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REVIEW ARTICLE

Causes and feedbacks to widespread grass invasion into chaparral shrub dominated landscapes

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Abstract

Context This study provides a unified, holistic framework for predicting the dynamics of shrub-grass conversion throughout Mediterranean-climate shrublands. This work focuses specifically on the California chaparral, which until recently has been considered resistant to invasion by exotic grasses, but in recent years appears to have undergone substantial type conversion.

Objectives To synthesize current understanding of the feedbacks and anthropogenic impacts that both enhance and reduce the susceptibility of southern California chaparral to invasion and its corresponding ability to recolonize invaded areas.

Methods We review the existing literature pertaining to the factors that enhance or reduce the susceptibility of chaparral to invasion, and organize these factors and their interactions into a single unified framework of environmental drivers, ecological interactions, and historical legacies associated with the distribution and rate of such invasion.

Results A myriad of processes interact to mediate the invasion of exotic grasses into intact chaparral. In addition, we demonstrate that feedbacks exist within both chaparral shrublands and exotic grasslands that modify the landscape in ways that can enhance their own survival, act as barriers to conversion into alternate cover types, and in some cases weaken the resistance of adjacent vegetation to invasion. We posit a methodological framework from which the many climatic, anthropogenic, edaphic, and biotic feedbacks that determine the mosaic of invasion can be modeled.

Conclusions This study demonstrates that substantial conversion of chaparral into deciduous grasslands has recently occurred in southern California and presents a unified framework for forecasting the dynamics of shrub-grass conversion throughout Mediterranean-climate shrublands.

Keywords Chaparral · Invasion · Ecological forecasting · Alternate stable states · Landscape restoration

Introduction

While woody plant encroachment into grasslands is a global phenomenon, grass invasion into communities previously dominated by closed canopy woody plants is also occurring (D'Antonio and Vitousek 1992;

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Costello et al. 2000). California chaparral represents an ideal study system for examining the dynamics of grass invasion into closed canopy woodlands, as it represents a highly diverse vegetation formation that is situated at a nexus of factors disrupting their historical assemblage including climate change, increasing encroachment and fragmentation, grazing, more rapid fire cycles, and pressure from invasive species. While chaparral has been considered uniquely resistant to grass invasion (Knops et al. 1995; Minnich and Bahr 1995), grass invasions into shrub communities are increasing in extent (Keeley 2004; Syphard et al. 2019) and represent a significant portion of landscapes formerly classified as intact chaparral (Park et al. 2018). Examinations of the distribution of grass and herbaceous cover throughout National Forests of southern California that were conducted at 30-m scale using newly developed remote sensing methods (Park et al. 2018) suggest that grasses and herbaceous cover now compose approximately 34% of land cover within historically chaparral shrublands, with 24% of areas classified as chaparral exhibiting over 50% cover by grasses and herbaceous species (Fig. 1). Human encroachment progressively fragments chaparral, providing corridors for invasion (Lambrinos 2006), while nitrogen (N) pollution improves the competitive ability of many exotic species (Fenn et al. 2010), and climate change threatens to disrupt the historical conditions in which chaparral thrived (Kelly et al. 2008). As a result of the combined pressures associated with encroaching development, progressive fragmentation, accelerating fire cycles, and increasing proximity to invasive seed sources, chaparral and other Mediterranean shrublands are experiencing increased encroachment and conversion into invaded grasslands (D'Antonio and Vitousek 1992; Figueroa et al. 2004; Gritti et al. 2006). Thus, although relatively intact until recent decades, this unique ecosystem is at increased risk of invasion and conversion into grasslands throughout much of its remaining range.

Due to the historical resilience of chaparral ecosystems to invasion and most research emphasizing woody plant encroachment into historic grasslands, the causes and consequences of grass invasion and chaparral type-conversion, the long-term replacement of chaparral vegetation by exotic-dominated grasslands, remain uncertain. The mechanisms facilitating or hindering invasion of closed-canopy chaparral likely differ substantially from processes facilitating grass invasion other open-canopy Mediterranean shrublands, such as coastal sage scrub, that have historically been vulnerable to invasions. As a result, the risk, distribution, and extent of future displacement of many of the species that constitute chaparral vegetation by exotic grasses, as well as the means by

