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Cumulative effects of fire and drought in Mediterranean ecosystems

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Abstract. The occurrence of multiple disturbances can jointly affect the recovery capacity of ecosystems, potentially leading to changes in vegetation dynamics or loss of resilience. The effects of interacting disturbances on ecosystems are, however, not well understood. We use a model system based on Mediterranean-type ecosystems (MTEs) to examine how the interplay between vegetation regeneration traits and compound, stochastic disturbances modulate ecosystem dynamics. We developed a state-and-transition simulation model including two tree species with contrasting regeneration strategies (seeder vs. resprouter) and a shrubland formation. We aim to assess potential compositional switches under contrasted scenarios of compound fire–drought regimes, and to characterize the cumulative effects of fire–drought (synergism vs. antagonism) relative to the effects of individual disturbance regimes. Our simulation results indicate that interaction between moderate fire and sporadic drought recurrence—as opposed to chronic dryness—can act as a strong mechanism generating highly heterogeneous landscapes in which different regeneration types coexist, as observed in MTEs. Resprouters dominated under individual, moderate disturbance regimes of fire or drought, whereas the interaction of the two disturbances promoted the long-term coexistence of both tree regeneration strategies. However, shrubland expansion and persistence at the expanse of forests was favored by increases in drought recurrence and associated fire–drought interactions, highlighting the potential for important vegetation changes in MTEs under climate change. Overall, the cumulative effects of fire and drought can lead to distinct landscape configurations under moderate disturbance regimes that are otherwise only attained under high frequency of individual disturbances. At the ecosystem level, however, we suggest that disturbance-induced vegetation dynamics can modify vegetation sensitivity and resilience to further disturbances precluding the prevalence of synergistic effects of the two disturbances.

Key words: additive model; climatic change; compound disturbance regimes; cumulative effects; drought; ecosystem resilience; fire; Mediterranean ecosystems; regeneration traits; sequence of events.

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Introduction

Most ecosystems are subject to natural disturbances that operate across a range of temporal and spatial scales and shape their structure and function. Extreme drought events, understood as exceptionally severe episodes of water deficit, and fire are two major disturbances that affect the dynamics and composition of ecosystems worldwide (e.g., Bond et al. 2005, Allen et al. 2010). As temperature and precipitation directly influence water deficits and vegetation flammability, climatic changes are likely to trigger substantial alterations in the scale, frequency, and intensity of drought and wildfire (Moritz et al. 2012, Allen et al. 2015).

Despite general understanding of the impacts and climate-related alterations of specific disturbance regimes on ecosystems, the influence of possible interactions among different disturbance types is not well understood (Seidl et al. 2011, Enright et al. 2014). Interactions among disturbances may be seen as compound perturbations (Paine et al. 1998), because the occurrence of several disturbances jointly affects the recovery capacity of ecosystems. The combined effects of multiple disturbances can be higher (synergism) or lower (antagonism) than the additive sum of effects elicited by the disturbance regimes acting in isolation (additive model, Folt et al. 1999, Crain et al. 2008, Piggott et al. 2015). Potentially complex synergistic or antagonistic interactions among disturbance types may lead to long-lasting impacts on ecosystem structure and function (Turner 2010, Buma 2015). A better understanding of the cumulative and interacting effects of multiple disturbances on ecosystem dynamics is therefore a pressing issue in ecology and conservation (e.g., Mouillot et al. 2013, Côté et al. 2016, Foster et al. 2016).

The response of vegetation to disturbance regimes is strongly influenced by species' capacity to persist by resprouting and/or regenerating from a persistent seed bank. The tight relationship between regeneration strategies and disturbance regimes suggests that any changes in the frequency and intensity of disturbances might differentially affect the abundance of species with these two major regeneration traits (e.g., Lloret et al. 2005, Vilagrosa et al. 2014). In this study, we used a model system based on Mediterranean-type ecosystems (MTEs) to increase our understanding of multiple disturbance interactions on long-term vegetation dynamics, which can be characterized by contrasting regeneration strategies of woody plants in MTEs. Also, given their climatic characteristics, MTEs may be especially sensitive to projected changes in climate leading to increased aridity (e.g., potential increases in fire occurrence, mediated by productivity, Batllori et al. 2013, Bedia et al. 2015, higher recurrence of extreme droughts, IPCC 2014).

Functional, quantitative classification of plant traits provides a powerful framework to model landscape–disturbance interactions and to assess potential changes in vegetation composition, structure, and function (Lavorel et al. 2007, Enright et al. 2014). Existing modeling approaches that assess the coexistence of seeding and resprouting species (e.g., Bradstock et al. 1998, Zavala and Zea 2004, Pausas and Lloret 2007, Miller and Chesson 2009, Esther et al. 2010) do not incorporate compound disturbance effects on the dynamics of vegetation. We developed a state-and-transition simulation model (STSM; Daniel et al. 2016) to assess how the interplay of disturbance interactions and regeneration traits influence long-term vegetation responses. The model, extended from Batllori et al. (2015), is comprised of two tree species with contrasting regeneration traits (seeder vs. resprouter) and a shrubland formation composed by a mix of species and regeneration strategies. Our intent is to incorporate general ecological principles into the model so that the underlying mechanisms, and thus simulation results, depend less on the specific biology of the species being represented than on the qualitative features of regeneration traits and the effects of interacting disturbance regimes.

In this investigation, we aim to identify key patterns in ecosystem dynamics under compound fire–drought disturbance regimes in MTEs, as mediated by regeneration traits and vegetation characteristics (fuel load and flammability). We hypothesize that the effects of interacting fire and drought disturbance events drive landscape configurations in ways that differ from considering these two disturbances separately. To test this general hypothesis, we assess the effects of disturbances on long-term vegetation dynamics (i.e., over multiple disturbance events) under fifteen individual and compound fire–drought regimes. Specifically, we (1) examine the influence of interacting disturbances on vegetation composition relative to individual disturbance regimes; (2) test whether the effects of interacting fire and drought on vegetation composition are synergistic or antagonistic following the additive effects model (Folt et al. 1999); and (3) evaluate the influence of simultaneous and consecutive disturbance events as mechanisms contributing to observed vegetation dynamics. Regeneration traits (seeder vs. resprouter) are widely recognized in MTEs, where major disturbances such as fire and extreme drought events shape vegetation characteristics and landscape dynamics (e.g., Keeley et al. 2012, Allen et al. 2015). However, given the prevalence of disturbance interactions—both biotic and abiotic—and similar regeneration traits in many other ecosystem types, findings from this model system can provide relevant insights for the dynamics of a broad range of environments (e.g., austral and boreal forests, savanna systems, subalpine forests; Weber and Flannigan 1997, Bigler et al. 2005, Midgley et al. 2010, Landesmann et al. 2015).

