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RESEARCH ARTICLE

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Minimal mortality and rapid recovery of the dominant shrub *Larrea tridentata* following an extreme cold event in the northern Chihuahuan Desert

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Abstract

Questions: Woody encroachment into grasslands is a worldwide phenomenon partially influenced by climate change, including extreme weather events. *Larrea tridentata* is a common shrub throughout the warm deserts of North America that has encroached into grasslands over the past 150 years. Physiological measurements suggest that the northern distribution of *L. tridentata* is limited by cold temperatures; thus extreme winter events may slow or reverse shrub expansion. We tested this limitation by measuring the response of individual *L. tridentata* shrubs to an extreme winter cold (−31°C) event to assess shrub mortality and rate of recovery of surviving shrubs.

Location: Sevilleta National Wildlife Refuge, Socorro County, New Mexico, USA.

Methods: Canopy dieback and recovery following an extreme cold event were measured for 869 permanently marked individual *L. tridentata* shrubs in grass–shrub ecotone and shrubland sites. Individual shrubs were monitored for amount of canopy dieback, rate of recovery, and seed set for three growing seasons after the freeze event.

Results: Shrubs rapidly suffered a nearly complete loss of canopy leaf area across all sites. Although canopy loss was high, mortality was low and 99% of shrubs resprouted during the first growing season after the freeze event. Regrowth rates were similar within ecotone and shrubland sites, even when damage by frost was larger in the latter. After three years of recovery, *L. tridentata* canopies had regrown on average 23–83% of the original pre-freeze canopy sizes across the sites.

Conclusions: We conclude that isolated extreme cold events may temporarily decrease shrubland biomass but they do not slow or reverse shrub expansion. These events are less likely to occur in the future as regional temperatures increase under climate change.

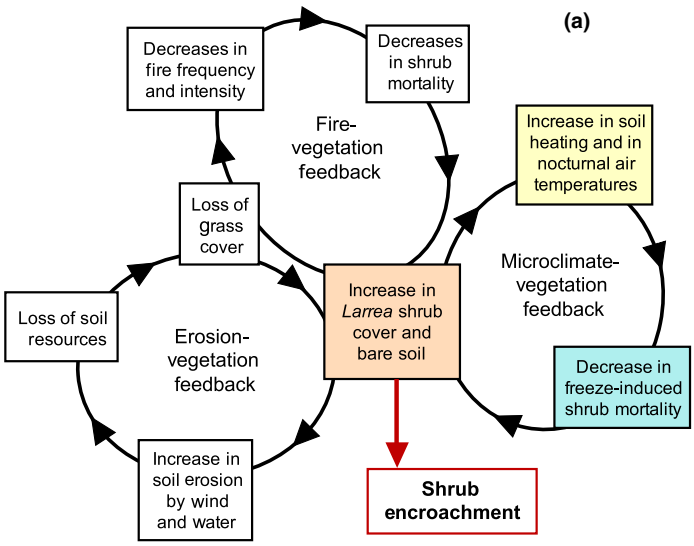
KEYWORDS

Chihuahuan Desert, creosote bush, extreme cold, grass–shrubland ecotone, *Larrea tridentata*, regrowth, winter

1 | INTRODUCTION

Throughout the world, woody vegetation is encroaching upon herbaceous-dominated systems, often transforming grasslands to shrublands (Briggs, Schaafsma, & Trenkov, 2007; Fredrickson, Estell, Laliberte, & Anderson, 2006; Van Auken, 2009). Ecological impacts and social perceptions of shrub encroachment vary widely. Negative consequences of shrub encroachment include decreased plant cover and diversity (Báez & Collins, 2008; Ratajczak, Nippert, & Collins, 2012), loss of soil nitrogen and carbon (Turnbull, Wainwright, & Brazier, 2010; Turnbull, Wainwright, Brazier, & Bol, 2010), increased nighttime temperatures (D'Odorico, Okin, & Bestelmeyer, 2012), decreased faunal diversity (Menke, 2003; Sirami, Seymour, Midgley, & Barnard, 2009), and less available forage for livestock (Passera, Borsetto, Candia, & Stasi, 1992). In contrast, positive implications of the conversion of grasslands to shrublands can include increased faunal abundance and diversity (Ceballos et al., 2010; Dettmers, 2003; Fuller & DeStefano, 2003; Whitford, 1997), increased plant diversity (Eldridge et al., 2011; Troumbis & Memtsas, 2000), reversal of desertification (Maestre et al., 2009), and higher C sequestration (Eldridge et al., 2011; Petrie et al., 2016). Whether perceived as positive or negative, human activities coupled with climate change and increased atmospheric CO_2 (Buitenwerf, Bond, Stevens, & Trollope, 2012) facilitate shrub encroachment in grasslands worldwide (Briggs et al., 2007; Fredrickson et al., 2006; Van Auken, 2009). In the context of alternative stable states, conversion of grassland to shrubland is generally considered to be irreversible over ecological time frames (D'Odorico et al., 2012, but see Peters, Yao, Sala, & Anderson, 2012).