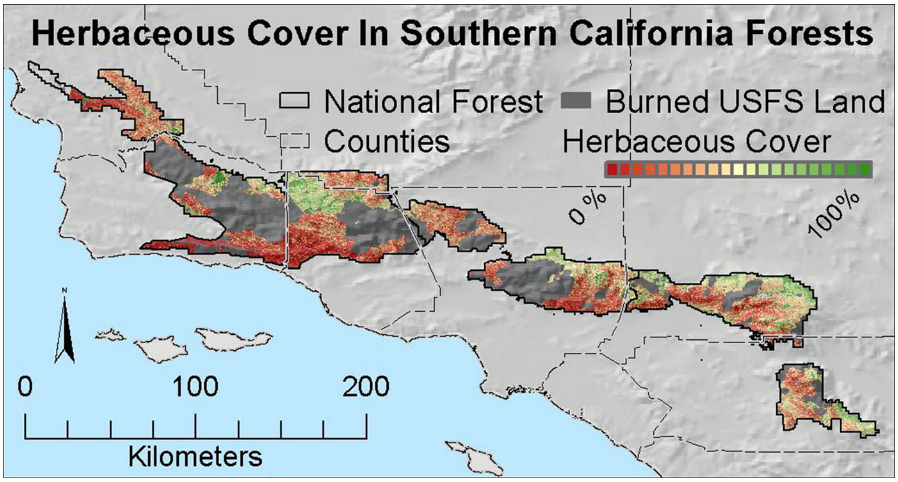

Fig. 1 Estimated % cover by grasses and other herbaceous cover throughout National Forest lands across southern California as of 2008. Grey areas indicate recently burned locations in which cover estimates are unreliable. Percent herbaceous cover was estimated using a recently developed remote-sensing method that leverages intra-annual phenological differences in normalized difference vegetation index (NDVI) between herbaceous forbs and grasses and evergreen shrublands using Landsat remote-sensing imagery (Park et al. 2018)

which such invasion may be delayed, restricted, or reversed, remain poorly understood.

Identifying the potential for future invasion requires a systematic examination of the feedbacks that promote or hinder invasion, as well as the factors that may disrupt the resilience of chaparral vegetation to invasion and displacement by exotic grasses. Here, we review the growing literature that has identified the many factors governing the invasion and type-conversion of closed canopy chaparral to invasive annual grasses. We organize these factors and their interactions into a single unified framework of environmental drivers, ecological interactions, and historical legacies associated with the distribution, magnitude, and rate of such invasion. In so doing, we identify the network of feedbacks that reinforce the resistance of chaparral to invasion, the anthropogenic drivers that disrupt shrub feedbacks and provide opportunities for grass invasion, and the subsequent feedbacks of the new vegetation type to restrict the recolonization of shrubs throughout a landscape.

Reinforcing feedbacks promoting chaparral resistance to invasion

Historically, attempts at deliberate conversion of most forms of chaparral vegetation have met with mixed success. Intentional conversion of chaparral to grasslands for grazing has been found to require a combination of physical brush removal or herbicidal application and controlled burns conducted in combination with deliberate seeding of exotic annual grasses to successfully convert intact chaparral into grasslands (Bentley 1967; Murphy and Leonard 1974; Green 1977). Moreover, invasions occurred almost exclusively along the edges of intact chaparral stands, while the invasion front proceeded only slowly, if at all (Zink et al. 1995; Davies et al. 2013) except in cases or repeated burning at rapid intervals (Haidinger and Keeley 1993; Keeley and Brennan 2012). Thus, barring intense or frequent disturbance, the interior of chaparral is historically highly resistant to invasion and type conversion. This resistance to invasion is likely the result of a combination of climatic and biotic factors that are associated with intact chaparral. Intact chaparral has been found to produce specific regimes of fire frequency and intensity, soil moisture, and small mammal herbivory that generate positive feedbacks which prevent invasion by exotic grasses, and may also provide a barrier to invasion by intercepting sufficient light to outshade any seedling of exotic species. These barriers may be removed or disrupted, however, once alternate cover types are established.

Historical fire cycle

Chaparral is often referred to as a fire-adapted system due to the extreme intensity of fires in chaparral ecosystems. However, California chaparral has historically exhibited long intervals between fires, with median fire return intervals of 24–65 years prior to Euro-American settlement (Van de Water and Safford 2011). Many chaparral species have seeds that require scarification or are tolerant of the extreme heat events associated with the burning of old growth chaparral (Borchert and Odion 1995). Soil heating or burning have also been found to significantly enhance the emergence of many chaparral species (McPherson and Muller 1969; Christensen and Muller 1975a; Keeley et al. 1985; Keeley and Keeley 1987; Parker 1987). Other species regrow from rootstock, allowing rapid recolonization and canopy closure even after intense burn events (Keeley and Zedler 1978).