Methods

Model overview

The simulation model, programmed in R statistical language (R version 3.2.2; R Core Team 2015), corresponds to a STSM integrated in a landscape of 400 (20 × 20) cells where vegetation dynamics is influenced by stochastic regimes of fire (implemented as a spatially explicit process) and sporadic, extreme drought. Each cell is described by the following state variables: the proportion of six major vegetation types, their corresponding live and dead biomass values, and a cell-level counter of time since disturbance that modulates processes of vegetation state change. Vegetation types are defined by broad formations, constituted by sparse vegetation, shrublands, and two developmental stages (young vs. mature) of a tree seeder and a tree resprouter. The time counter is applied at the cell level, assuming that ecological properties (i.e., biomass level and sensitivity to fire and drought) are equivalent irrespective of the age within a given vegetation state, once that vegetation state is reached.

For this investigation, we assumed that shrublands are dominated by a mix of fire- and drought-adapted species with high capacity to resprout or recover from seed after disturbance (Vilà-Cabrera et al. 2008), whereas sparse vegetation is considered a formation with low vegetation cover. The tree seeder is characterized by traits of pioneer species: fast growth, early maturity, and massive seed production and dispersal (Sheffer 2012). The young seeder vegetation type corresponds to seedlings and saplings that are highly sensitive to fire and drought and that are not able to produce seeds, so their recovery after disturbance depends on seed inputs from the mature seeder class (Bradstock et al. 1998, Moya et al. 2008). On the other hand, the tree resprouter incorporates traits of late-successional species such as low chance of germination in open environments and high persistence of established individuals (Sheffer 2012). The mature resprouter class corresponds to plants with high basal resprouting capacity after the disturbance-induced death of the aboveground biomass and moderate ability of crown re-greening after drought (e.g., Lloret et al. 2004, Catry et al. 2010). Finally, the young resprouter vegetation type corresponds to individuals recently established or regrowing that exhibit lower capacity for basal resprouting compared to mature resprouters due to a smaller amount of accumulated carbon reserves, resulting in a higher sensitivity to fire and drought than mature individuals (e.g., Lloret et al. 2004).

We considered that the tree resprouter is less sensitive to both fire and extreme drought—as opposed to low or moderate and long-term dryness—than the seeder (Pausas et al. 2016), but both resprouting and seeding capabilities are modulated by disturbance occurrence and recurrence. Seeds are only produced in mature seeders, incorporating maturation time, whereas resprouters gradually recover their resprouting capacity after disturbance, incorporating the effect of repeated disturbances on the ability of plants to accumulate reserves and resprout (e.g., López et al. 2009). We assume that neither seed germination nor resprouting occurs in drought years (e.g., Galiano et al. 2013).

While extremely simplified, we believe the basic vegetation types described above, along with their different response to disturbances, are suited to simulate the main patterns of landscape dynamics in MTE forests such as the natural or seminatural pine–oak systems that dominate extensive areas in the Mediterranean Basin (e.g., *Pinus halepensis–Quercus ilex*, Zavala et al. 2000; *Pinus brutia–Quercus calliprinos*, Sheffer 2012; *P. halepensis–Q. calliprinos*, Sheffer et al. 2013). Characterization of vegetation traits in the model may be modified to apply to other environments where regeneration traits are correlated differently to other life-history traits (e.g., pioneer vs. late-successional species).

The spatial scale of the model is not explicitly fixed, but it would correspond to a regional landscape affected by major synoptic weather conditions (e.g., extreme drought episodes) where each cell would represent an area large enough (e.g., 0.5–1 km^2) to encompass a mix of vegetation types with shared environmental conditions and capabilities to respond to the ecological processes incorporated in the model. Vegetation processes are implemented cell by cell, but each cell's dynamics is coupled with the rest of cells both by disturbance regimes and by the influence of landscape properties (e.g., fraction of mature forests, biomass) on the rate of vegetation succession and replacement processes or the likelihood of fire. For instance, the system recovery rate is modulated by the fraction of mature forests, as a lower fraction of mature forests (at both the cell level and landscape level) results in a lower rate of shrubland to forest succession. Succession to forest stops if the mature tree seeder and resprouter disappear completely from the landscape. Therefore, although colonization is not explicitly incorporated in the model, the influence of landscape-level properties on the rate of vegetation processes is intended to implicitly incorporate landscape-scale processes such as dispersal in modulating vegetation dynamics (Zavala and Zea 2004).

Changes in each cell's vegetation composition (Fig. 1a) are driven by succession to forest (e.g., change from shrubland to forest), maturation (e.g., change from young to mature classes), and replacement processes (e.g., change among forest types). Fire and drought events (Fig. 1b, c), both defined as sporadic mortality factors, can set vegetation back to earlier successional stages (e.g., change from forest to shrubland). Shrublands and seeder-dominated forests are not successionally stable in the current formulation of the model; if disturbance processes do not occur, they transition to resprouter-dominated forests, representing major successional pathways across the Mediterranean Basin MTEs.

In this study, one time step of the model represents one year, and model parameterization and the environmental conditions of the system (except disturbance stochasticity) are held constant over all cells and over time. The overall environment determines the baseline rate of change among the vegetation types and the baseline disturbance regime characteristics, which consist of the frequency and intensity of fire risk and drought.

Process scheduling and ecological principles

The overall model procedure and the basic ecological principles associated with each rule are outlined below. See full model description and formalization following the Overview, Design concepts, Details protocol (ODD; Grimm et al. 2010) and sensitivity analysis in the Supporting Information (see Appendices S1 and S2, respectively; Batllori et al. 2015).

To accommodate multiple transition types derived from vegetation succession and disturbances, processes that determine the state of each cell between time steps are applied sequentially (Daniel et al. 2016). At each time step (a year), the model first determines whether drought, understood as episodes more severe than the typical summer dryness of MTEs, will occur. Sporadic drought episodes are implemented through the generation of random deviates with a certain inter-drought interval (see *Modeling scenarios*). Drought influences the entire landscape at a given model step (i.e., all cells are simultaneously affected), and vegetation succession, maturation, and replacement processes stop during such episodes to incorporate the limitations imposed by water deficit in vegetation growth and biomass accumulation (e.g., Beer et al. 2010). If drought does not occur, processes of vegetation change occur first (Rule 1), followed by updating of live and dead biomass (Rule 2), to simulate the growing season. In drought years, drought-induced mortality takes place (Rule 3). Then, if ignition occurs, fire spreads through the landscape from a random starting point (Rule 4; see details of each model's

