthy and dying stands was heterogeneous across the landscape, shrub abundance, cover, and volume were higher and abundance of herbaceous species, cover, and volume were lower in dying aspen stands. Shrub cover and volume increased from 2009 to 2011 in dying stands, which suggests that shrub growth and expansion is ongoing. Species richness of herbs declined by 23% in dying stands. Composition of herbs differed significantly between dying and healthy stands. Richness of non-native species did not differ between stand types. The understory community in dying aspen stands was not similar to other shrub-dominated plant communities in the region and may constitute a novel community. Our results suggest that changes in understory plant communities as forests die off could be a significant indirect effect of climate change on biological diversity and forest communities.*

**Keywords:** biodiversity, climate change, community composition, herbaceous species, species richness, understory

Efectos de la Mortalidad Extensiva de Álamos Inducida por Sequía sobre Plantas del Sotobosque

**Resumen:** *Se espera que la desaparición de bosques aumente en las próximas décadas a medida que incrementa la temperatura debido al cambio climático. La desaparición de bosques probablemente afecte a las comunidades de plantas de sotobosque, que tienen influencia sustancial sobre la diversidad biológica regional, el funcionamiento de ecosistemas y las interacciones tierra-atmósfera, pero casi no se conoce como afecta la desaparición a estas comunidades de plantas. Examinamos los cambios en las comunidades de plantas de sotobosque después de una mortalidad extensiva, inducida por sequía, de álamo (*Populus tremuloides*) en el occidente de Estados Unidos. Evaluamos la cobertura y volumen de arbustos y hierbas en cuadrantes en 55 parcelas localizadas en un amplio rango de niveles de mortalidad de álamos. Medimos la riqueza y composición de especies de comunidades de plantas herbáceas mediante el registro de la presencia y ausencia de especies en 12 conjuntos de parcelas pareadas de álamo (1 sana, 1 moribunda). Aunque la composición del sotobosque en parcelas sanas y moribundas fue heterogénea en el paisaje, la abundancia, cobertura y volumen de arbustos fueron mayores y la abundancia, cobertura y volumen fueron menores en parcelas de*

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*álamo moribundo. La cobertura y volumen de arbustos incrementó de 2009 a 2011 en parcelas moribundas, lo cual sugiere que esta en marcha el crecimiento y expansión de arbustos. La riqueza de especies de hierbas declinó 23% en las parcelas moribundas. La composición de hierbas difirió significativamente entre parcelas moribundas y sanas. La riqueza de especies no nativas no difirió entre tipos de parcelas. La comunidad del sotobosque en las parcelas de álamo moribundo no fue similar a otras comunidades de plantas dominadas por arbustos en la región y pueden constituir una comunidad nueva. Nuestros resultados sugieren que los cambios en las comunidades de plantas de sotobosque a medida que mueren los bosques pudiera ser un efecto indirecto significativo del cambio climático sobre la diversidad biológica y las comunidades de bosques.*

**Palabras Clave:** biodiversidad, cambio climático, composición de especies, especies herbáceas, riqueza de especies, sotobosque

## Introduction

Global environmental change, such as climate change and shifting pathogen and insect loads, is predicted to have wide-ranging effects on forest ecosystems. In addition to gradual shifts in tree distributions and demographics due to climate change (Parmesan 2006; Lenoir et al. 2008; van Mantgem et al. 2009), rapid and widespread tree die-off associated with drought and temperature stress has been documented on all vegetated continents in the last several decades (Allen et al. 2010). Deciduous and evergreen species in the United States and Canada have recently experienced die-off associated with severe drought accompanied by elevated temperatures, termed “climate change-type” droughts (Breshears et al. 2005; Worrall et al. 2008; Anderegg et al. 2012). More severe droughts accompanied by higher temperatures are expected in large areas of western North America within several decades (Seager et al. 2007). Such conditions may trigger further tree die-off (Overpeck & Udall 2010).