Winter climate is influential in many ecosystems (Ladwig et al., 2016) and experimental manipulations help examine the response of ecological systems to changing winter conditions (Kreyling, 2010). Snow manipulations test for the ecological consequences of altered winter precipitation (Kreyling, Haei, & Laudon, 2012; Loik, Griffith, & Alpert, 2013), and warming manipulations track ecosystem changes following gradual increases in temperature (Collins et al., 2017; Wu, Dijkstra, Koch, Penuelas, & Hungate, 2011), yet our understanding of the response of plant communities to winter climate extremes is often limited to opportunistic studies following extreme climate events, as large-scale cooling experiments are generally not practical. For example, ice storms in hardwood forests can temporarily increase canopy openness and shift community composition based on species shade tolerance (Arii &



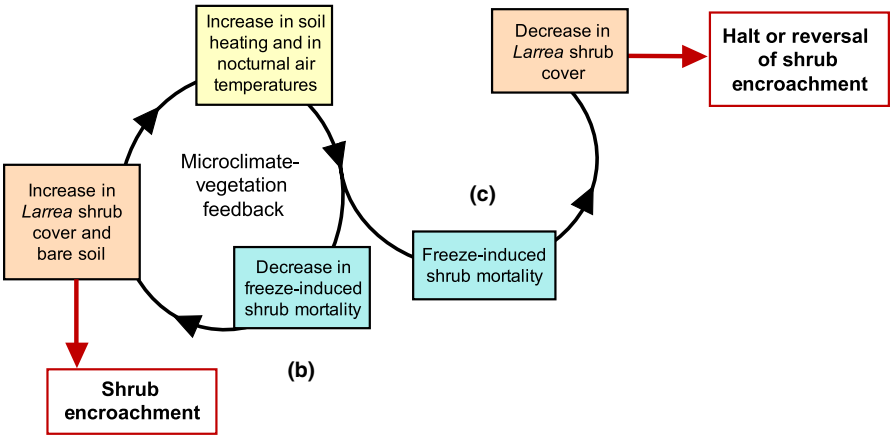


FIGURE 1 Positive feedbacks associated with *Larrea tridentata* shrub encroachment (a) proposed by D'Odorico et al. (2010). In this study, we assessed how extreme weather events may interact with the microclimate–vegetation feedback loop. Specifically, we asked, do the warmer temperatures in shrublands buffer shrubs from damage following an extreme cold event (b), or does an extreme cold event overpower the microclimate–vegetation feedback and damage individuals in the shrubland (c)? Figure modified from D'Odorico et al. (2010) [Colour figure can be viewed at wileyonlinelibrary.com]

Lechowicz, 2007; Rhoads et al., 2002; Shao, Huang, Liu, Kuang, & Li, 2011; Weeks, Hamburg, & Vadeboncoeur, 2009). Extreme warm events during winter can cause dormant trees and shrubs to break bud exceptionally early (Ladwig, Chandler, Guiden, & Henn, 2019), exposing young tissue to damaging cold temperatures later in the season (Augspurger, 2009; Muffler et al., 2016). Examples of how winter climate extremes influence natural communities are largely limited to snow and ice storm events in forests, since many of these forests regularly experience cold and occasional extreme cold temperatures. In contrast, most warm desert species are limited by cold (e.g., Pockman & Sperry, 1996; Smith, Monson, & Anderson, 1997), so plant responses may be more severe in deserts than forests. Yet, the extent to which extreme cold events shape desert community structure and function remains unknown.