In contrast, the long-interval and high-temperature burn cycles that characterize historical chaparral communities have several negative impacts on exotic herbs and grasses. The years immediately following fires may be critical opportunities for grass invasion due to reduced ground cover (Keeley et al. 2003), and long-interval fires limit the number of these occurrences, thereby limiting invasion opportunities. When fires do occur in mature chaparral, they are associated with surface temperatures in excess of 700 °C (Borchert and Odion 1995; Odion and Davis 2000), and soil temperatures that reach 200–300 °C even at 3 cm depth (Christensen 1985). While these temperatures are sufficient to incinerate most seeds at surface level regardless of species, most native shrub species do experience successful post-fire germination from cached or buried seeds after even extreme fire events (Christensen and Muller 1975b; Moreno and Oechel 1991; Borchert and Odion 1995). However, species not adapted to extreme temperatures often experience substantial seed mortality as a result of the intense heating associated with shrubland fires (Keeley 2001; Brooks 2002; DiTomaso et al. 2006), including the invasive species *Taeniatherum caput-medusae,* and multiple *Bromus* species. Thus, if these seeds are able to accumulate from nearby areas in intervals between fire, the historical pattern of infrequent but intense fires may act as a filter to invasion by limiting opportunities for colonization by many exotic species, while also purging them from the seedbank.

Herbivory

While changes in the fire regime disrupt a key element of chaparral resistance to invasion, herbivory also plays a key role. Cattle grazing, for example, has been found to prevent recolonization of recently converted grasslands by native shrubs (Johnson and Fitzhugh 1990). Deliberate grazing by cattle and other ungulates is currently limited in California chaparral, however, and thus likely plays a minimal role in the broad-scale invasion history of California chaparral. In contrast, herbivory by rodents and other small mammal herbivores may be essential in mediating the competitive dynamic between shrubs and grasses. In nearby California grasslands, herbivory by native rodents has been found to both facilitate and maintain invasions by some exotic grass species through increased predation of native seeds adjacent to stands of invasive grasses (Orrock et al. 2008). Rodents typically browse primarily underneath the chaparral, where they are more protected from birds and other large predators than in open grasslands (Bartholomew 1970; Davis and Mooney 1985; Tyler 1995). As a result, the number of herbs and grasses that occur within intact chaparral stands are dramatically reduced (Davis and Mooney 1985). Similarly, exclusion of herbivores within mature chaparral has been found to dramatically increase the abundance and biomass of herbaceous species (Tyler 1995, 1996).

In chaparral, rodent herbivory has been observed to reduce survival of invasive grasses *Cortaderia jubata* and *Cortaderia selloana* to nearly zero (Lambrinos 2002, 2006). Similarly, rabbit herbivory may also be capable of excluding annual grasses from intact chaparral stands (Bartholomew 1970). As small herbivorous mammals typically browse grasses and shrubs both underneath and immediately adjacent to chaparral shrubs, where the shrub canopy protects them from predators, rodents are also likely responsible for a 1–2 m ‘bare zone’ often observed at the edges of chaparral stands where the dominant cover transitions from chaparral to grass (Bartholomew 1970). However, rodent herbivory has been found to be reduced post-fire (Tyler 1995), indicating that fire-related rodent mortality may play a critical role in the post-fire success of chaparral invasion by exotic herbs and grasses.

Rodent herbivory may also explain the low abundance of grass seedlings under open chaparral canopies in which light interception is unlikely to exclude such species (Muller 1982). In contrast, similar rates of seedling survivorship have been observed in bare soil and under intact chaparral canopies in cases where herbivores were artificially excluded (Lambrinos 2006). Thus, the action of small mammal herbivores in restricting establishment of exotic herbs and grasses underneath chaparral may do much to explain the resistance often observed by chaparral to invasion by exotic grasses and the ability of chaparral shrubs to displace exotic grasslands once established.

Soil nitrogen

Chaparral shrubland has historically been considered to be an N limited system (McMaster et al. 1982; Vourlitis et al. 2009). Many plant species include traits promoting nutrient conservation, including long leaf lifetimes, nutrient-poor sclerophyllic tissues, and nutrient resorption during senescence, which lead to conservation of N within plants and high N use efficiencies (Mooney and Rundel 1979; Gray and Schlesinger 1983). The paucity of soil nutrients, particularly N, may also limit the ability of rapidly growing, potentially invasive species to colonize and outcompete local species that are more adapted to low-nutrient conditions.