Although much research has focused on the physiological mechanisms of drought-induced tree mortality (e.g., McDowell et al. 2008; Anderegg et al. 2012), the multifaceted consequences of widespread tree mortality have been studied less. Results of recent research indicate widespread tree mortality can transform regional land cover (Breshears et al. 2005), alter nutrient cycling (Xiong et al. 2011), affect land-atmosphere interactions (Royer et al. 2011), and decrease carbon sequestration by these ecosystems (Kurz et al. 2008). Because ecological communities that are shaped by a particular species (e.g., dominant tree species) tend to be structured by a small number of relatively strong species interactions (Ellison et al. 2005a), drought-induced mortality of a dominant tree species can disproportionately affect ecosystem processes and functions. These effects include alteration of nearby aquatic ecosystems and assemblages (Snyder et al. 2002), regional homogenization of floral and faunal assemblages (Ellison et al. 2005b), changes in soil ecosystem processes (Jenkins et al. 1999), and shifts in hydrological regimes (Sun et al. 2001).

The effects of tree mortality on understory plant communities and species richness have received little attention despite the prominent roles understory plants can

play in forest biological diversity, ecosystem function, wildlife food and habitat, and land-atmosphere interactions (Classen et al. 2005; Harrison et al. 2010; Kane et al. 2011). Unlike other disturbances that remove the forest canopy, such as land-use change (Benítez-Malvido & Martínez-Ramos 2003), logging (Haeussler & Bergeron 2004) and fire (Brockway & Lewis 1997), tree mortality generally does not directly disturb understory plant communities. Thus, effects on understory plant communities following forest overstory changes are likely to be mediated by changes in microclimate and competition between overstory and understory (Classen et al. 2005; Bartemucci et al. 2006).

Understory plants may be particularly vulnerable to tree mortality because they are considered sensitive to microclimate and have low colonization rates (DeFrenne et al. 2011). The extensive literature on loss of a dominant tree species from other disturbances (e.g., insect infestation) indicates that overstory loss typically alters understory plant communities and may lead to, for example, increases in invasive non-native species and decreases in species richness (Ellison et al. 2005a). Results of the only study on understory plant communities following drought-driven overstory mortality in an arid conifer woodland, however, showed increases in understory species richness and abundance (Kane et al. 2011). Understory plant growth may also affect regrowth of forests by competing with understory tree seedlings and saplings, thereby altering community trajectory. Thus, the effects of drought-induced tree mortality on understory plants are uncertain and could be an indirect effect of climate change on biological diversity (e.g., Martin 2007).

Trembling aspen (*Populus tremuloides*) is a clonal, deciduous tree species and is the most widespread tree in North America (Peterson & Peterson 1992). Trembling aspen forests support high levels of species richness relative to co-occurring forest types (DeByle & Winokur 1985; Bartemucci et al. 2006). For example, in Rocky Mountain National Park, Colorado (U.S.A.), Stohlgren et al. (1997) found that aspen stands constitute <2% of the studied landscape but hosted 45% of all plant species recorded. We examined the response of understory shrubs and herbs to widespread drought-induced

mortality of trembling aspen: sudden aspen decline (SAD) (Worrall et al. 2008, 2010).

SAD was triggered by a climate change-type drought that occurred from 2000 to 2003 (Anderegg et al. 2012). It now affects >17% of Colorado aspen forests and has been documented throughout the western United States and western Canada (Worrall et al. 2010; Michaelian et al. 2011; Huang & Anderegg 2012). Very low aspen regeneration has been observed in areas affected by SAD and may be related to responses of understory plants or mortality of roots from which aspens resprout (Worrall et al. 2010). SAD provides an ideal case with which to examine the effects of drought-induced widespread forest die-off on understory plant communities. We examined changes in understory shrub abundance associated with aspen mortality; changes in shrub and herbaceous growth associated with overstory mortality; effects of SAD on understory herb species richness, including changes in non-native species; and understory changes related to aspen regrowth during SAD.