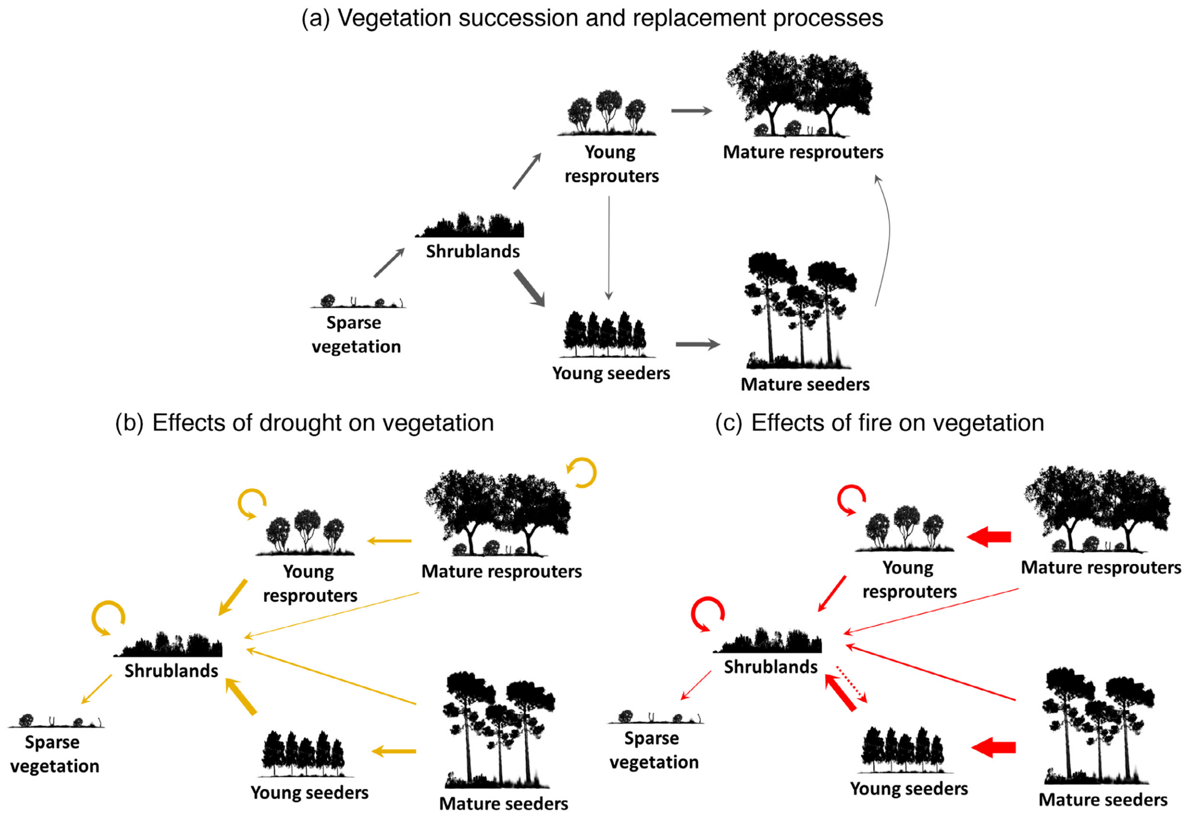

Fig. 1. Model structure: (a): successional, maturation, and replacement pathways among the six vegetation types of the system (gray arrows), (b) and (c) effects of drought and fire, respectively, on vegetation dynamics (red arrows). Arrowheads depict the direction of change from one vegetation state to the other, irrespective of the ecological mechanism behind it, and arrow widths are representative of the rate of each process. The six vegetation types used in this implementation correspond to sparse vegetation, shrublands, and two developmental stages (young and mature) of a tree seeder and a tree resprouter.

rule). Random patterns of ignition alleviate the influence of initial landscape configuration, and we assume they better capture the human influence to fire occurrence in most MTEs, as opposed to natural ignitions that would be more influenced by the spatial patterning of vegetation types (Syphard et al. 2007, Ganteaume et al. 2013, San-Miguel-Ayanz et al. 2013). Stochastic ignitions are driven by a baseline landscape-level environmental fire risk (i.e., probability of ignition) that is increased by cell vegetation characteristics (fuel load and flammability) and fuel dryness. At the cell level, fires are implemented as high-intensity, stand-replacing crown fires characteristic of MTEs (Keeley et al. 2012). At the landscape level, burned area (i.e., the number of cells burned) is drawn from scenario-defined distributions (see *Modeling scenarios*) and fire spread to neighboring cells is determined by their fuel load and vegetation composition. Finally, vegetation proportions, as well as live and dead biomass levels, are updated at each time step after accounting for disturbance effects.

Rule 1.—Succession, maturation, and vegetation replacement processes. This rule determines new proportions of the six vegetation types within cells. Such vegetation changes not driven by disturbance (Fig. 1a) are constrained by the differential behavior of pioneer and late-successional vegetation types included in this parameterization. The tree seeder corresponds to a pioneer, shade-intolerant forest species with relatively high establishment rates in shrublands (i.e., succession to forest) and moderate establishment rates on young stands of the tree resprouter (i.e., replacement; Zavala et al. 2000). Contrastingly, the shade tolerance of the late-successional tree resprouter leads to a lower ability to recruit in shrublands but a competitive advantage at later successional stages to colonize adult stands of the tree seeder (e.g., Curt et al. 2009, Sheffer 2012, Carnicer et al. 2014).

Rule 2.—Biomass update. Live biomass, expressed as a 0–1 index, depends on the proportion of the different vegetation types within the cell. Negligible biomass as in sparse vegetation is expressed as 0 (i.e., no contribution to cell fuel load), whereas 1 corresponds to the maximum biomass level that vegetation states can achieve (i.e., mature seeder and resprouter classes). Young forests and shrublands have intermediate maximum biomass levels: young resprouter > young seeder > shrublands. Cell and landscape live biomass changes as succession and vegetation replacement processes occur (Rule 1), indirectly leading to biomass accumulation through time.

Dead biomass (produced by drought-induced mortality, see *Rule 3*) is updated on the basis of a constant decomposition rate following a negative exponential function. Drought-induced mortality is likely to generate dead fuel from different diametric classes, but in this investigation we aimed to incorporate the short-term effects of increased fire likelihood as a result of increased fine, dead fuels (that disappear relatively fast) resulting from drought (shoot dieback, McDowell et al. 2008 and references therein). Fine fuels are the ones with a highest influence in vegetation ignitability, and they also influence fire behavior (Rothermel 1972, Scott and Reinhardt 2001, Fernandes and Loureiro 2013). In the model, it is assumed that drought-induced biomass mortality mostly corresponds to shoot dieback, and thus, dead biomass within cells decreases rapidly (most of it disappears in ~10–15 yr), capturing the relatively high biomass decomposition rates characteristic of some MTEs (Verkaik and Espelta 2014).