Anthropogenic factors that alter competitive dynamics between shrubs and grasses

Increasingly, human activity is altering chaparral ecosystems in multiple ways that may disrupt barriers to invasion through increasing fragmentation, increased fire ignitions, and increased N deposition. These changes interactively have altered the resistance of many components of chaparral to invasion, and have also increased the competitive ability of invasive grasses. In recent years, the majority of ignitions in

California chaparral have been attributed to human activity that has dramatically accelerated the frequency of fire (Conard and Weise 1998; Syphard et al. 2007), while simultaneously opening previously intact shrublands to invasion (Syphard et al. 2007; Keeley and Syphard 2018). More rapid fire cycles also reduce the amount of time that many shrub species have to replenish the seedbank (Zedler et al. 1983; Zammit and Zedler 1988). In cases where fires occur with sufficient frequency to re-burn chaparral before it reaches reproductive maturity, repeat ignitions may even preclude the reseeding of many chaparral shrubs, with particularly deleterious effects on obligate seeders (Zedler et al. 1983). Rapid fire cycles also result in lower burn intensities due to reduced fuels as compared to mature chaparral, thereby removing filters that limit the presence of invasive species in the seedbank.

Human development and land use change is progressively encroaching into and fragmenting chaparral vegetation. Development is frequently associated with increases in the presence of exotic and invasive species used in landscaping, thereby placing a much larger area of chaparral in close proximity to invasive vegetation and reducing the area of chaparral interior that is not in close proximity to invasive species. The increasing presence of human development within chaparral also results in increased rates of ignition, as well as increased concern about fire prevention. The construction of firebreaks intended to control fire can cause further fragmentation of chaparral and act as corridors for invasive species (Merriam et al. 2006). Increased concern about the danger of fires within the urban-wildland interface has also dramatically increased the rate of mechanical fuel removal treatments since the year 2000 (Brennan and Keeley 2015). Such treatments are intended to reduce the risk of intense fires to built structures (Agee and Skinner 2005), but are also associated with reduced cover by chaparral and corresponding increases in the presence of exotic herbs and grasses within the treated areas (Brennan and Keeley 2015). Thus, human development is simultaneously fragmenting chaparral and increasing its exposure and proximity to potentially invasive exotic species, while also removing many of the barriers that typically exist within chaparral to hinder invasion.

Human activity also impacts the competitive balance between native shrubs and invasive grasses through increased N deposition that results from atmospheric pollution. This is particularly evident in southern California, where increased atmospheric pollution has led to nitrogen deposition rates exceeding 90 kg ha^{-1} year^{-1} (Fenn et al. 2008; Bytnerowicz et al. 2015). Studies of nearby open canopy coastal sage scrub and desert communities have found that increased N deposition enhanced the growth rates of invasive grasses, many of which often threaten chaparral, while not benefitting native shrubs that are adapted to the historically N-poor soils of the region (Allen et al. 1998; Weiss 1999; Fenn et al. 2010; Vourlitis 2017). Artificial N fertilization of soil from mature (90 + year old) chamise chaparral was observed to more than double biomass production of barley and ryegrass seedlings (Hedrick 1951). Many if not most non-native annual grass species respond strongly to soil N additions by increasing growth and seed production (Huenneke et al. 1990; Allen et al. 1998; Weiss 1999; Yoshida and Allen 2004; Fenn et al. 2010). Increased N deposition in combination with drought may even lead to increased shrub mortality (Valliere et al. 2017). The intense atmospheric pollution experienced by much of California chaparral is therefore likely to increase the ability of invasive grasses to compete with native shrub seedlings, particularly after major disturbances when mature chaparral cover has been removed.

Reinforcing feedbacks of established grasslands

In addition to anthropogenic changes to the landscape that enhance the ability of grasses to colonize landscapes historically dominated by chaparral, established grasslands also exhibit multiple feedbacks that hinder recolonization by chaparral species and result in the converted grasslands acting as a new stable state (Schultz et al. 1955; Allen 1999). This occurs through not only alterations to the fire regime, but also changes in local fauna and biogeochemical feedbacks that alter the competitive dynamics between the two vegetation types.