## Methods

### Field Sites

Our study area was the aspen-dominant forests of the San Juan National Forest (915 km<sup>2</sup>) in southwestern Colorado, an area that has had exceptionally high levels of SAD (Huang & Anderegg 2012). Mean annual temperature in these mountains is 3.2 °C, and mean annual precipitation is 508 mm at high elevations (Elliot & Baker 2004). In the San Juan National Forest, aspen forests occur at approximately 2350–3250 m. They co-occur with ponderosa pine (*Pinus ponderosa*) forests at lower elevations and with Engelmann spruce-subalpine fir (*Picea engelmannii*/*Abies lasiocarpa*) forests at higher elevations (Worrall et al. 2008). Understory shrub abundance varies greatly across these aspen forests, and the shrub community is dominated by mountain snowberry (*Symphoricarpos oreophilus*).

### Vegetation Surveys

We surveyed the understory plant community at 55 aspen forest plots in the San Juan National Forest across a range of SAD severity from June to August 2011. Stands were selected to cover a diversity of geographic and topographic areas in aspen distribution within 1 km of an accessible road. Plot locations within a stand were selected randomly. To minimize short-term effects of cattle grazing, we sampled most (>75%) of our plots in each growing season before when cattle were allowed on a specific pasture of forest. We assessed overstory crown mortality and measured diameter at 1.37 m height (dbh) of all trees >5 cm dbh in plots with an 8.8-m radius (0.02 ha). We estimated each tree's crown mortality vi-

usually as in other studies of SAD (Worrall et al. 2008; Anderegg et al. 2012) and supplemented these data with plot-level measurements of canopy leaf area index from fisheye photographs taken at the center of each plot. We defined SAD plots as those with  $\geq 30\%$  crown mortality averaged across all measured trees. We considered plots with <30% mortality healthy. This threshold has been used effectively in remote-sensing studies of aspen die-off (Huang & Anderegg 2012). Using identical methods, we resurveyed 20 plots previously surveyed in 2009 to assess understory growth and changes in volume from July 2009 to August 2011.

At each site, we recorded abundance, percent cover, and maximum height of mountain snowberry, other shrubs, and herbs and determined percent cover of bare ground. We performed these measurements in 1-m<sup>2</sup> quadrats: 8 quadrats in the 20 plots surveyed in 2009 and 12 quadrats in all other plots (i.e., not surveyed in 2009). We delineated a 12-m transect through the center of the plot in which tree-stem mortality was measured. At 4 randomly selected sites along that transect we located 3 1-m<sup>2</sup> quadrats perpendicular to the transect and separated by either 1 or 2 m. We partitioned these quadrats into 16 sectors with string to estimate percentage cover. Within these quadrats, we estimated percentage cover of each understory vegetation class (snowberry, other shrub, herb, bare ground) visually and measured the maximum height with a tape measure. We estimated volume of a vegetation class by multiplying percentage cover and height and averaging the product across quadrats to generate volume (cubic meters) of vegetation per square meter. Within a subset of 4 quadrats, we lowered a straight wire in 5 fixed places within the quadrat and counted the times that each vegetation class touched the wire. This point-intercept method has been used in many studies as a way to assess grass and shrub abundance (Jonasson 1988).

To assess changes in herb species richness and diversity, we chose 12 plots with severe SAD (>50% crown mortality in a 5-m radius) and 12 plots that contained a healthy group of aspen (<25% crown mortality) within 100 m of each other (24 paired plots total). We noted grazing intensity (visibly grazed, visible damage to herbs; grazing possible, grazing may have occurred but no signs detected) in these plots and selected one plot from which cattle had been excluded for >10 years for use as an ungrazed reference site. From June to August 2010, we assessed canopy health as described above, except that the plot radius was 5 m. We identified all herbs in 5 1-m<sup>2</sup> quadrats randomly located within each plot. We recorded the presence or absence of each species within each quadrat and calculated species richness in each plot (for diversity calculations see Supporting Information). We determined whether each herbaceous species recorded during the field study was native or non-native (Komarek 1995).