Rule 3.—Drought impacts. Drought severity determines changes in live and dead biomass as well as changes in vegetation composition (i.e., changes in the proportion of the six vegetation types; Fig. 1b). For a given drought event, higher biomass in a cell will result in a higher total amount of drought-induced biomass mortality. In such a framework, drought–density relationships are thus incorporated indirectly. Importantly, drought-induced changes from live to dead biomass are higher than changes in vegetation composition, to account for the capacity of MTE species to endure drought. For a given drought event, shrublands are assumed to be rather resistant (low mortality rates) because they include many drought-deciduous and drought-tolerant species, whereas the young seeder and resprouter classes are the most sensitive given their shallower rooting depths and lower levels of stored reserves, respectively (e.g., Pratt et al. 2014).

Rule 4.—Ignition and fire spread. When it occurs, fire burns all vegetation within affected cells changing their vegetation composition (Fig. 1c). The probability of ignition is modulated by environmental factors through the influence of drought episodes on fuel moisture, as well as by landscape levels of live and dead biomass (i.e., fuel load; Duane et al. 2015) and the proportion of flammable vegetation types (shrublands, Barros and Pereira 2014, seeders, e.g., Cowan and Ackerly 2010, Saura-Mas et al. 2010). This incorporates climatic and fuel accumulation effects and the influence of vegetation traits (e.g., fine needles, resin) on fire risk. Drought episodes affect fire occurrence through an increased likelihood of ignition of live biomass during such episodes, implicitly simulating more severe drying of fuels than in non-drought years. When fire occurs in a cell, it affects all vegetation types and all live and dead biomass is consumed (i.e., high-intensity, stand-replacing crown fire). Burned area of each fire event is drawn from a uniform distribution spanning the range of fire sizes within the scenario-defined fire regimes.

Modeling scenarios

We defined three contrasting regimes for fire and three regimes of increasing drought recurrence. Each of these six regimes was applied in a corresponding individual disturbance scenario, and nine additional compound scenarios resulted from all the possible combinations of fire and drought regimes (Appendix S3: Table S1 and Appendix S1: Table S1). A no-disturbance scenario was implemented as control. This scenario design allows testing the effects of interacting fire and drought—synergism vs. antagonism—following the additive model (Folt et al. 1999), in which the effects of interacting disturbances are compared with the additive sum of effects of the corresponding disturbance regimes acting in isolation.

The three implemented fire regimes are defined on the basis of fire size and recurrence. They correspond to (1) LI100, regime of large, infrequent fires with a mean recurrence of 100 yr and where all fires correspond to large events, burning 80–100% of cells in the landscape; (2) SF20, regime of small to medium, frequent fires with a mean recurrence of 20 yr and where all fires correspond to small–medium events, burning 5–25% of cells in the landscape; and (3) M20, a mixed fire regime with a mean fire recurrence of 20 yr but in which both large and small–medium fires occur; in this scenario, 25% of the fires correspond to large fire events (burning 80–100% of the cells) and the remaining 75% correspond to small to medium fires (burning 5–25% of the cells). Because surface fires are rare in MTEs (Keeley et al. 2012), we thus made the simplifying assumption that all fires correspond to high-intensity, stand-replacing fires.

From an ecological perspective, the mixed fire regime resembles disturbance regimes discussed in recent fire assessments, suggesting that large fires, in combination with small frequent fires, may be characteristics of fire-prone MTEs areas irrespective of and/or promoted by ongoing firefighting efforts and strongly influenced by human-driven ignitions (San-Miguel-Ayanz et al. 2013). On the other hand, the LI100 and SF20 fire scenarios were included to better assess the range of major fire regime components such as recurrence and extent, and to conceptually incorporate scenarios with a strong control on fire by humans. The large infrequent fire regime would thus correspond to a scenario where most ignitions are successfully controlled, but when a fire does escape, it is one that overcomes firefighting capacity (i.e., a large fire). Contrastingly, the small to medium fire regime would correspond to a scenario where fire size is effectively controlled, and thus, fires are allowed to regularly burn the landscape, but they are successfully limited to small–medium fires.

The three drought regimes correspond to mean drought return intervals of 40, 30, and 15 yr (D40, D30, and D15, respectively), with drought events of variable length drawn from a Poisson distribution with $\lambda = 1$ and a stochastically defined drought intensity causing 10–25% biomass mortality. We set such conservative drought intensity because, in MTEs, events causing over than 30% of vegetation die-off are relatively rare (Allen et al. 2010). Note that in this implementation, drought severity is held constant irrespective of drought recurrence, as our aim was to simulate the potential effects of increased high-intensity droughts under projected climate change scenarios (IPCC 2014, Merino et al. 2015). Mean drought recurrence of 40 yr roughly corresponds to the historical frequency of exceptional periods of climatic water deficit reported for some Mediterranean regions (Tejedor et al. 2016). Drought regimes at a mean recurrence of 30 and 15 yr would thus correspond to scenarios of increased drought frequency under climate change projections.

For each disturbance scenario, we conducted 100 model replicates to account for the effects of disturbance stochasticity and thus variance in realized disturbance sizes and intervals (e.g., Stephens et al. 2014, Enright et al. 2015 and references therein), which may be critically important for ecosystem dynamics and resilience (Buma et al. 2013). The landscape was always initialized as a mosaic equally composed of cells 100% dominated by the adult seeder and resprouter classes, and each run consisted of a model simulation of 600 model steps. Baseline values of each model's parameter are described in Appendix S3: Table S1 (see also Appendix S1: Table S1).

Analysis of model outputs

Landscape-level vegetation composition in each model simulation was described by means of the average abundance of each vegetation type, lumping together young and mature classes for the tree resprouter and the tree seeder. We discarded the initial 100 model steps of each simulation replicate to allow the system to be representative of the modeled disturbance regime and not the initial conditions. We used principal component analysis (PCA) to summarize landscape configurations under individual and compound disturbances scenarios. The PCA was performed on the matrix containing the average vegetation composition for each simulation replicate.

To test for synergistic and antagonistic effects of compound fire and drought regimes, we examined whether the cumulative effects of interacting fire and drought are higher (synergistic) or lower (antagonistic) than the additive sum of the corresponding individual disturbance regimes. Thus, we assessed the effect of individual and compound disturbance regimes on the composition of vegetation types with respect to the composition obtained under the no-disturbance scenario. Predictions of ecosystem response to multiple stressors are influenced by the response variable that is measured, and complicated by stochasticity (Crain et al. 2008 and references therein). As we aimed to assess the effects of stochastic, compound disturbances on long-term system dynamics, we used the average landscape-level vegetation composition over each model replicate to assess the response of the system. This procedure probably results in more conservative estimates of the cumulative effects of disturbances than if a given vegetation type was used (Folt et al. 1999).

