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Extensive drought-associated plant mortality as an agent of type-conversion in chaparral shrublands

Authors for correspondence:
Anna L. Jacobsen
Tel: +1 661 654 2572
Email: ajacobsen@csub.edu

R. Brandon Pratt
Tel: +1 661 654 2033
Email: rpratt@csub.edu

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Anna L. Jacobsen* and R. Brandon Pratt*

Department of Biology, California State University, Bakersfield, 9001 Stockdale Hwy, Bakersfield, CA 93311, USA

Contents

	Summary	498
I.	Introduction	498
II.	Ecological drought and vegetation type-conversion	499
III.	Chaparral mortality during extreme drought events	501
IV.	Some species survive drought and others do not	501
V.	Recovery potential	502
VI.	Conclusions	503
	Acknowledgements	503
	References	503

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Summary

California experienced an intense drought from 2012 to 2015, with southern California remaining in drought to the present. Widespread chaparral shrub mortality was observed during the peak of the drought in 2014. Some species were more impacted than others and shallow-rooted shrub species were the most vulnerable to drought-associated mortality. This type of drought represents what is termed an 'ecological drought' during which an ecosystem is driven beyond thresholds of vulnerability, triggering impairment of ecosystem services and feedbacks that may result in long-term type-conversion of natural communities. The ability of shrublands to recover will depend on the timing, intensity and seasonality of future extreme climate events, post-fire recruitment potential of species with obligate fire-associated recruitment, and interactions with other stresses.

I. Introduction

California experienced an intense 3-year drought from 2012 to 2015 that attracted widespread attention. The drought was the most intense in the last 1200 yr (Griffin & Anchukaitis, 2014). Drought-associated affects were apparent across many ecosystems. Forests were transformed by an estimated mortality of > 100 million trees (USDA, 2016). Even large and exceptionally long-lived tree species, such as the iconic giant sequoia (*Sequoiadendron giganteum*), were affected (Stephenson *et al.*, 2018).

One biotic community in California that was not widely discussed during the ongoing drought was chaparral shrubland, the most extensive biotic community in California. Chaparral shrublands are abundant in the mountains of southern California, and also occur sporadically throughout the state (Parker *et al.*, 2016). This closed-canopy community, dominated by evergreen shrubs, is

*These authors contributed equally to this work.

recognized for being highly biodiverse (Parker *et al.*, 2016) and includes many endemic species (Rundel *et al.*, 2016). Drought events, where below-average annual rainfall occurs, are not uncommon in southern California (Cowling *et al.*, 2005). Chaparral shrub species display a range of adaptations to tolerate periodic low soil moisture, high temperature and dry air conditions (Esler *et al.*, 2018).

Heavy precipitation in 2016 and 2017 in northern California has mitigated drought in that region; however, drought has continued for the southern third of the state (2012–present, Fig. 1). As of December 2017 significant rains had yet to fall in much of southern California. During these ongoing dry conditions, the largest fire in state history, the Thomas fire, burned in December 2017 in what would typically be the winter-wet season.

In this paper, our objective was to evaluate how intense droughts affect chaparral communities. We focused on mortality of dominant species including an evaluation of why some species are more sensitive to drought-induced mortality than others. Finally, we considered the prospects for recovery of chaparral communities that have already been strongly affected by drought.

II. Ecological drought and vegetation type-conversion

Ecological drought refers to droughts that lead to water deficits that drive ecosystems beyond thresholds of vulnerability, impair ecosystem services, and trigger feedbacks in natural and human systems (Crausbay *et al.*, 2017). One manifestation that ecosystem thresholds have been surpassed is when a system converts from one vegetation type to another in what has been called vegetation type-conversion, as illustrated in Fig. 2. Chaparral type-conversion occurs when this closed-canopy community transitions to one that is more open; ruderal sage scrub species or invasive grasses often colonize the newly created open spaces between shrubs (Fig. 2). Type-conversion is a continuum rather than a binary and the defining continuous feature for chaparral shrublands is the degree of canopy openness (Keeley *et al.*, 2005). Altered fire regimes have led to widespread type-conversion in chaparral (Jacobsen *et al.*, 2004; Keeley & Brennan, 2012). When fires occur in short-return intervals, the species that rely on a dormant fire-cued seedbank to recover cannot persist because the seedbank has not had time to recover from the previous fire. Drought may also type-convert chaparral (Park *et al.*, 2018), as has been described for forests (Millar & Stephenson, 2015).