## Aspen Regeneration Surveys

To examine possible interactions between aspen regrowth and understory responses to SAD, we measured aspen regeneration in the 55 stands where shrubs were assessed. In each stand we tallied all aspen sprouts <1.3 m in height (considered browsing height) within a 6-m-radius circle from the overstory plot center. We cut a sub-sample of sprouts (approximately 6/plot) and aged trees by counting tree rings under a hand lens. Most (>90%) sprouts <1.3 m had sprouted because of the onset of SAD around 2004. We calculated the number of sprouts per hectare. Because we were interested in understory competition with aspen regeneration in SAD stands, we examined the relation between sprouts per hectare and shrub variables in stands with >30% canopy mortality.

## Statistical Analyses

We used *t* tests or Wilcoxon signed-rank tests (for non-normally distributed data) ( $\alpha = 0.05$ ) to compare understory cover and volume within the 55 sites surveyed in 2011 and to analyze changes in vegetation cover and volume over time between SAD and healthy plots in the 20 revisited sites. We used paired *t* tests ( $\alpha = 0.05$ ) to compare species richness of herbs and invasive species between paired SAD and healthy plots. We performed ordinary least-squares linear regressions ( $\alpha = 0.05$ ) on shrub and herb cover as a function of overstory tree mortality to examine whether there were any threshold effects in mortality levels and to examine shrub cover in relation to aspen regeneration. We compared the point-intercept touches within a quadrat with the estimates of cover and volume via ordinary least-squares linear regression ( $\alpha = 0.05$ ) to determine whether our cover and volume measurements accurately captured abundance.

To assess the consequences of SAD on herbaceous community composition, we computed Jaccard dissimilarity of species composition between all possible pairs of healthy and SAD sites. We then used permutational multiple analysis of variance (PERMANOVA,  $\alpha = 0.05$ ) to assess whether SAD and healthy stands hosted significantly different communities and visualized these differences with nonmetric multidimensional scaling (Anderson 2001). We ran all analyses of herbaceous communities for all sites, for only visibly grazed sites, and for only possibly grazed sites to examine the effects in the presence and absence of grazing. All statistical tests were performed in R software (R Core Development Team 2010).

## Results

Because mountain snowberry constituted >90% of shrubs documented at all plots and other shrub response was similar to that of mountain snowberry, we pooled

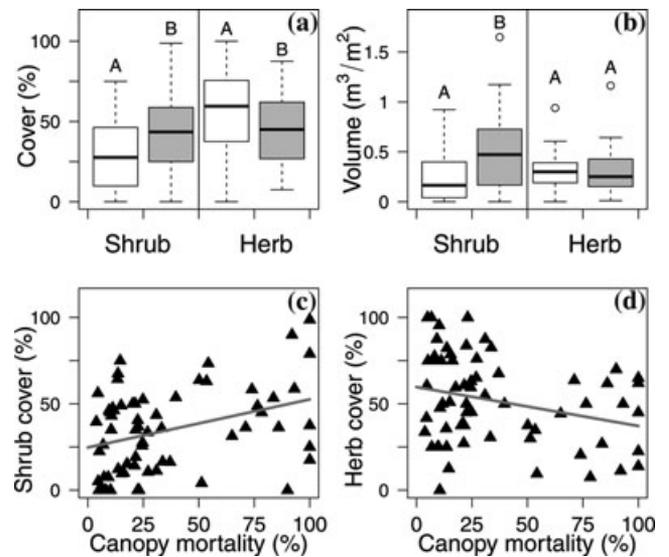
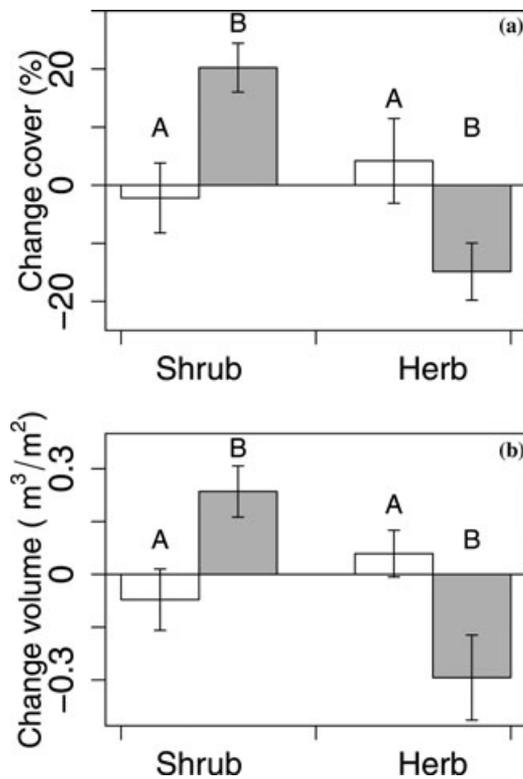