In our model, the vegetation compositional space is multivariate, so that distances in this space can occur in many directions (e.g., change from resprouter to seeder vs. change from resprouter to shrubland) and, hence, they are not amenable to directly test for antagonistic or synergistic effects. To solve this issue, we projected the average composition of vegetation types of each simulation replicate onto a new axis defined by w = 1·% tree resprouter + 2·% tree seeder + 3·% shrubland + 4·% sparse vegetation. In w, the multiplicative weights 1–4 indicate the inverse position in the successional sequence: sparse vegetation → shrubland → tree seeder → tree resprouter. Subsequently, we quantified the response of the system for any given simulation replicate as the absolute difference between the value of w for the replicate and the value of w for the no-disturbance scenario. Following this approach, the highest value of system response (*response* = 3) would occur among a system dominated by 100% tree resprouter (i.e., $w = 1$, no-disturbance scenario) and a complete dominance of sparse vegetation (i.e., $w = 4$ and *response* = $|4 - 1| = 3$). Similarly, the response of the system among 100% resprouter dominance and 100% dominance of the tree seeder or the shrubland would equal to 1 and 2, respectively. Intermediate values in the abundance of the different vegetation types would derive in intermediate values of the response of the system, incorporating information on both the direction and magnitude of vegetation change.

To compute the response of the system under each of the implemented disturbance scenarios, first we computed system's response in each simulation replicate, and then we averaged the response of the system across the 100 simulation replicates in each disturbance scenario. Finally, we examined the relationship between the response of the system and the occurrence of simultaneous and consecutive fire–drought events. Given the varying relationship between weather (extreme drought) and fire in MTEs (e.g., Pausas 2004, Koutsias et al. 2013, Duane et al. 2015), we opted for not fixing an a priori prevailing sequence of events (e.g., drought followed by fire as opposed to fire followed by drought). In each model replicate, we computed the number of simultaneous events as the number of times fire and drought occurred in a given year, followed by a year without disturbance. The number of consecutive events reflects the number of times a drought or fire year was followed by a fire or drought year, respectively. The relationship between the number of consecutive and simultaneous disturbance events and the average response of the system was summarized by disturbance regime.

Results

Individual disturbance scenarios

The individual effects of a mixed fire regime—with no drought—including both small frequent and large infrequent fires resulted in heterogeneous landscapes with similar abundances of shrublands and the two regeneration traits (resprouter and seeder; M20 and No drought in Fig. 2). In contrast, the tree resprouter dominated under individual scenarios of large infrequent and small frequent fires. However, the stochastic nature of fire (e.g., inter-disturbance period) resulted in substantial variability in resprouter abundance under regimes encompassing large infrequent fires (LI100 and M20), favoring the persistence, and in some cases dominance, of the other vegetation types under such fire regimes. As expected by our modeling assumptions, individual effects of drought recurrences of 40 and 30 yr favored resprouter dominance, whereas high drought frequencies (15 yr) lead to landscapes with similar abundances of all vegetation types (Fig. 2).

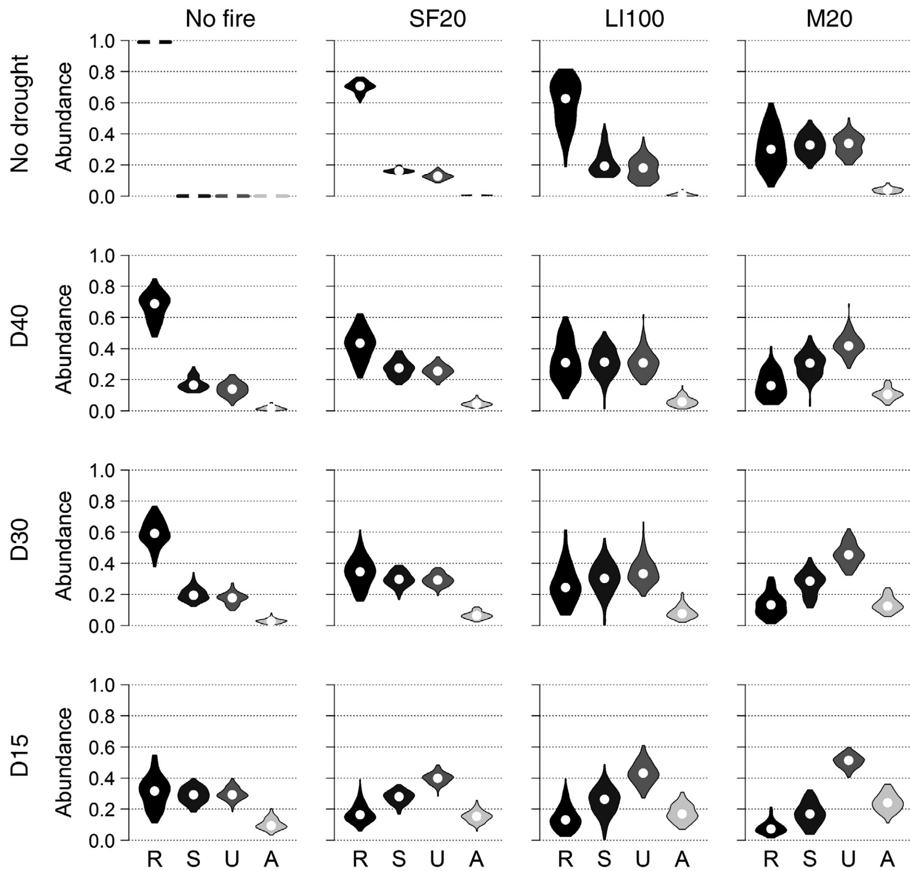

Fig. 2. Abundance of the major vegetation types incorporated in the model in relation to three individual disturbance scenarios of fire (top row, no drought) and drought (left column, no fire), and nine scenarios of compound fire and drought regimes (see *Modelling scenarios* for details). For each vegetation type, a kernel density distribution represents its mean abundance over each of the 100 replicates for each scenario; the white dot in each graph depicts the median over all replicates. Note that *R* and *S* corresponds to the young and adult classes lumped together, LI100 to large infrequent fires, SF20 to small frequent fires, M20 to mixed fire regime of small frequent and large infrequent fires, and D40, D30, and D15 correspond to mean drought recurrences of 40, 30, and 15 yr, respectively. *R*, tree resprouter; *S*, tree seeder; *U*, shrublands; and *A*, sparse vegetation.