An important aspect of community change, separate from stand structure, is the loss of certain functional groups from communities that we refer to as ‘functional type-conversion’. Chaparral communities are composed of species with different life history types that are characterized with respect to their modes of post-fire recovery. Obligate seeding species do not resprout after fire and regenerate through germination of fire-cued seed banks. Facultative seeding species regenerate through post-fire seed germination and also resprout after fire from their root crown. Obligate resprouting species regenerate following fire solely through resprouting and their seeds do not survive fire. These different life history types represent different functional types (Pratt *et al.*, 2007). Obligate seeding species are highly dehydration tolerant, whereas obligate resprouting species include the most dehydration-avoidant taxa found in chaparral, and facultative seeding species tend to be intermediate to the other types (Jacobsen *et al.*, 2007). Obligate seeding *Ceanothus* spp. are also nitrogen fixers, and thus their loss

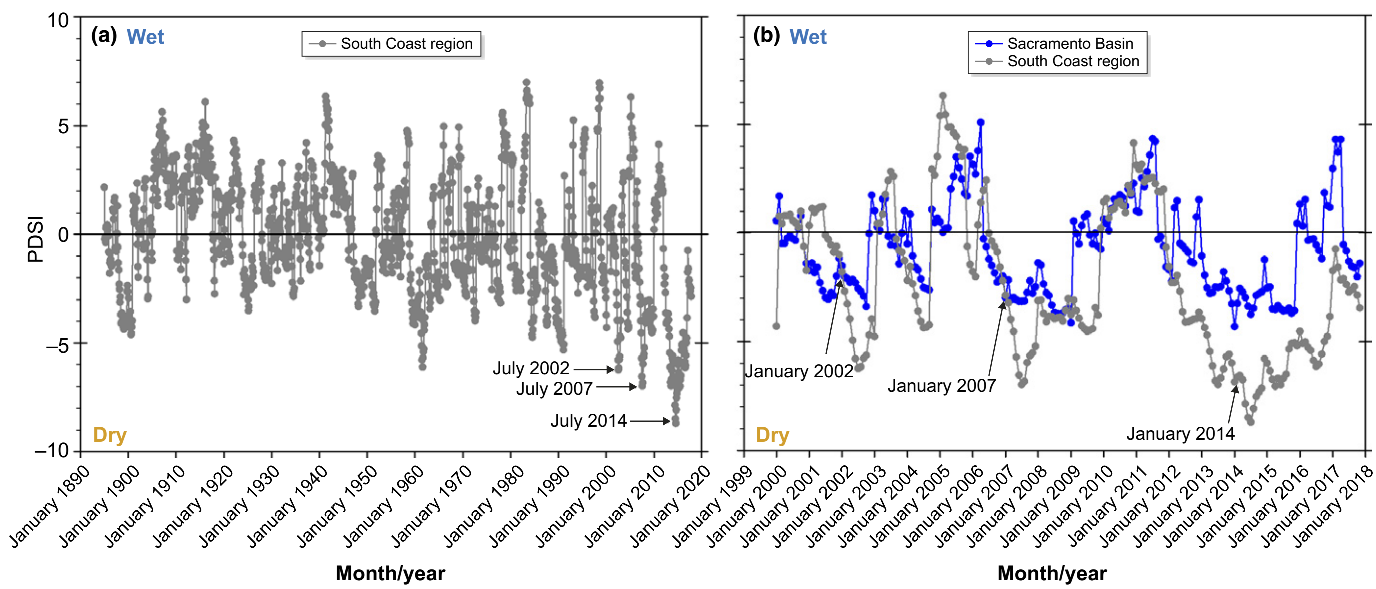

Fig. 1 Palmer Drought Severity Index (PDSI) values from (a) the last 121 yr and (b) since 2000 for the southern coast region of California. This region includes the cis-montane areas from about Pismo Beach to San Diego and is dominated by chaparral. For comparison, data are also shown from northern California, represented by the Sacramento Drainage Basin (b). PDSI values are based on precipitation inputs and temperature to measure drought conditions and this index is correlated with soil moisture. Negative PDSI values indicate drought, positive values indicate wet years and zero is the average. In recent years, dry season (July) PDSI has reached a series of new record lows (a). In the most recent extreme drought period, there was also intense drought during the normally moist winter (January 2014) (b). From 2016 to the present, southern California has remained in drought, while northern California has had wet periods (b). Data are from the National Oceanographic and Atmospheric Administration (NOAA) National Centers for Environmental Information.