Altered fire dynamics

The increased presence of exotic grasses in and around chaparral has been observed to increase the frequency of fire by allowing more rapid regeneration of groundcover (D'Antonio and Vitousek 1992; Keeley 2001), increasing the ease of ignition (Bradshaw et al. 1983), and by extending the length of the fire season (Keeley 2000). At the same time, grass cover limits the total amount of fuels in comparison to stands of intact chaparral, which in turn reduces fire intensity in comparison to chaparral. These departures from the long-interval, high-intensity fires that are the historic norms for chaparral are often detrimental to the survival and recruitment of many chaparral shrub species (Zedler et al. 1983; Haidinger and Keeley 1993; Keeley et al. 2005a), while also providing direct benefits to invasive forbs and grasses (Keeley 2001; Keeley and Brennan 2012).

First, grasslands generate fires that burn with far less intensity than intact chaparral, with peak soil surface temperatures of only 170–245 °C (Rundel 1983) and peak soil temperatures under 50 °C at 5 cm soil depth (Neary et al. 1999). These low-temperature fires result in much lower fire-related mortality among grasses and invasive herbs than the more intense fires experienced by chaparral. Additionally, rapid fire cycles benefit exotic grasses by removing competing species that require longer time periods to reseed, and benefiting species that are capable of the most rapid recolonization and maturation, particularly annual grasses. While annual grasses require only a single year to produce seed, shrubs will often require many years between germination and reseeding (Keeley 1992). As chaparral shrubs require longer periods of time to regenerate than grasses and annual herbs, fires that recur at 5–10 year intervals may kill shrub saplings before they have the ability to replenish the seedbank (Zedler et al. 1983; Zammit and Zedler 1988). Examinations of short interval fires have found that reseeding shrubs typically germinate profusely after the first fire event, but are almost completely extirpated if a second fire occurs before seedlings can mature enough to replenish the seedbank (Zedler et al. 1983; Keeley 1992; Haidinger and Keeley 1993; Keeley and Brennan 2012).

Short intervals between fires can also reduce the ability of native shrub species to regenerate rapidly post-fire. As resprouting shrubs invest a large portion of their belowground energy stocks in post-fire resprouts, long intervals between fires allow those belowground energy reserves to replenish. Short-interval fires, which may destroy recently resprouted plants before they recover their carbon investment, can lead to high mortality among resprouting species due to the energy loss sustained from regenerating after repeated fires (Zedler et al. 1983; Haidinger and Keeley 1993; Keeley and Brennan 2012). Thus, as the fire interval shortens, the ability of both seeding and some resprouting shrubs to compete is reduced, thereby increasing the success of exotic weeds (Haidinger and Keeley 1993; Lippitt et al. 2012).

Altered soil moisture availability

Differences in the use of soil moisture by intact chaparral and grasslands also produce feedbacks that alter the availability of soil moisture both to themselves and to their competitors. Moisture availability has also been found to be critical in the success of post-fire chaparral recolonization. Low moisture would typically benefit exotic herbs and grasses, while high moisture availability, particularly in the years immediately following fire, benefits native shrubs (Frazer and Davis 1988; Keeley et al. 2005b).

This simple relationship is complicated, however, by the fact that grasses are shallow-rooted in comparison to many chaparral shrubs. As grasses are unable to access water at depths below their roots (Williamson et al. 2004b), they intercept far less moisture than chaparral shrubs (Rowe 1963; Corbett and Crouse 1968; Williamson et al. 2004a). As a result, conversion of chaparral into grasslands results in increased moisture availability in the soil below 0.6 m (Davis and Mooney 1985; Eliason and Allen 1997), within the rooting depth of most chaparral shrubs. Throughflow and downstream soil moisture (Bentley 1967; Hibbert 1971; Davis 1984) as well as groundwater recharge (Williamson et al. 2004b) have also been found to increase after conversion from chaparral into invaded grasslands, and even to convert streams from intermittent to perennial (Orme and Bailey 1970). Increased throughflow and moisture availability at depths below the root horizon of grasses and herbs may benefit chaparral shrubs that occur at downstream sites or harden mature shrubs that persist within areas that have largely type-converted to grasses.