Compound disturbance scenarios

Some landscape configurations only emerged as a result of the interacting effects of fire and drought (Figs. 2, 3; Appendix S3: Fig. S2), which promoted drastic alterations of landscape composition compared to individual disturbance regimes. In general, the interplay of fire and moderate drought recurrence (40–30 yr) produced highly heterogeneous landscapes in which the two regeneration traits, tree resprouter and tree seeder, tend to co-dominate with shrublands. However, under mixed fire regimes (M20), shrublands tended to become dominant in the long term irrespective of drought recurrence. Fluctuations in interacting disturbance regimes (stochasticity of occurrence) made possible the transient dominance of any of the vegetation types under most of the scenarios assessed (results not shown). On the other hand, for a given fire scenario, increased drought recurrence inevitably led to increased shrubland dominance. Interestingly, the tree seeder was less affected than the tree resprouter to increasing drought recurrence, despite its higher sensitivity to extreme drought.

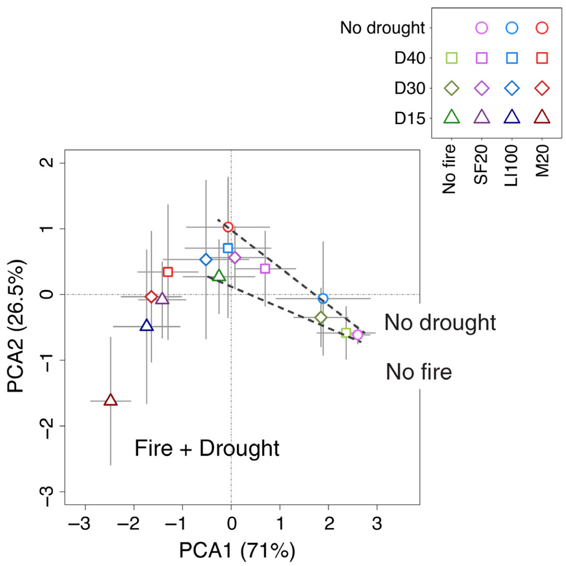

Fig. 3. Summary of the landscape configurations under the implemented individual and compound fire–drought regimes. Each symbol corresponds to the mean value of the 100 replicates of each disturbance regime (see legend in the upper right corner) and gray lines depict standard deviations in each scenario. Principal component analysis (PCA) was performed on the basis of the abundance of each vegetation type. Abbreviations are as follows: SF20, small frequent fires; LI100, large infrequent fires; M20, mixed fire regime; mDRI15, 30, 40, drought recurrence of 15, 30, and 40 yr, respectively.

Despite the above-mentioned compositional heterogeneity under compound fire and drought regimes, the tree seeder and shrublands became —on average—dominant in six out of the nine scenarios of compound disturbances. The tree resprouter tended to become the least abundant vegetation type, especially under mixed fire regimes and high drought recurrence (15 yr), but still dominated under small, frequent fire regimes and moderate drought recurrence (40 and 30 yr). However, even under these scenarios, the tree seeder and shrublands reached abundances similar to resprouter's abundance level. Long-term landscape dominance by shrublands occurred under high drought recurrence (15 yr) irrespective of fire regime, although the tree seeder could still dominate under large infrequent fires (LI100) and such frequent drought regimes. Under scenarios of high disturbance recurrence, sparse vegetation represented a substantial portion of the landscape, reaching values up to ~35% in the most extreme cases (Fig. 2).

Cumulative effects of fire and drought

Our assessment revealed that in most cases, the average effects of interacting fire and drought on vegetation composition are not far from the additive sum of the effects of fire and drought regimes acting in isolation (Fig. 4a). However, antagonistic effects prevailed under mixed fire regimes irrespective of drought recurrence; compound effects of fire and drought were less than the additive sum of the corresponding individual disturbance regimes. In contrast, slightly synergistic effects (i.e., compound effects greater than the additive sum of individual disturbances) were more common under fire regimes of either frequent small fires or large infrequent fires, especially at moderate drought recurrence. Interestingly, the assessment of individual model replicates showed that the stochastic nature of disturbances promoted both synergistic and antagonistic effects under any given compound fire–drought regime (Fig. 4b; Appendix S3: Fig. S3), though results indicate a trend of increasing antagonistic effects associated with higher disturbance frequencies in all scenarios.

We found that the effects of consecutive events on the response of the system were significantly higher than the effects of simultaneous events (*t*-test, H_0: The slopes are equal, *P*-value <0.05; Fig. 5) under compound regimes of drought and small frequent fires (SF20; *P*-value <0.01) or drought and large infrequent fires (LI100; *P*-value <0.01). Simultaneous and consecutive fire–drought events had a similar influence under mixed fire regimes (M20)—involving both small frequent and large infrequent fires (*P*-value = 0.126).

Discussion

The simulation results presented here highlight that the interplay of regeneration strategy and other ecological traits (e.g., successional dynamics), combined with the inherent stochasticity of disturbances, can dominate ecosystem dynamics. Our findings agree with the observed advantage of resprouters under individual, moderate disturbance regimes (e.g., Clarke et al. 2015). However, despite the capacity of

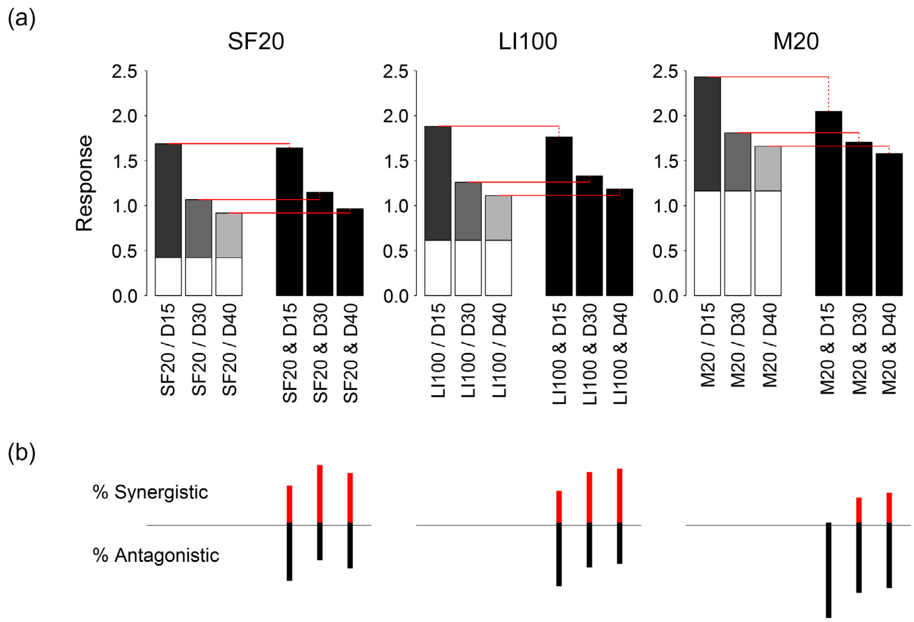

Fig. 4. Interacting effects of compound fire and drought regimes on vegetation composition relative to fire and drought acting in isolation. For each disturbance regime, mean interaction effects are presented in panel (a), where individual fire and drought effects are depicted by white and gray bars, respectively, their additive sum is shown by the horizontal red lines, and the corresponding effects of interacting fire and drought regimes are depicted by the black bars. The proportion of synergistic and antagonistic effects at the simulation replicate level is presented in panel (b), where red and black bars depict the proportion of synergistic and antagonistic effects, respectively, across the 100 simulation replicates performed for each disturbance regime. From left to right, subplots show interaction types in each of the three fire scenarios assessed: SF20, small frequent fires; LI100, large infrequent fires; and M20, mixed fire regime, respectively. D15, D30, and D40 correspond to drought frequencies of 15, 30, and 40 yr, respectively.