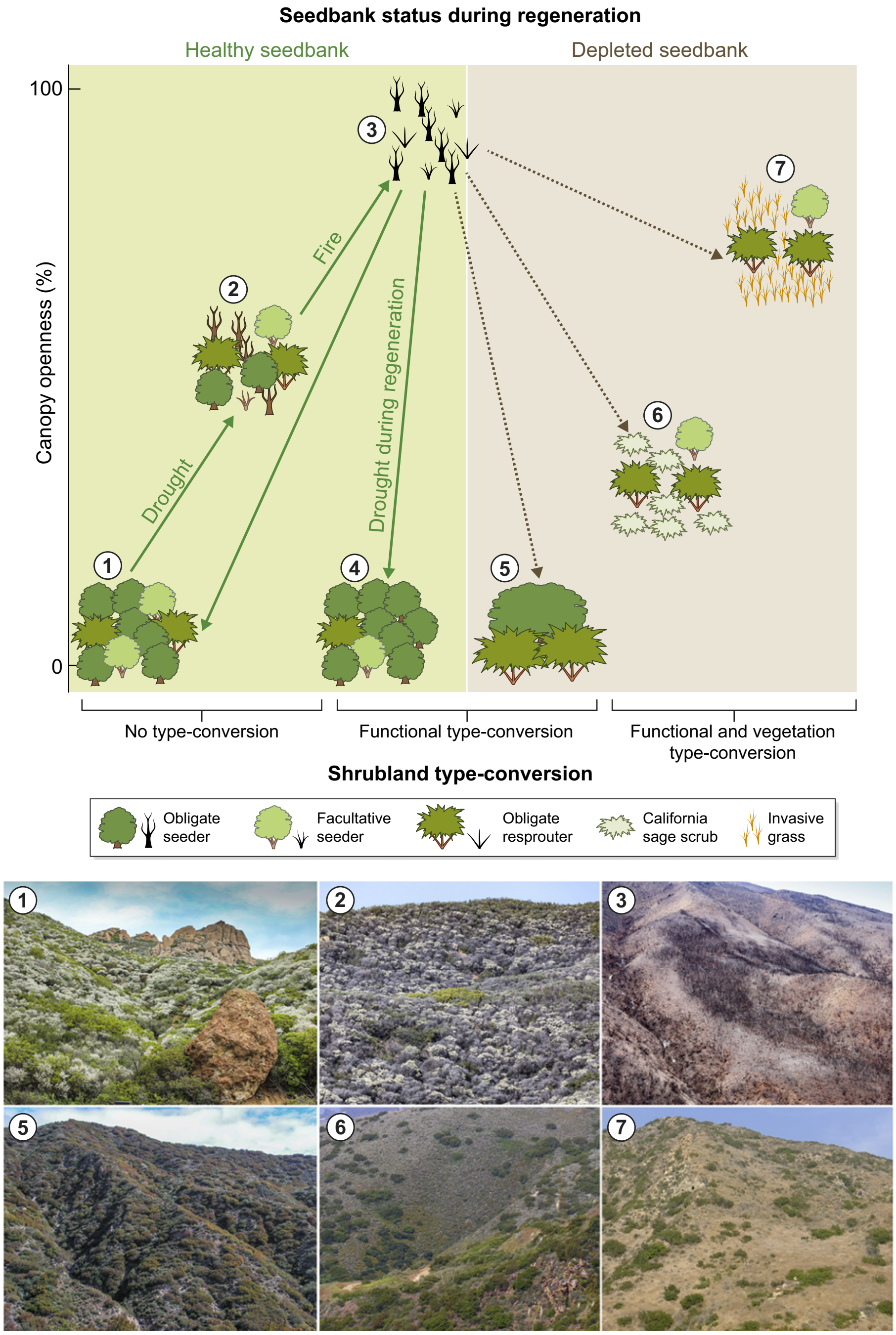

Fig. 2 Vegetation type-conversion of chaparral occurs along a continuum of canopy openness, while functional type-conversion occurs when species representing distinct functional types are lost or decrease in abundance. While some changes may be reversible, through the process of post-fire succession, other changes may be permanent without active restoration. An intact and mature mixed chaparral stand (1) contains both seeding and resprouting species. A chaparral stand (1) that experiences drought and subsequently contains individuals that experienced drought-associated mortality (2) may be able to recover back to the same state (1) following a fire (3), provided that the seed bank at the site is not limited. If intense drought occurs during the post-fire recovery period, resprouting species abundance may become reduced (4), creating gaps for obligate seeding species to establish (Pausas & Keeley, 2014; Pratt *et al.*, 2014), and thus the community remains a closed-canopy shrubland. The progression leading to type 4, a closed-canopy seeding species-dominated shrubland, would probably take more than one fire cycle as depicted. If the seed bank is limited, then drought and fire will lead to an alternative series of possible post-fire community types. Resprouting species may thrive in the absence of abundant obligate seeding species and, over time, resprouting shrubs may expand to fill in the gaps left by the loss of obligate seeding shrubs (5; Lucas *et al.*, 2017). The vegetation may type-convert to a resprouter-dominated open-canopy shrub savannah with coastal (California) sage scrub species colonizing the openings (6) or with invasive grasses and forbs colonizing open spaces (7). Photos show examples of different stages of canopy openness across sites historically dominated by closed-canopy mixed chaparral shrublands. Numbers on the photo panels correspond to the similar community type in the diagram above. Photos 1 and 2 were taken in the same area of the western Santa Monica Mountains before the drought (February 2013) and after the peak of the drought (February 2016) when abundant dead shrubs of obligate seeding *Ceanothus megacarpus* are visible as gray branches amidst the white flowering survivors.

represents a further functional transformation of the system. Vegetation type-conversion always leads to functional type-conversion in chaparral, but there are cases where the loss of obligate seeding species does not lead to vegetation type-conversion (Fig. 2, type 5). Recent droughts have created a series of natural experiments by which to study how drought might contribute to chaparral type-conversion, which is valuable because there has been very little research on the link between drought and type-conversion.