Figure 1. (a) Percent cover and (b) volume of shrub and herbaceous understory classes in healthy stands (unshaded) and stands affected by sudden aspen decline (shaded) (letters, statistically significant differences between groups,  $p < 0.05$ ; whiskers, minimum and maximum values without outliers [circles], i.e., twice the interquartile range subtracted and added from the first and third quartile [bounds of boxes]; solid line, means) and relation between (c) shrub and (d) herb percentage cover as a function of aspen overstory mortality.

shrubs measurements and presented them as total shrub abundance, cover, and volume. Shrub cover and volume were highly correlated with the point-intercept measures of abundance ( $R^2 > 0.85$ ;  $p < 0.001$ ) (Supporting Information). This result suggests our measures of cover and volume accurately captured shrub abundance in our stands. Shrub cover and volume were 52% and 96% higher, respectively, in SAD plots than in healthy plots (cover:  $t = 2.41$ ,  $df = 55$ ,  $p = 0.02$ ; volume:  $W = 305$ ,  $p = 0.01$ ), although shrub cover and volume in both SAD and healthy stands varied substantially across the landscape (Fig. 1). Shrub cover increased as aspen canopy mortality increased, and there was no indication of a threshold of shrub response to canopy mortality ( $R^2 = 0.13$ ;  $p = 0.004$ ). Herbaceous cover was 22% lower in SAD plots than in healthy plots ( $t = 2.03$ ,  $df = 55$ ,  $p = 0.04$ ) and declined as canopy mortality increased, although the relation was weak ( $R^2 = 0.08$ ,  $p = 0.02$ ). Herbaceous volume, however, was similar in SAD and healthy plots ( $t = 0.1$ ,  $df = 55$ ,  $p = 0.94$ ) (Fig. 1). Herbaceous cover and shrub cover were strongly and negatively correlated across plots ( $R^2 = 0.57$ ,  $p < 0.0001$ ) (Supporting Information).

Resurveyed plots revealed substantial differences in changes in cover and volume (a proxy for growth or



**Figure 2.** Change in (a) percentage cover and (b) volume of shrub and herbaceous understory classes from 2009 to 2011 in healthy aspen stands (unshaded) and in stands affected by sudden aspen decline (shaded) (letters, statistically significant differences between groups,  $p < 0.05$ ).

expansion or contraction of the understory vegetation class) over time between SAD and healthy plots. Shrub cover and shrub volume increased significantly in SAD plots compared with healthy plots (cover:  $t = 2.6$ ,  $df = 19$ ,  $p = 0.02$ ; volume:  $t = 2.96$ ,  $df = 19$ ,  $p = 0.01$ ) (Fig. 2). Similarly, herbaceous cover and volume declined significantly in SAD plots compared with healthy plots from July 2009 to August 2011 (cover:  $t = 2.48$ ,  $df = 19$ ,  $p = 0.03$ ; volume:  $t = 2.54$ ,  $df = 19$ ,  $p = 0.03$ ) (Fig. 2).