vegetation to endure individual disturbance effects through specific regeneration strategies (in our case, resprouters and seeders), fluctuations in disturbance regimes (as in the combined small frequent and large infrequent fires scenario) promote the coexistence of different regeneration traits (Tucker and Cadotte 2013). On the other hand, the interplay and cumulative effects of multiple interacting disturbances—fire and drought—further strengthen such coexistence in the long term, and it may thus be a key ecosystem property. Although the effects of compound disturbances effectively modify vegetation composition at the landscape scale, the interacting effects of fire and drought are not predominantly synergistic. In fact, we found that antagonistic effects were somehow prevalent, especially under high disturbance scenarios. The nature of fire–drought interactions seems to vary with the properties of the disturbance regimes (e.g., event frequency, extent) and their effects on the sensitivity and response capacity of the system to further disturbances.

Compound disturbance scenarios

Our investigations suggest that the interaction of moderate fire and drought recurrence can act as strong mechanism in generating highly heterogeneous landscapes in which tree resprouters and seeders tend to co-dominate with shrublands. Resprouting species show high resistance to exceptional episodes of water deficit (Pausas et al. 2016) and they are highly resilient to fire (e.g., Lloret et al. 2005, Pausas et al. 2008). However, our analysis indicates that expected increases in drought recurrence under climate change, in conjunction with fire, could lead to considerable declines in the abundance of late-successional, obligate resprouters with low colonization ability (such as *Quercus ilex* or *Quercus*

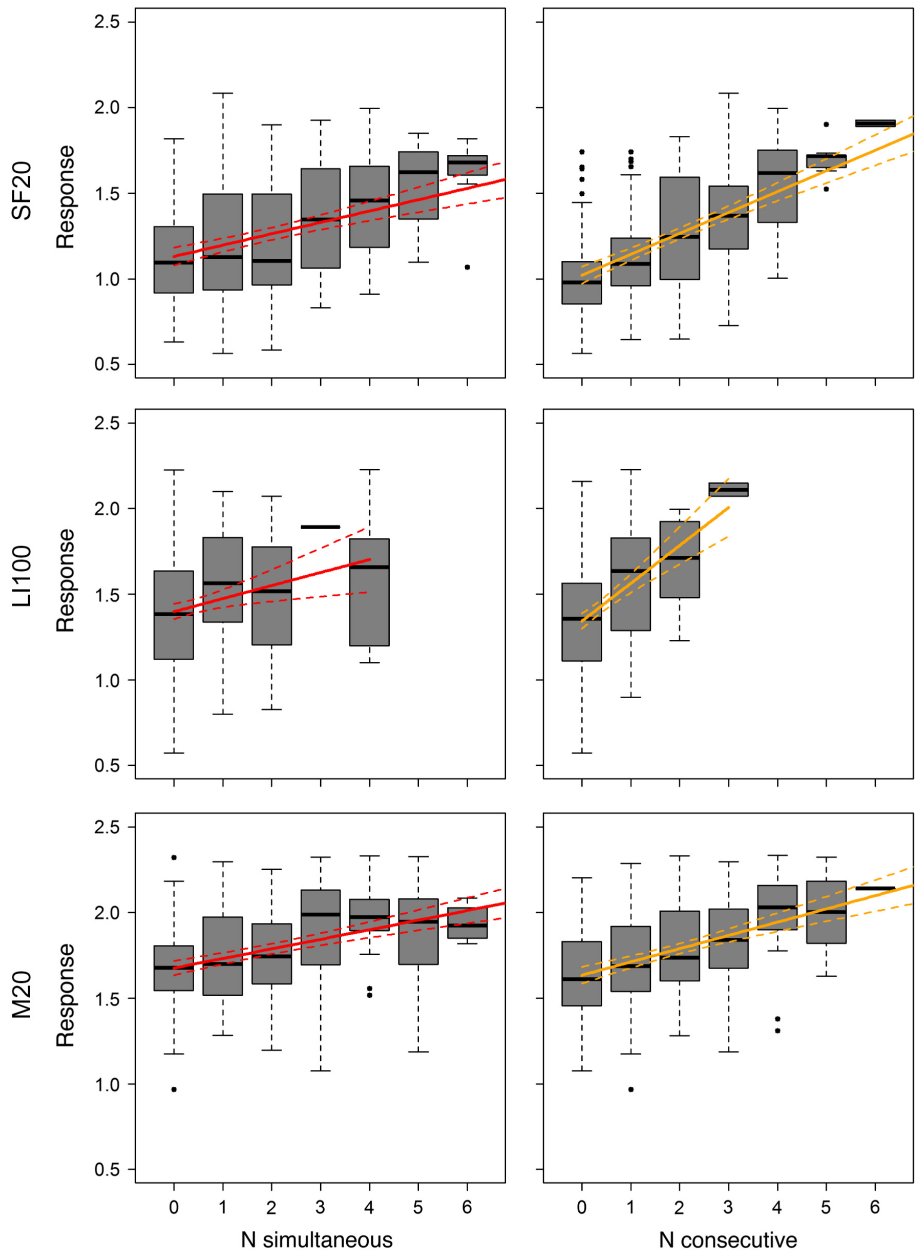

Fig. 5. Effects of the number of simultaneous and consecutive fire–drought events on the response of the system summarized by fire regime: small frequent fires (top row, SF20), large infrequent fires (middle row, LI100), and mixed fire regime of small frequent and large infrequent fires (bottom row, M20). In each subplot, boxplots depict the response of the system relative to the number of simultaneous or consecutive disturbance events over all model replicates in each fire regime. Solid lines show lineal relationships among variables and dashed lines the 0.95 confidence level.

calliprinos in the Mediterranean region). In contrast, the persistence and abundance of pioneer, fast-growing tree seeders with high colonization ability (such as *Pinus halepensis* or *Pinus brutia*; Zavala et al. 2000, Sheffer 2012) may increase as a result of altered fire–drought regimes, provided that these regimes do not constrain seed production as a result of too short inter-disturbance periods (Pausas and Lloret 2007). Such species may thrive where the interacting effects of multiple disturbances promote a recurrent turnover among forested states and shrubland communities.