III. Chaparral mortality during extreme drought events

In recent decades, southern California has experienced a series of extreme and record-setting drought events (Fig. 1). In 2001–2002, Los Angeles experienced what was then the lowest rainfall-year recorded since records began in 1877 (112 mm compared to the 375 mm average). An even lower amount of precipitation was recorded (82 mm) for the 2006–2007 rainfall-year. Both of these droughts were associated with the lowest Palmer Drought Severity Index (PDSI) values in the last 121 yr, indicative of extreme drought.

The most recent drought, 2012–present, differed from previous ones in several important ways. The drought was more protracted and intense than other recent droughts, driven by a combination of above average temperatures and below average precipitation (Diffenbaugh *et al.*, 2015; Luo *et al.*, 2017). At the peak of this drought, January–October 2014, PDSI values were lower than all previous records (Fig. 1a). The period of extreme drought also extended into the winter months, with very low PDSI values in the two coldest months, December and January 2014 (Fig. 1b). Subzero temperatures can lead to freeze–thaw stress and this stress is exacerbated when plants are also dehydrated (Ewers *et al.*, 2003). This interaction between drought and freeze–thaw stress was probably a key driver of mortality for many winter-active evergreen chaparral shrubs.

Chaparral mortality patterns have differed during recent drought events. During the 2001–2002 drought, mortality of chaparral shrubs was observed along a desert–chaparral ecotone (Paddock *et al.*, 2013). In areas of higher average annual precipitation, in the center of chaparral distribution, effects were observed as a sharp decline in the Normalized Difference Vegetation Index (NDVI) (Sims *et al.*, 2006) and net ecosystem flux measures indicated that a chaparral community, which had been a CO_2 sink, became a strong CO_2 source during the drought (Luo *et al.*, 2007). During the 2006–2007 drought, some mortality was observed away from arid ecotones and one study found considerable mortality of resprouting shrubs after fire (Pratt *et al.*, 2014). These past drought events suggested that chaparral communities were relatively resilient to short-term high-intensity droughts. Mortality was observed in arid ecotones and dry microsites, already at the extreme of the distribution for chaparral, and when drought interacted with other stressors such as fire.