Larrea tridentata (creosote bush) is an ideal species for studying relationships between shrub encroachment and changing winter climate. Native to North American warm deserts, *L. tridentata* is present throughout the southwestern USA and northern Mexico and alters ecosystem function as it expands into neighboring desert grasslands (Pockman & Small, 2010; Turnbull, Wainwright, & Brazier, 2011). *Larrea tridentata* has continued to expand northward over the past two centuries (Kelly & Goulden, 2008), presumably due to increasingly warmer climate combined with altered land use practices. Warmer winter temperatures may strengthen the positive microclimate feedback between temperature and shrub cover (D'Odorico et al., 2010; He, D'Odorico, De Wekker, Fuentes, & Litvak, 2010; Figure 1) and further contribute to range expansion by *L. tridentata*. Although many future global changes may support continued encroachment of *L. tridentata*, periodic extreme cold events may interrupt feedbacks between temperature and shrub cover to delay or even reverse shrub expansion (Figure 1). Although *L. tridentata* commonly experiences sub-freezing temperatures, low temperatures are thought to influence the northern range boundary of this species (Martínez-Vilalta & Pockman, 2002; Medeiros, Marshall, Maherali, & Pockman, 2012; Pockman & Sperry, 1996). *Larrea tridentata* shrublands are year-round carbon sinks (Anderson-Teixiera, Delong, Fox, Brese, & Litvak, 2011; Petrie et al., 2016), yet cold temperatures increase leaf folding, decreasing leaf area, and severely reducing photosynthetic rates at temperatures below 0°C (Gutschick & BassiriRad, 2003; Naumburg, Loik, & Smith, 2004). Based on laboratory trials, cold temperature can be lethal to young *L. tridentata* plants, with −20°C causing cell lysis and xylem embolism in nearly all young plant stems (Pockman & Sperry, 1996) and −24°C causing 100% mortality of one-year-old seedlings (Medeiros & Pockman, 2011). Anecdotal observations following an extreme freeze in the 1930s indicated massive canopy dieback (Cottam, 1937) and recovery (Fosberg, 1938) of *L. tridentata* throughout the Mojave Desert, yet quantitative evaluation of shrub response to natural extreme cold events is lacking.

We took advantage of a natural extreme cold event to examine how *L. tridentata* individuals responded to extreme cold at its northern range boundary at a scale unapproachable by lab or field manipulations. During February 2011, temperatures fell to 20°C below the 20-year average low temperature for February and remained below average for a week. This event allowed for the examination of naturally cold-adapted, mature plant response within both established shrublands and shrub–grassland ecotones. Our specific research questions included: (a) After an extreme cold event, does shrub survival differ between dense shrublands and sparsely populated ecotones? and (b) How long does it take surviving shrubs to recover their canopies after freezing damage?

2 | METHODS

2.1 | Study site

This research was conducted at the Sevilleta National Wildlife Refuge (SNWR; 34.3° N, 106.8° W; Figure 2) located in central New Mexico, USA. SNWR is also the site of the Sevilleta Long Term Ecological Research (LTER) program, which provided detailed long-term, site-specific climate data (http://sev.lternet.edu). Several ecosystems occur within the SNWR, including the northern extent of Chihuahuan Desert grasslands and shrublands, dominated by *Bouteloua eriopoda* and *L. tridentata*, respectively. Research was conducted in *L. tridentata* shrublands and ecotone regions co-dominated by shrubs and grasses. Annual precipitation over the past 22 years averages 240 ± 14 mm with approximately 60% falling as large summer monsoon events

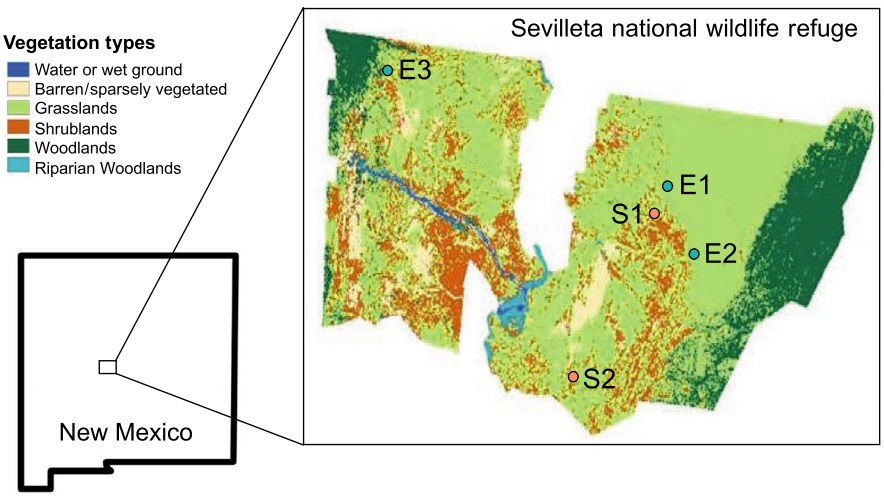


FIGURE 2 Vegetation types and survey locations within the Sevilleta National Wildlife Refuge [Colour figure can be viewed at wileyonlinelibrary.com]