However, while grasses remove less moisture from the soil overall, they dramatically reduce soil moisture at depths of less than 0.6 m (Davis and Mooney 1985), resulting in more xeric conditions within the soil at shallower depths than occur within intact chaparral. This decrease in near-surface soil moisture may increase drought stress and mortality among shrub seedlings whose roots have not yet penetrated into the deeper soil below where grasses cannot reach. Intensive seeding of exotic grasses after clearing of chaparral reduces moisture in the soil above 0.6 m, and has led to nearly 100% mortality of shrub seedlings due to severe drought stress (Schultz et al. 1955). Thus, while grasses may increase overall soil moisture, they also generate a layer of near-surface soil that is far more xeric than under intact chaparral. This shallow zone of highly xeric soil, which does not adversely affect mature shrubs, nevertheless acts as a bulwark against chaparral recolonization by inhibiting the survival of newly germinated chaparral seedlings.

Altered nitrogen cycling

While in neighboring open-canopy coastal sage shrub communities, grass invasion may tend to increase N storage (Wolkovich et al. 2010) and facilitate recolonization by shrubs (Wolkovich et al. 2009), grass invasion in closed-canopy chaparral potentially has the opposite consequences, leading to decreased available N for shrub recolonization by increasing rates of N loss from the ecosystem and increased immobilization of N during rapid grass growth during the wet season. Grass invasion can increase N losses through hydrologic pathways (Longstreth and Patten 1975; Davis and Debano 1986; Davis 1987) and possibly atmospheric pathways, especially during the wet-to-dry transition. In part increasing losses may be associated with annual grass litter, which is generally more labile and rapidly decomposed than evergreen perennial shrub litter (Cornwell et al. 2008).

Indirectly, grass may lead to N losses through increased erosion and increased water loss and the N stored in these soil and dissolved pools, by increasing fire frequency and therefore N volatisation, and by interfering with nitrogen fixing species that are common in many forms of chaparral, such as *Ceanothus*. During the wet season, however, the rapid growth of grasses may immobilize N and restrict N availability (Homyak 2012). Together, the influence of grass litter during the wet-to-dry transition, which promotes N losses, and the influence of grass immobilization during the growing season, which may restrict N availability, both act as a positive feedback that enhances grass invasion while restricting available N for shrub recolonization. Direct tests of N cycle feedbacks of grass invasion into chaparral are needed as current evidence is limited and chaparral biogeochemical dynamics are highly dynamic.

Toward a general framework of grass invasion into mediterranean-climate landscapes

Chaparral-grass conversion dynamics appear to be controlled by multiple simultaneous drivers, each of which increase or decrease the rate or likelihood of chaparral conversion into grass cover and whose states are influenced by external controls and internal feedbacks (Fig. 2). As such, the interactive effects of environment, ecological feedbacks, and historical legacies jointly influence trajectories of grass invasion or chaparral recovery. A state-transition framework that considers simultaneously how factors that reinforce either shrub or grass dominance and promote transition between states provides a synthetic approach. Such a framework can help assess the vulnerability of chaparral shrublands to conversion and invasion risk and also assist in better designing restoration efforts. Simultaneously assessing the likelihood of chaparral community in situations where herbivory, fire frequency, moisture availability, or soil N could be modified may allow for better assessments in chaparral dominated regions experiencing multiple drivers of environmental change.

Feedbacks are important drivers of shrub and grass resilience to state changes. Each vegetation type, once established, alters local conditions in a variety of ways that generally benefit that vegetation type or provide barriers to colonization by alternate vegetation types. In addition to acting as seed sources for the regeneration of nearby chaparral, established chaparral reduces invasion success by invasive species through facilitating rodent herbivory, promoting a longer, more intense fire regime which reduces invasion opportunities while also removing invasive seeds from the seedbank, and by increasing near-surface soil moisture in comparison to exotic-dominant grasslands, which is necessary for shrub seedling recruitment (Davis and Mooney 1985). In contrast, exotic grasslands promote frequent, low-intensity fire regimes, which increase invasion opportunity and do not produce sufficient soil heating to remove invasive seeds from the seedbank. Grasses also increase the aridity of near-surface soils, which increase drought