Stands affected by SAD exhibited a 23% decline in herbaceous species richness ( $t = 5.03$ ,  $df = 12$ ,  $p < 0.001$ ) (Fig. 3a). Herbaceous species diversity also declined in SAD plots (Supporting Information). Herbaceous community composition differed significantly between SAD and healthy stands (PERMANOVA:  $F = 2.24$ ,  $p = 0.009$ ) (Fig. 3b). Changes in species richness, diversity, and community composition were robust for both grazing statuses (Supporting Information). Despite these significant changes in community composition, non-native species richness did not differ significantly between SAD stands and healthy stands ( $t = 1.9$ ,  $df = 12$ ,  $p = 0.08$ ) and was relatively low in all plots (<3 species).

In SAD stands, aspen regeneration declined as shrub volume increased ( $R^2 = 0.42$ ,  $p = 0.0008$ ) (Fig. 4). Regeneration declined sharply as canopy mortality increased.

## Discussion

The differences between understory plant communities in SAD-affected aspen stands and healthy stands were striking. Community structure, as captured by the proportion and volume of shrubs in the understory, differed greatly between SAD and healthy stands. These differences could influence biogeochemical cycles and land-atmosphere interactions through their effect on albedo, transpiration, and land-surface properties (e.g. Hogg et al. 1997). For example, results of a study in which remote sensing was used to analyze SAD show that a typical greenness index (enhanced vegetation index) could not successfully detect SAD, likely due to the high greenness of understory plant communities (Huang & Anderegg 2012). The changes in the shrub understory we documented may explain these results. Our results suggest that the shrub understory may play a major role in ecosystem albedo and land-surface properties following SAD.

We could not definitively conclude that SAD caused the understory changes we observed because we could not compare understory communities before and after SAD. Yet the observed increases in shrub cover and volume (Fig. 2) in SAD stands provides strong evidence that dying stands favor more shrubby and less herbaceous communities. Healthy stands did not exhibit these increases in shrub abundance over the same period, which indicates the trends in SAD were not due to a universal increase in shrub abundance. These changes also suggest that the understory changes in SAD were ongoing through 2011 and will continue in the near future as mortality continues in SAD-affected stands (Anderegg et al. 2012). Similarly, SAD predominantly occurred at low elevations (Worrall et al. 2008), and the lack of relation between shrub volume and elevation in healthy stands ( $R^2 = 0.01$ ,  $p = 0.57$ ) (Supporting Information) suggests that preexisting differences in shrub abundance would not likely have led to our results.

Although changes in understory plants are expected with overstory mortality, the direction and magnitude of these changes are unknown for many species and communities. Depending on whether understory species are limited by light, water, temperature, competition, or other factors, their responses to tree die-off could differ greatly. Our results provide insight into the direction and magnitude of change in shrub and herb species after tree die-off in this diverse temperate forest type. The expansion of shrubs in SAD stands appears to have come at the expense of the herbaceous understory (Figs. 1 & 2). Our paired plots revealed a 23% decline in species richness of herbs, which is consistent with the documented