(Pennington & Collins, 2007; Petrie, Collins, Gutzler, & Moore, 2014). Average annual temperature is 13.2°C with highest average monthly temperatures in June, 33.4°C, and lowest in January, 1.6°C (Muldavin, Moore, Collins, Wetherill, & Lightfoot, 2008). Between 2001 and 2010, minimum air temperature (T_{min}) was −20°C within *L. tridentata* shrublands (Figure 3a). Based on longer temperature records in the region (1932–2016; Albuquerque International Airport, 80 km NNE of site), the mean temperature in February has steadily increased ~2°C over the past 84 years, from 3.5°C in the 1930s to 5.5°C in the 2010s (Figure 3b). During early February 2011, minimum low temperatures fell well below average for several days, reaching the lowest levels on February 3, 2011, when T_{min} ranged from −26°C to −31°C across SNWR (Figure 3a). This was the coldest daily T_{min} in February from the 84-year regional climate record and fell below the 5% quantile for February daily T_{min}, with the previous February daily T_{min} < −20°C occurring 60 years earlier in 1951 (Figure 3c).

2.2 | Field surveys and data analysis

We established five observation sites across SNWR to examine shrub response to extreme cold with regard to variation in T_{min} and shrub density (Figure 2). Criteria for site selection included the presence of *L. tridentata*, flat terrain, close proximity to an existing meteorological station, and variation in both shrub density and T_{min} among sites. Two of the five sites were in dense shrublands (S1 and S2) while the other three sites were in the grass–shrubland ecotone (E1, E2, E3) with lower shrub density and greater grass cover. We established circular plots (20 m diameter) at each site and measured all shrubs within the plots two months after the cold event and annually for three years thereafter. At least 200 individual shrubs were evaluated at each site and the number of plots per site varied with shrub density.

Leaves turned brown but persisted on canopy branches for many months after the cold event. Even when they broke into pieces if lightly pinched by hand, we were still able to measure pre-freeze canopy dimensions after the extreme event and estimate percent canopy mortality. We grouped the percentage of mortality within the canopy into canopy mortality classes (no canopy mortality, 1–25%, 25–50%, 50–75%, 75–99% and 100% canopy mortality). In an effort to standardize the mortality class assignment, one researcher performed all mortality group assignment estimates to increase the consistency of the measurements. Canopy volume, estimated by calculating the volume of an inverted cone, correlates with biomass (Ludwig, Reynolds, & Whitson, 1975) and was our measure of canopy size. Canopy measurements included height, maximum horizontal width, and the perpendicular width. Presence or absence of seeds was also recorded to determine if shrubs were reproductive during recovery. Although great care was taken to label and track individual shrubs through time, permanently marking the shrubs was difficult as many recovering shrubs shed dead branches and consequently tags. Individuals that could not be confidently identified were removed from the dataset, resulting in a total of 869 shrubs included in the study by the end of the three years of recovery.

To test if initial response to the cold event varied between shrubland and ecotone sites, we conducted an analysis of covariance (ANCOVA; "lm" function in the vegan package) with canopy death as the response variable and site and initial canopy volume