By contrast, the most recent drought (2012–present) triggered significant dieback and mortality of adult shrubs in many regions throughout southern California, including areas in the center of chaparral distribution. At one chaparral site, stand density was reduced by > 60%, primarily due to mortality that occurred during winter 2014, and some species exhibited > 90% mortality (Venturas *et al.*, 2016). The same patterns were also apparent at broader scales (Coates *et al.*, 2015).

The reasons why the most recent drought event was more severe are probably a combination of factors that include both drought duration and intensity (McDowell *et al.*, 2008; Pausas *et al.*, 2016). Peak mortality events were associated with very low PDSI values, with high chaparral mortality during winter 2014 during an especially intense period (Fig. 1; Venturas *et al.*, 2016). If drought duration was the key driver of chaparral mortality, one would predict mortality events to occur repeatedly as the drought continued, rather than the observed episodes of mortality during the periods of highest drought intensity. Nevertheless, drought duration may be linked to mortality for some species. Laurel sumac (*Malosma laurina*), a deep-rooted resprouting species, is often the dominant shrub still persisting in type-converted savannahs in coastal areas of southern California (Fig. 2, photo 7). This species has experienced ongoing mortality during the drought that has been linked to the opportunistic pathogen *Botryosphaeria dothidea* (Aguirre *et al.*, 2018). The mortality patterns for *M. laurina* are consistent with long-term drought limiting carbon gain and leading to a decline in energy reserves available to defend against pathogens.

Not all droughts are ecological droughts and understanding the characteristics of these droughts is an important area of research. Elevated temperatures play an important role in drought-induced mortality (Allen *et al.*, 2015). Higher temperatures reduce water vapor in the air leading to greater water losses from plants (Allen *et al.*, 2015; Diffenbaugh *et al.*, 2015), and they can lead to unsustainable negative carbon balances due to decreased photosynthetic rates and increased respiration rates (Oechel & Lawrence, 1981). Another important consideration are extremes in climate that occur over sub-annual time frames (e.g. Crimmins *et al.*, 2017).

IV. Some species survive drought and others do not

During drought, it is common that some species are more strongly affected than others (Martínez-Vilalta & Lloret, 2016) and this has been the case for chaparral species (Fig. 3a). Elucidating the physiological factors that determine drought resistance is an important research objective, especially for use in predictive models (Anderegg *et al.*, 2015; Adams *et al.*, 2017). Proposed mechanisms for differential drought resistance have focused on the ability to sustain water transport and to acquire and transport carbohydrates during drought (Anderegg *et al.*, 2015; Pausas *et al.*, 2016).

Among chaparral species, differences in rooting depth were strongly associated with levels of drought-associated mortality (Fig. 3b; Supporting Information Fig. S1). Species with more restricted root systems, such as *Ceanothus* spp., *Arctostaphylos* spp. and *Adenostoma fasciculatum* (Tables S1, S2), were particularly affected by drought and this included mortality of many individuals (Paddock *et al.*, 2013; Venturas *et al.*, 2016). More deeply rooted chaparral species (e.g. *Quercus* spp. and *Rhus ovata*) were less visibly affected.

Having shallow roots probably leads to increased vulnerability to drought-induced hydraulic failure due to cavitation. This has been