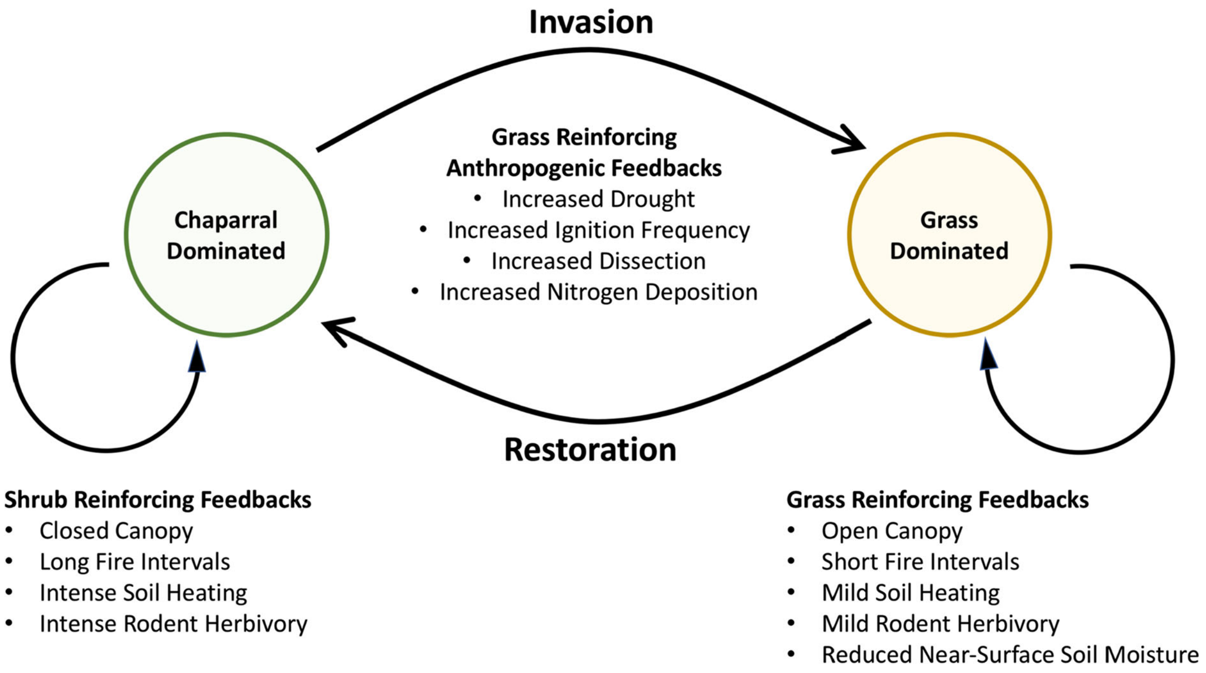

Fig. 2 Feedbacks among grass-dominated and chaparral-dominated vegetation, as well as anthropogenic disruptions, and their relative benefit to chaparral or grass cover

mortality among shrub seedlings, and hinder rodent herbivory through increased risk of predation. Thus, any attempt to model the likelihood of chaparral-grass conversion must ultimately incorporate the network of feedbacks that occur within each cover type that make them more or less resistant to colonization by alternate cover. As chaparral vegetation often occupies highly heterogeneous landscapes, the interaction these feedbacks and the local topography and soil types must also be accounted for. This is particularly true when examining vegetation in areas that are downstream in any given watershed, as the vegetation, fire history, and soils that are located upslope within a given watershed may impact not only the moisture availability (Dunn et al. 1988) but also the quantity (Orme and Bailey 1970) and nitrogen content (Goodridge et al. 2018) of soil runoff that may flow into downslope areas (Rowe 1963). In a systems framework the main effects of individual factors to changes in vegetation type, including herbivory, fire frequency, moisture availability, and other factors, are themselves dependent on vegetation dynamics. Thus, the predicted importance of each driver is continuously updating in response to changes in local shrub and grass cover.

By incorporating the ability of both chaparral shrubs and invasive grasses to alter local conditions in order to harden themselves against colonization by alternate vegetation types, we can evaluate not only the likelihood of local type-conversion, but also the effects of disturbances or climate abnormalities that may counteract, disrupt, or intensify those effects, and thereby open windows of opportunity for colonization by alternate vegetation types. As the quality and duration of large-scale climate, biophysical, and vegetative data continue to mount, the development and empirical testing of such models represent a promising future for developing our understanding of the dynamics underlying vegetation conversion both within chaparral and within analogous Mediterranean shrublands across the globe.