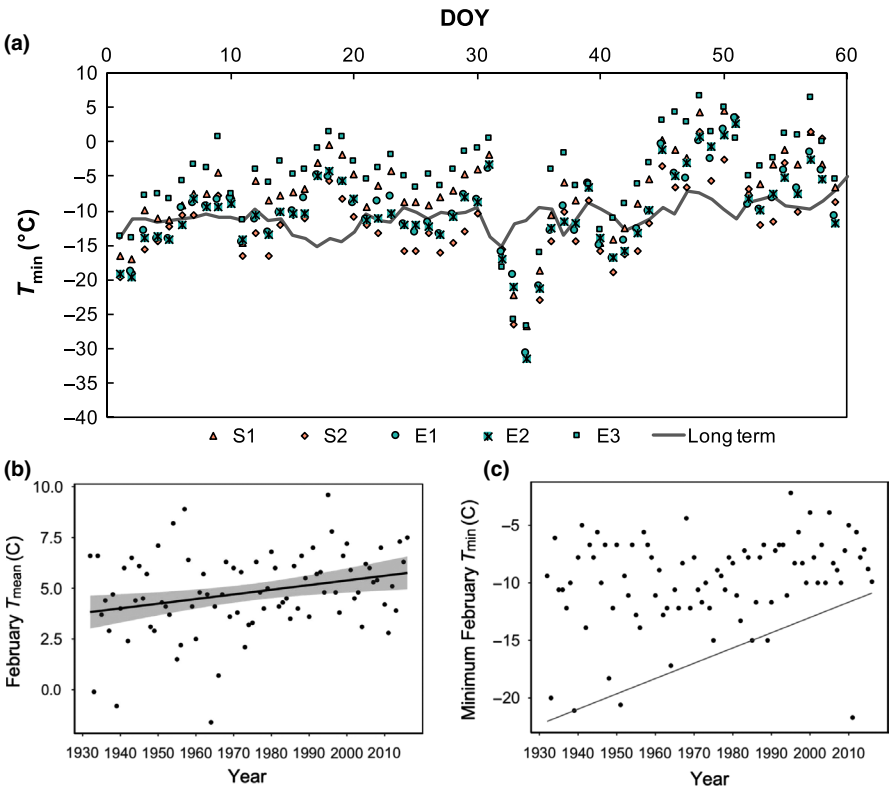


FIGURE 3 (a) Average long-term daily T_{min} (solid line) across the sites for the first 60 days of the year (DOY). Points on the graph indicate daily T_{min} from each of the five survey sites, each site indicated by a different shape. Longer-term regional data from the Albuquerque International Airport, 80 km NNE of the site, were used to compare the February of 2011 with a longer climate record (1931–2016). (b) Mean February temperatures have increased 2°C over the past 86 years. (c) Monthly minimum temperature for February with the 5% quantile indicated by the line. Temperatures falling below the line are extreme cold temperatures [Colour figure can be viewed at wileyonlinelibrary.com]

as effect variables. The extreme cold temperatures caused different amounts of damage to the shrubs, and the location of tissue regrowth indicated of the extent of damage. New leaves sprouting from the existing canopy indicated only partial canopy damage occurred. New tissues emerged from the base of the shrub indicated branch mortality. No new tissues indicated complete shrub mortality. To assess the amount of damage, the height of green leaves after a year of recovery was compared between sites with an ANOVA. Canopy recovery was assessed by comparing canopy volumes before and after the event. An individual was considered recovered when the size of its canopy matched or exceeded the canopy volume prior to the event (Year 0). Annual regrowth was calculated as:

$$(\text{Volume}_{\text{Year}X}/\text{Volume}_{\text{Year}0}) - (\text{Volume}_{\text{Year}x-1}/\text{Volume}_{\text{Year}0})$$

To test if regrowth varied between sites through time, annual growth was compared between sites and years with a two-way ANOVA. To determine whether floral buds were impacted by the event, the presence/absence of seeds and flowers were recorded annually for three years following the event. Statistical analyses were performed using R (R Core Team 2015) with an $\alpha = 0.05$.

3 | RESULTS

Initial canopy mortality of *L. tridentata* following the cold event was extensive, and all shrubs experienced some degree of canopy dieback. Of the 869 individual shrubs surveyed, nearly all (98.6%) had ≥50% canopy dieback. Initial dieback varied among sites ($F_{9, 859} = 57.9$, $p < 0.0001$, $r^2 = 0.37$; Figure 4) and was only related to canopy size at one site ($F_{4, 859} = 6.74$, $p < 0.0001$; negative association at site E1). Canopy mortality was related to shrub density, but opposite to our expectations. Shrublands are consistently warmer than grasslands (D'Odorico et al., 2010) and we thought this might buffer shrubland individuals from the cold event. Rather the two shrubland sites with highest shrub density (S1 and S2) experienced significantly more dieback than the three ecotone sites (E1, E2, E3; Figure 4). Height of canopy regrowth also varied with shrub density. Individuals in shrublands had lower regrowth from the base of the plant while, in the ecotone, regrowth was higher and largely within the existing canopy ($p < 0.001$, $F_{4, 864} = 301$, $R^2 = 0.58$; Figure 5).

Shrub mortality following the extreme cold event was exceptionally rare. During the first year of recovery, when precipitation was well below average, only seven of the 869 shrubs did not have new growth. Canopy recovery varied with regard to site and time (model $p < 0.001$, $F_{9, 2597} = 3.9$, $r^2 = 0.01$; site*year $p < 0.001$, $F_{4, 2597} = 6.45$). Specifically, the site with lowest shrub density experienced less initial damage (Figure 4) and therefore could recover sooner (Figure 6). Seed set varied among sites (Figure 7) and ranged from 0.5% to 82% of shrubs producing seeds during the first year of recovery, increasing to 17–96% following the third year of recovery.