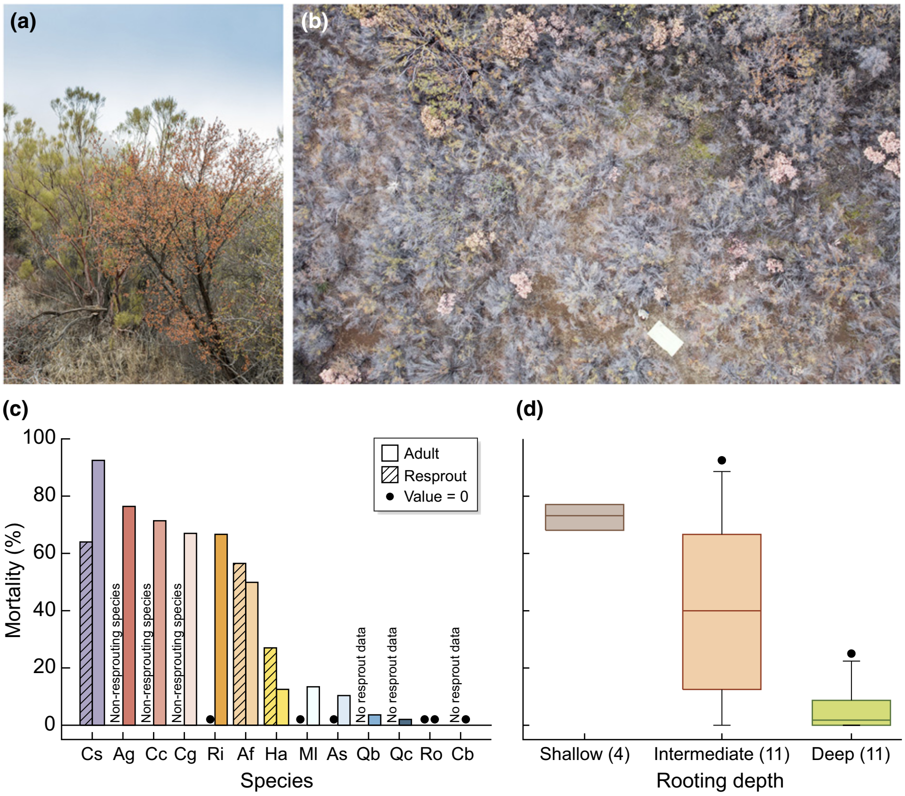

Fig. 3 During the recent extreme California droughts, shrub mortality differed among species. A dead shallow-rooted, obligate seeding *Ceanothus megacarpus* shrub is visible in the foreground while a still living deep-rooted, obligate resprouting *Adenostoma sparsifolium* shrub is visible behind it (a). The combination of mortality and canopy dieback resulted in openings in the canopy of chaparral shrublands, which are typically closed-canopy evergreen systems (b). The light-colored rectangle visible in the aerial photo view is *c.* 1 m by 2 m in size (b). Species mortality during the drought ranged from over 90% to 0% (c; different colors indicate different species). The species with the highest mortality tended to have shallow roots, while deeply rooted species exhibited low mortality levels (d; different colors indicate different rooting depth categories in this boxplot). Key to species mortality and rooting depth data, and sources for these data are included in the Supporting Information (Tables S1–S3; Notes S1). Cs, *Ceanothus spinosus*; Ag, *Arctostaphylos glauca*; Cc, *Ceanothus cuneatus*; Cg, *Ceanothus greggi*; Ri, *Rhamnus ilicifolia*; Af, *Adenostoma fasciculatum*; Ha, *Heteromeles arbutifolia*; Ml, *Malosma laurina*; As, *Adenostoma sparsifolium*; Qb, *Quercus berberidifolia*; Qc, *Quercus cornelius-mulleri*; Ro, *Rhus ovata*; Cb, *Cercocarpus betuloides*.

well documented for chaparral shrubs (Paddock *et al.*, 2013; Venturas *et al.*, 2016). Shallow-rooted species are the most dehydration tolerant, are highly resistant to xylem cavitation and are adapted to extract the maximum amount of moisture from dry soils (Pratt *et al.*, 2007; Pausas *et al.*, 2016). However, these highly cavitation-resistant shrubs are the ones that are the least resistant to high-intensity drought (Paddock *et al.*, 2013; Pausas *et al.*, 2016). This result confounds a simple view of cavitation resistance as a key trait that determines drought resistance.

The species that were most affected by the drought were predominantly obligate seeding species (Table S3). Because of the high diversity represented by this group, high mortality of these species represents a threat to chaparral biodiversity. In the short term, drought has reduced the abundance of these species from chaparral stands and altered the composition of some communities, leading to partial functional type-conversion (Venturas *et al.*, 2016; Fig. 2).