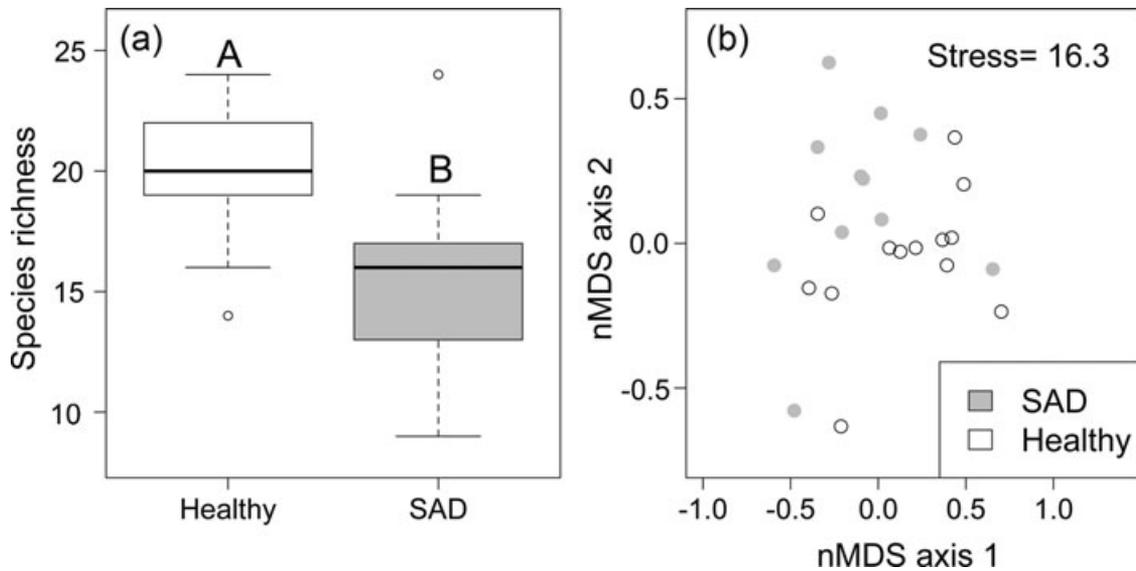


Figure 3. (a) Species richness of herbs in healthy aspen stands and in stands affected by sudden aspen decline (SAD) (letters, significance difference in paired *t* tests or Wilcoxon signed-rank tests,  $p < 0.001$ ; whiskers, minimum and maximum values without outliers [circles], i.e., twice the interquartile range subtracted and added from the first and third quartile [bounds of boxes]) and (b) nonmetric multidimensional scaling (nMDS) plot of herbaceous community composition between aspen stands affected by SAD and healthy stands (distance between points, dissimilarity in species compositions).

15% decline in herbaceous cover (Fig. 3). These declines might have occurred because preexisting shrub height allowed shrubs to take advantage of increased light in areas with tree die-off. The volume of herbs, however, was

not significantly different in SAD stands, which suggests that herbs were generally taller in SAD stands where they did occur.

These changes were likely due in part to changes in the microclimate following overstory mortality, but may also have been mediated by changes in grazing by ungulates, particularly domestic cattle, following SAD. We did not explicitly test the mechanism of understory changes, although grazing intensity appeared to have little effect on our results (Supporting Information). In the paired-plot analyses of herbaceous communities, observed changes were similar across all plots, seasonally grazed plots, and the plot that was not grazed for >10 years (Supporting Information), which suggests that recent grazing pressure was not enough to drive reported trends. The behavior and grazing intensity of domestic cattle in SAD stands over multiple years, however, could still affect changes in SAD understory communities and merits further study, especially its effects on aspen regeneration.

SAD was associated with a decline in understory species richness and diversity and changes in understory community structure, as has been observed with other disturbances (Holdenreider et al. 2004; Ellison et al. 2005a). These changes have particular regional relevance because other co-occurring shrub, grass, and conifer-dominated vegetation types typically support much lower levels of species richness than aspen forests (Stohlgren et al. 1997). The resultant vegetation community in SAD stands did not appear similar to other similar understory plant or shrub-dominated communities in

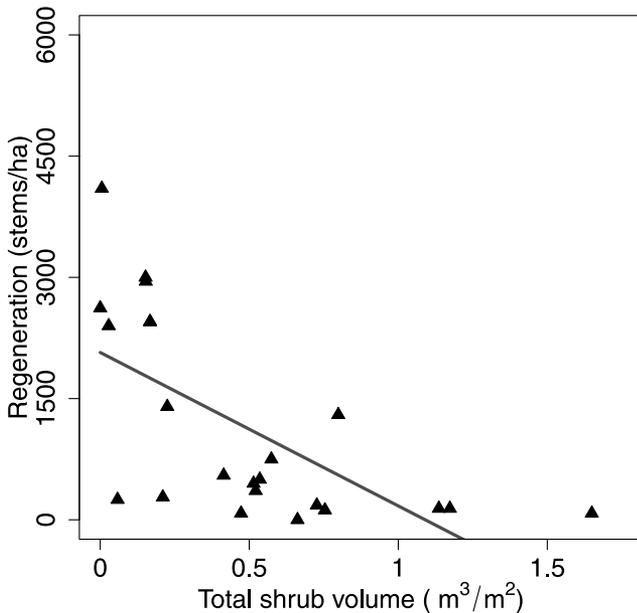


Figure 4. Relation between aspen regeneration and shrub volume in stands affected by sudden aspen decline (line, best-fit ordinary least-squares linear regression equation).