4 | DISCUSSION

This extreme cold event had a significant but short-term impact on *L. tridentata* canopies. Most individuals experienced nearly complete loss of canopy leaf area similar to that reported for the cold event in the 1930s (Cottam, 1937; Fosberg, 1938) but plant

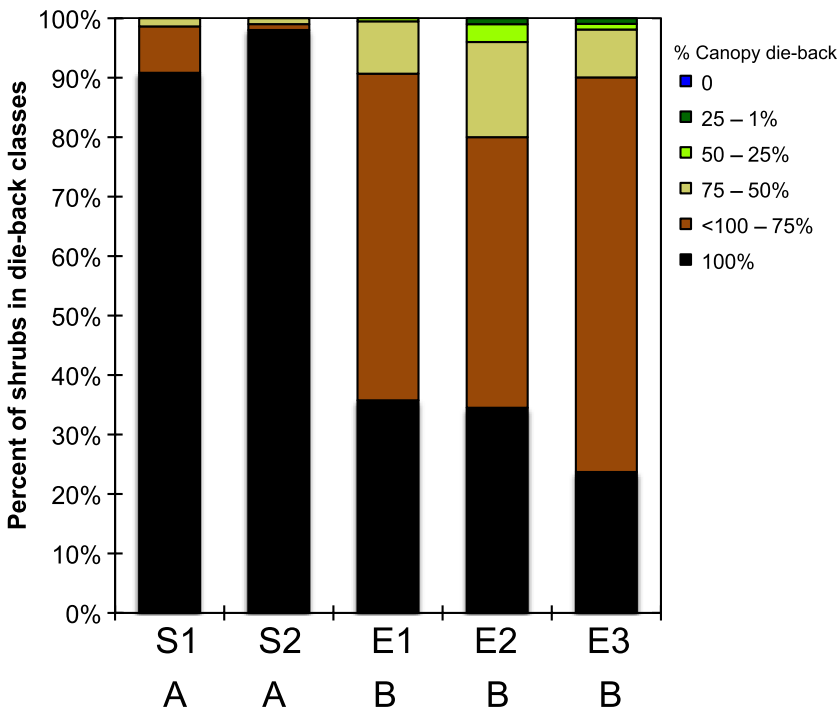


FIGURE 4 Canopy dieback based on the percentage of shrubs at each site in each canopy dieback class. There were >150 shrubs surveyed at each site, and sites are ordered according to decreasing shrub density. The letters below site names indicate statistically significant ($p < 0.05$) differences in canopy death between sites [Colour figure can be viewed at wileyonlinelibrary.com]

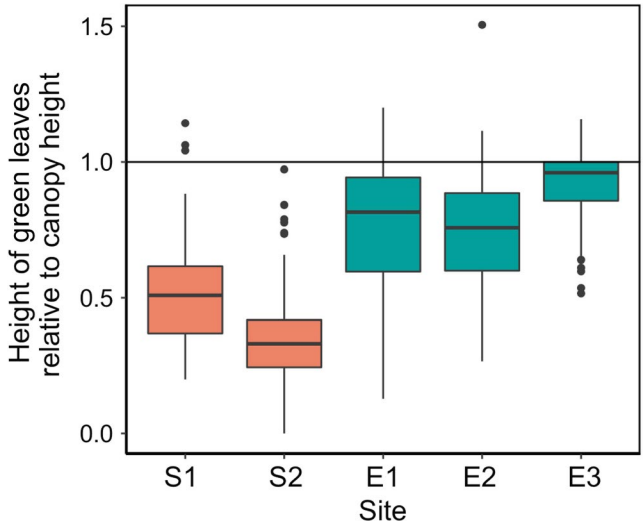


FIGURE 5 Height of green leaves after one year of recovery relative to canopy height prior to the event. Points at or below the horizontal line indicate regrowth within the existing canopy. Sites are organized from high (shrubland; coral) to low (ecotone; turquoise) shrub density [Colour figure can be viewed at wileyonlinelibrary.com]