Shrubland expansion and persistence at the expanse of forests would also be favored by fire–drought interactions and increased drought recurrence, according to our results. Increases in drought severity would further strengthen such trends (Appendix S3: Fig. S4). Dominance of shrubland formations in frequently disturbed landscapes is characteristic of some MTEs such as Australia, California, and South Cape (Keeley et al. 2012). Overall, our findings show that the interacting effects of fire and drought can produce distinct landscape configurations in which shrublands dominate under moderate disturbance regimes that, otherwise, are only attained under high recurrence of individual disturbances (Appendix S3: Fig. S5).

Cumulative effects of fire and drought

The significantly larger effects of consecutive vs. simultaneous events suggest that specific sequences of events may modulate the response of the system (Miao et al. 2009, Gower et al. 2015). This could indicate the existence of short-term synergistic effects of fire and drought if, for instance, forest regeneration is precluded in a drought year right after a large fire (e.g., mortality of recruits; Pratt et al. 2014) or in a fire year after a drought year (e.g., lack of seed sources; Meng et al. 2015). Other studies suggest synergistic effects of fires and abiotic (extreme weather; Gouveia et al. 2016) or biotic (herbivory; Midgley et al. 2010) disturbances. However, in the long term, we did not find prevalent synergistic effects of fire and drought on vegetation composition in MTEs. Although disturbance interaction promoted drastic changes in vegetation composition (Figs. 2, 3), those tended to be lower than the additive effects of the individual disturbance regimes (Fig. 4). Antagonistic interaction has been also reported for other ecological properties such as plant richness and the interacting effects of climate change and erosion (García-Fayos and Bochet 2009).

At the biological level, additive effects in our modeling framework would derive from the fact that regeneration mechanisms (e.g., reserve mobilization, bud or seed bank formation) are expected to be similar for any disturbance destroying biomass. Interestingly, our simulations indicate a trend toward increasing antagonistic effects as fire and/or drought frequency increases (Fig. 4b). Similar to components of individual tree resilience (e.g., Lloret et al. 2011), we suggest that such trends are related to a change in the overall resistance and resilience of the system as shrublands increase (and, paradoxically, sparse vegetation) relative to forests (tree resprouters and seeders). Shrublands can cope with higher disturbance recurrence and intensity than many forests (e.g., Odion et al. 2010), which may explain how the cumulative effects of fire and drought become buffered as the abundance of this vegetation type increases. At the system level, our assessment indicates that the cumulative effects of compound disturbance regimes (synergism and antagonism) are modulated by disturbance-induced changes that alter the capacity of the system to further respond to stressors. Therefore, whereas synergistic effects may occur at the population level, we hypothesize that they are less likely to prevail at the community or ecosystem level, unless all species or components of the system show equivalent sensitivity and capacity of response to disturbance.

Framework considerations

In this study, we focused on regeneration strategies and other ecological traits of tree species to assess major compositional dynamics and potential loss of resilience of forests in relation to compound disturbances and climatic alterations (i.e., increased recurrence of extreme drought). We did not assess the relative frequency of seeding, resprouting, or facultative seeding species among shrubs, which is another pressing issue that requires further investigation. For simplicity, we assumed that shrublands, as a major vegetation type, were less sensitive to fire and drought regimes than forest-forming species. This is because the combination of facultative species and the presence of multiple shrub-like seeding and resprouting species make these formations more resistant to disturbance (Vilà-Cabrera et al. 2008). However, disturbance frequencies higher than those implemented here may threaten the persistence of these communities as well (Enright et al. 2014, Batllori et al. 2015). On the other hand, drought limits survival of young recruits of both tree seeders and resprouters in our framework, but additional post-disturbance weather conditions that may affect them are not considered. This could somehow overstate the importance of seeders, since they are more sensitive to post-disturbance weather than resprouters (Pausas et al. 2008). Also, we did not incorporate other changes likely associated with scenarios of increased extreme drought such as decreased long-term productivity (due to limited precipitation) that could limit the rate of vegetation changes. Fire–drought productivity feedbacks are certainly a key area of research under climate change scenarios that require further investigation.

In this implementation, we used random ignition points, although plant trait–flammability feedbacks could influence the spatial patterning of ignition (e.g., Cowan and Ackerly 2010, Saura-Mas et al. 2010, Barros and Pereira 2014) leading to a higher degree of landscape heterogeneity (i.e., different fire recurrence would occur in different parts of the landscape, modulating vegetation successional processes). Given the currently limited occurrence of natural ignitions in MTEs (e.g., San-Miguel-Ayanz et al. 2013), we opted to include random ignition patterns which, in turn, alleviate the influence of specific configurations in the patterning of the initial landscape and highlight the relative abundance of each vegetation type in relation to compound disturbance regimes. Additionally, ignition patterns may have a relatively small influence in our investigation given the relative scale of the modeled landscape and burned area within the fire regime scenarios (excepting in regimes of small, frequent fires); the drought-induced mortality acting at the landscape scale would further minimize such effects through vegetation homogenization. We believe that vegetation flammability–fire feedbacks may be of greater importance in assessments of vegetation dynamics at large, biogeographical spatial scales (e.g., over climatic gradients).

Conclusions

The cumulative effects of fire and drought produce distinct landscape configurations under moderate disturbance regimes that are otherwise only attained under high recurrence of individual disturbances. Therefore, ecosystem assessments based on the impact of individual disturbance regimes will not capture potential alterations caused by interactions between multiple disturbance types. Despite the high resilience of late-successional, resprouting MTE tree species to sporadic disturbance events and thus individual disturbance regimes, they may nevertheless be more vulnerable to the effects of interacting disturbances such as fire and drought, and to long-term changes in compound disturbance regimes. We suggest this is related to their ecological characteristics (e.g., low colonization ability) and to the intrinsic stochasticity in the realized interval of multiple disturbances and minimum inter-disturbance periods. Overall, our simulations emphasize that the projected increase in drought recurrence under climate change may promote shrubland persistence and expansion at the expense of forest cover in Mediterranean landscapes. Such changes in vegetation will promote, in turn, an overall increase in landscape resistance and resilience to disturbance, which may preclude synergistic effects of interacting fire and drought relative to their individual regimes. Therefore, as climates become further altered, shrubland cover may ultimately become a highly valued ecosystem characteristic in many MTEs.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1906/full