the region. In general, the SAD understory community was different from the shrub-forb community of Ponderosa pine (*Pinus ponderosa*) (Sørensen's similarity index on reported species lists: 0.16) and Engelmann spruce-subalpine fir (*Picea engelmannii-Abies lasiocarpa*) (0.21) forests and from tall shrublands (0.25) and Utah serviceberry (*Amelanchier utahensis*) shrublands (0.2) of southwestern Colorado (DeVilice et al. 1986; Johnston et al. 2001). Although the SAD understory community may be transient, it appears to represent a novel community in this region. If drought-triggered aspen die-off recurs or spreads in the future due to climate change, as climate envelope projections indicate (Rehfeldt et al. 2009), habitat availability for some herbaceous species would further decrease, potentially decreasing habitat connectivity. Changes in herbaceous community composition, species richness (shrub richness was <3 species in 95% of all stands), and species diversity (Supporting Information) suggest SAD could have a large effect on regional plant richness and composition.

The effects of drought-induced tree mortality on understory plant communities have been considered, to our knowledge, in only one previous study. Kane et al. (2011) found significant increases in understory plant diversity and increases in invasive species' dominance following mortality of Utah juniper (*Juniperus osteosperma*) in an arid woodland in Arizona (U.S.A.). In contrast, we found significant decreases in species richness but no increases in non-native species richness in SAD stands, although we did not consider non-native species' dominance. This suggests that the effects of tree mortality on understory plants differ across systems, perhaps in accordance with the diversity already present in the understory, shrub abundance, and role of the overstory tree species in the system. In aspen forests species richness of understory plants is high and this facilitates growth of other species (DeByle & Winokur 1985). However, juniper stands generally have less diverse understory plant communities and may suppress growth through shading and litter depth (Horman & Anderson 2003; Kane et al. 2011).

Aspen regeneration declined substantially as understory shrub volume increased (Fig. 4). Nearly all regeneration densities were an order of magnitude below (200–4000 stems/ha) those documented in other studies of aspen regeneration following logging or fire (10,000–40,000 stems/ha) (e.g., Haeussler & Bergeron 2004). Low regeneration in SAD (typically 200–4000 stems/ha) is also highly related to root mortality (aspens reproduce vegetatively from roots), which increases as canopy mortality increases (Worrall et al. 2010). The relation we found between shrub volume and regeneration is stronger ( $R^2 = 0.42$ ) than previously reported relations between canopy mortality and regeneration ( $R^2 = 0.05$ ) (Worrall et al. 2010). Nevertheless, further research is needed to disentangle the extent to which decreased regeneration is due to increased

competition with shrubs for light or water and to intrinsic decreases in regeneration ability of SAD-affected stands. Aspen-regeneration densities we documented of 200–4000 stems/ha were substantially lower than the typical 10,000–80,000 stems/ha observed following other disturbance (Shepherd & Smith 1993). The relative contributions of root mass versus shrub competition constrain understory responses, aspen regrowth, and the demographic trajectory of tree populations in SAD areas.

We found widespread and pervasive changes in understory plant communities following drought-induced aspen die-off. These changes altered the plant community structure, composition, and species richness. The effects of drought-induced forest die-off on plant communities and diversity have been studied in very few systems, yet could constitute a large indirect effect of climate on ecological communities and species. Understanding these changes will be increasingly important if forest mortality accelerates in coming decades triggered by changes in climate.

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## Supporting Information

Methods used to determine herb species diversity and results of these methods and information on diversity of herb species and effects of grazing on it are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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