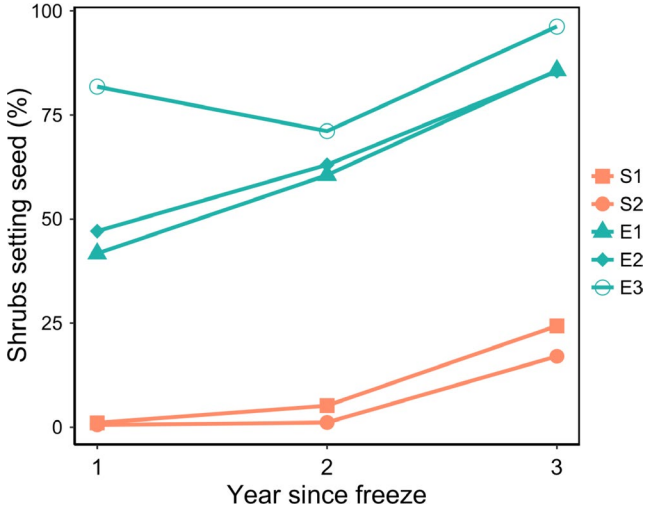


FIGURE 7 Percentage of shrubs setting seeds at each site during the three years following the extreme cold event. Each site is represented with a different line. Shrubland sites are in coral and ecotone sites in turquoise [Colour figure can be viewed at wileyonlinelibrary.com]

death was minimal (0.8% mortality). Although below-average temperatures triggered canopy damage, minimum temperature alone did not explain the variation in degree of dieback among the surveyed populations. The site that experienced the lowest T_{min} (E2; −31.4°C) also had relatively low canopy damage; therefore factors beyond minimum temperature influenced the degree of canopy dieback within sites.

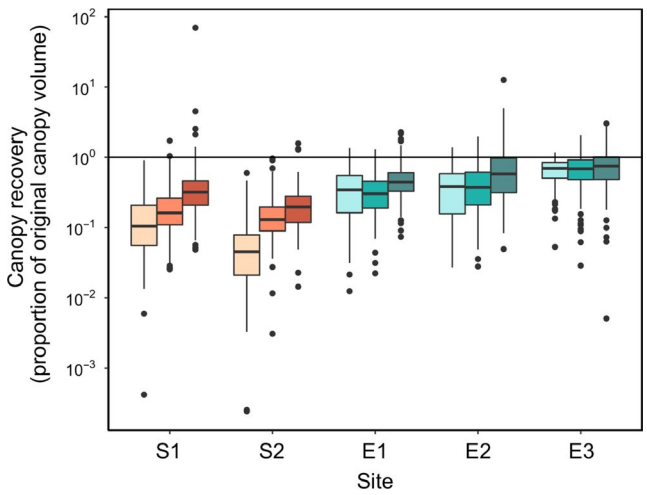


FIGURE 6 Canopy recovery, measured as the canopy volume during that year divided by initial canopy volume prior to the freeze, during the three years immediately after an extreme cold event. The horizontal line at 1 indicates complete canopy recovery. Sites are organized from high (shrubland; coral) to low (ecotone; turquoise) shrub density. For each site, boxes represent values from each year post event, with successive years of recovery in progressively darker shades [Colour figure can be viewed at wileyonlinelibrary.com]

Shrublands are generally warmer than both neighboring grasslands and ecotones (D'Odorico et al., 2010), but T_{min} during the extreme event was unrelated to shrub density. Therefore, the positive feedback between shrub encroachment and temperature (D'Odorico et al., 2010; He, D'Odorico, & De Wekker, 2015), was not enough to buffer *L. tridentata* from extreme cold, and several days of extreme cold temperatures presumably overpowered positive temperature feedbacks within shrublands (Figure 1). Shrubs may benefit from temperature feedbacks during average conditions, but the advantage disappears during extreme events when temperatures are well below physiological tolerances. Canopy dieback was related to shrub density, as shrubs in the high-density sites experienced more extreme dieback. Canopy size likely influenced this response, as smaller shrubs are more vulnerable to stress, such as drought (Reynolds, Virginia, Kemp, de Soyza, & Tremmel, 1999). Ecotone shrubs were generally larger and had less extensive canopy mortality. However, size was only negatively related to canopy dieback at one site and only accounted for a small percentage (6–14%) of the variation in dieback; therefore the response was not completely driven by plant size.

Cold temperatures led to extensive canopy dieback but not complete shrub mortality. After three years of recovery, shrub canopies covered 40% of the area they previously covered in the shrublands, and 63% of the area in ecotones (Figure 6). The height of new leaf tissue highlighted the variation in stem tissue damage between shrublands and ecotone sites. Stem damage was extensive in the shrublands, evident by most canopies re-forming via basal regrowth (Figure 5). Meanwhile, stem damage was less extensive in ecotone regions and many ecotone individuals were able to resprout from the tips of existing stems (Figure 5) and set seed within the first year (Figure 7). Location of regrowth also influenced canopy dimensions as shrubs with only basal regrowth had small, dense canopies while shrubs with branch resprouting had larger, more dispersed canopies.