V. Recovery potential

If the shrubs lost due to the drought cannot be replaced by recruitment, then drought becomes an agent of type-conversion (Fig. 2). Many of the most affected chaparral species (i.e. *Ceanothus* spp.) have fire-cued seeds with limited dispersal, so local seedbank dynamics will be key in determining replacement of drought losses. *Arctostaphylos* spp. fruits are dispersed by vertebrates and may be able to disperse longer distances into affected sites, albeit in limited numbers. Most obligate resprouting species recruit seedlings during inter-fire periods in the shady understory of closed chaparral canopies; thus, newly open canopies will limit recruitment opportunities (Parker *et al.*, 2016).

Successful recruitment from the seed bank will be affected by several factors, many of which are not well studied and represent important areas for future research (Del Cacho & Lloret, 2012; Parker, 2015). One key factor is the seed input from surviving individuals: where survival numbers are low and seed predation is high, inputs may not be sufficient for recovery (Fig. 2). Seed banks may be further depleted by atypical germination and failed recruitment between fires (Del Cacho & Lloret, 2012). Adult mortality creates gaps in the canopy and this can lead to warming of the soil surface. For some species (e.g. *Ceanothus* spp. and *A. fasciculatum*), this warming is sufficient to break dormancy, but seedling recruitment fails, leading to a reduction in the available post-fire seed bank (Burns, 2014).

Recovery also depends on the interaction between drought and fire, which will affect the ability of recruited seedlings to survive and persist. Importantly, resprouting species may also be affected by drought during the post-fire recovery period (Pratt *et al.*, 2014; Pausas *et al.*, 2016), making the combination of fire and drought particularly likely to lead to type-conversion. Finally, the creation of canopy gaps in drought-affected stands opens up formerly closed-canopy chaparral systems and facilitates invasion by non-native annual species (Fig. 2), which may impact fire regimes, nutrient dynamics, and species interactions that feedback and reinforce type-conversion (Dickens & Allen, 2014).

VI. Conclusions

Climate change models predict an increase in extreme climatic events, and these extreme events are likely to lead to ecological droughts. Following recent widespread mortality, many chaparral stands have thinned, which should reduce competition for water and make them more resilient to subsequent drought-driven losses over the short term (Gleason *et al.*, 2017). However, future drought events, especially those occurring with increased intensity and/or frequency, are likely to move these systems further along the type-conversion continuum. With drought continuing in southern California, large areas of chaparral shrublands may be at risk of type-conversion.

Extensive surveying during the recent California drought was undertaken for California's forests (USDA, Office of Communications, 2016), but the same intense surveys of shrublands were lacking. Increased information on the extent of impacts on this important system is critical for addressing a wide range of questions. Understanding the links between plant and community traits, landscape heterogeneity, and risk of mortality are important in predicting the impacts of future extreme events and planning appropriate conservation, mitigation or adaptation strategies, especially in the context of extensive land use change, degradation and interactions with other stresses (Keeley *et al.*, 2009).

One important way that chaparral ecosystems interact with society is through periodic wildfire. Dehydrated plants contain less moisture and will ignite more readily, and dead biomass is drier for more of the year, extending the fire season. These factors may contribute to more frequent, larger and more dangerous fires (Keeley *et al.*, 2009), similar to that in December 2017. Type-converted landscapes, with flashy fuels (senesced grass shoots), may permanently alter fire regimes and increase the frequency of fires on the landscape. Changes in fire regime further increase losses of the vulnerable obligate seeding species (Jacobsen *et al.*, 2004; Keeley & Brennan, 2012). For some of these species, active restoration may be required to maintain them within these heavily impacted systems. Many of these same patterns are occurring in shrublands that occupy other mediterranean-type climate regions (Esler *et al.*, 2018).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article:

Fig. S1 The relationship between rooting depth and mortality for selected chaparral species.

Table S1 Maximum and mean rooting depth of selected chaparral species and data sources

Table S2 Rooting depth categories (shallow, intermediate, deep) of selected chaparral species and data sources

Table S3 Species, abbreviations, life history type and reported levels of drought-associated mortality for selected chaparral species and mortality data sources

Notes S1 References for all data included within supporting information Tables and Figures.

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