Shared dynamics across worldwide Mediterranean-climate shrublands

Many drivers and feedbacks influencing grass invasion into southern California chaparral shrublands may also be common among other closed-canopy shrublands, especially in other areas that experience Mediterranean climates. This is particularly true in relation to fire, as increased fire frequency has been associated with increases in invasion across Mediterranean-climate shrublands throughout five continents (van Wilgen and Richardson 1985; D'Antonio and Vitousek 1992; Haidinger and Keeley 1993; Vilà et al. 2001; Brooks et al. 2004; Gómez-González et al. 2011). Grass cover in other Mediterranean shrublands has been associated with more rapid fires, which in turn promote additional expansion by grasses into adjacent shrublands (Grigulis et al. 2005). Although the relationship of fire frequency to the survival of native shrubs in the South African fynbos is mixed (van Wilgen and Richardson 1985), likely due to simultaneous invasion by both exotic shrub and grass species, increased cover by exotic shrubs has been found to reduce fire frequency while increasing fire intensity (van Wilgen and Richardson 1985), as in chaparral. Similarly, increased cover by invasive grasses is associated with increased fire frequency, and lower fire intensity (Brooks et al. 2004). Fire in Chilean mattoral, which until recently was largely absent (Muñoz and Fuentes 1989; Holmgren 2002), has been associated with increased dominance by both native and exotic annuals (Gómez-González et al. 2011). However, as native shrubs in mattoral are not as fire adapted as many other Mediterranean shrublands, high fire intensities can result in extreme mortality in the seedbank of native shrubs, thereby limiting post-fire recovery among many species (Segura et al. 1998). Thus it is clear that, while some differences do exist, fire often plays a similar role as a driver of grass invasion across Mediterranean shrublands worldwide.

Unlike chaparral, large mammal grazing appears to play a major role in most other Mediterranean shrublands. However, the effects of large mammal grazing vary depending on the relative palatability of local shrubs and grasses. In Australian shrublands, grazing has been one of the major factors promoting invasion into native grasslands by native shrubs that are unpalatable to grazers (Costello et al. 2000). In California coastal sage scrub, however, the elimination of ungulate grazing has been found to promote conversion of exotic grasslands back into shrublands (Johnson and Fitzhugh 1990). The unpalatability of most chaparral shrubs to many large ungulates, and resulting lack of intensive grazing, is potentially responsible for the relative absence of large mammal herbivory as a major factor in chaparral shrub-grass invasion dynamics.

Management implications

Collectively, these results indicate that no single driver should be viewed as a 'silver bullet' when it comes to predicting type-conversion or restoration potential. Instead, any attempt to forecast the impacts of future conditions on chaparral invasion or post-disturbance recovery will require an overlay of the impacts among all factors that may contribute to the invasion success of exotic grasses, or to the recolonization success of chaparral shrubs into invaded areas (Allen et al. 2018). Characterizing the site-specific impact of each factor that alters the likelihood of vegetation conversion will require local characterization of site-specific conditions, such as are provided by sources such as the National Cooperative Soil Survey and the Ecological Site programs, in combination with remote sensing tools and local meteorological information (Park et al. 2018).

Future research needs

The framework presented here provides a systems approach for studying and forecasting the dynamics of shrub and grass invasion across Mediterranean-climate shrub dominated landscapes. A key need for future research is to quantify the magnitude of feedbacks that occur as the composition of the local vegetation changes in the context of landscape distributions of invasion and environmental conditions. Shrub-grass transition may introduce many feedbacks that lead to alternate stable state dynamics (Stylinski and Allen 1999; Lett and Knapp 2003; Cox and Allen 2008). The potential for nonlinearities among these relationships are high, particularly in cases such as drought stress, where thresholds of soil moisture may result in sudden increases in seedling mortality (Oechel 1988). Prediction of grass invasion into chaparral also requires improved monitoring tools capable of identifying the current status of chaparral environments in order to facilitate predictions of future vegetation change. Newly available metrics for examining the coverage by grasses and shrubs across the landscape at both fine scales and broad areas show potential for providing the broad scale, fine-resolution mapping of vegetation cover that will be needed to conduct large-scale prediction of future grass invasion into chaparral (Park et al. 2018). Advances in computing power available to ecological researchers are now sufficient to overcome much of the intensive amount of processing that have thus far prevented such data from being incorporated into spatially explicit predictive models. As the quality and availability of fine-scale and broad-scope climate, topographic, and vegetation data are increasingly available to power generalized models capable of predicting the dynamics of grass and shrub invasion, the primary barrier to the implementation of broad-scale predictive models is now largely one of merging big data computational techniques with ecological modelling and remote sensing analysis. By using the emerging linkages between ecological modelling and recent advances in spatiotemporal analysis and big data techniques, a unified framework for assessing landscape distributions of chaparral shrub vulnerability to grass conversion throughout Mediterranean-climate landscape.

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Data availability Example code used to produce estimates of herbaceous cover in this study are available through: https://doi.org/10.6084/m9.figshare.6203366.

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