Canopy volumes increased during recovery, and three years after the cold event 12% of the shrubs had completely recovered to pre-freeze canopy volumes predominantly through branch resprouting. It is unclear how long complete recovery will take, but the timing may be similar to recovery from other disturbances. For example, after repeated vehicle damage, *L. tridentata* experienced no mortality and canopy size recovered within five years (Gibson, Sharifi, & Rundel, 2004), and following roller-chopping, productivity of the related species *Larrea divaricata* recovered to pretreatment levels in four years (Marchesini, Fernández, Reynolds, Sobrino, & Di Bella, 2015). Resprouting patterns of *L. tridentata* are also linked to disturbance severity (Bellingham & Sparrow, 2000). Since shrubland individuals experienced more severe damage, they will presumably take longer to fully recover than ecotone individuals. Rate of recovery is also presumably influenced by soil moisture availability, with greater soil moisture leading to faster recovery. The cold event occurred during a prolonged drought, and drought not only slows recovery of *L. tridentata* following disturbance (Gibson et al., 2004) but can intensify the influence of extreme temperatures (Hamerlynck, Huxman, Loik, & Smith, 2000). Even though *L. tridentata* is more drought-resistant than other desert shrubs (McAuliffe & Hamerlynck, 2010), extensive drought can lead to *L. tridentata* mortality in the Sonoran Desert (Bowers, 2005). Both drought and cold temperatures initially decrease plant performance, but can also increase the stress tolerance of individuals to future stressful events (Medeiros & Pockman, 2011). Soil moisture on average is lower in shrublands than ecotones (Bhark & Small, 2003); therefore shrubland individuals may be more drought stress-adapted than ecotone shrubs, yet the opposite pattern in cold damage was observed. Instead, the slightly cooler average temperatures in ecotones might have conditioned ecotone individuals to colder temperatures, which increased their resistance to the extreme cold event.

With regard to shrub encroachment, a single extreme cold event may have limited impacts on colonization of *L. tridentata* in neighboring grasslands. Even when coupled with long-term drought, established shrubs did not die from this extreme cold event. Additionally, during the first year of recovery when canopies were a fraction of their initial size, the majority of ecotone shrubs still produced seeds. High seed set during recovery was not surprising since *L. tridentata* flowers when stressed (Cunningham, Syvertsen, Reynolds, & Willson, 1979; Sharifi et al., 1988). Even though *L. tridentata* seed viability can be low (McGee & Marshall, 1993) and successful seedling establishment is rare (Ackerman, 1979), seed production following the stressful winter provided the potential for seedling establishment and shrubland expansion. Furthermore, many plant–plant interactions occur belowground, and although air temperatures greatly decreased, soil temperatures remained fairly constant throughout the cold event (unpublished data). Belowground tissues presumably experienced less, if any, damage from the extreme event and therefore belowground plant–plant interactions could continue during canopy recovery. Cold temperatures kill *L. tridentata* seedlings (Medeiros & Pockman, 2011) and successful establishment requires a narrow set of conditions (Ackerman, 1979; Moreno-de las Heras, Turnbull, & Wainwright, 2016; Reynolds et al., 1999). Therefore, although one event may have limited impacts on shrub expansion, clustered cold events, such as the several cold events between 1930s and 1950s (Figure 3c), could both decrease mature shrub performance and kill seedlings. As temperatures continue increasing, the frequency of extreme cold events clustered in subsequent years is likely to decrease, thus limiting the influence of extreme cold temperatures on future range limits.

Plant communities are changing in response to a rapidly changing climate, and species responses at range boundaries are likely to be most sensitive to climate extremes. Therefore, it is important to examine how communities along ecotones respond to climate variation to predict the rate of community dynamics in the future (Peters et al., 2006). Understanding the shrubland to grassland ecotone is particularly timely because the mostly irreversible switch from grasslands to shrublands causes ecological and economical concern worldwide (Eldridge et al., 2011). Although periodic and short-lived, extreme events can influence shrubland dynamics differently than gradual, constant changes. Initial response of *L. tridentata* to extreme cold was much more dramatic than initial response to drought (Báez, Collins, Pockman, Johnson, & Small, 2013), yet shrubs were quick to regrow, particularly in ecotones. Understanding how foundation species, such as *L. tridentata*, respond to extreme events, particularly along transition zones, will help elucidate the potential for shrub encroachment to continue under future climate change scenarios that include warmer winter minimum temperatures on average, along with more frequent extreme events.

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DATA AVAILABILITY STATEMENT

Data are available on the Sevilleta Long Term Ecological Research website (https://sevlter.unm.edu/data), Data set ID 244.

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