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RESEARCH ARTICLE

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# Compound fire-drought regimes promote ecosystem transitions in Mediterranean ecosystems

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## Abstract

1. Understanding ecosystem responses to compound disturbance regimes and the influence of specific sequences of events in determining ecosystem shifts remains a challenge.
2. We use a modelling framework for Mediterranean-type ecosystems to assess the effects of fire–drought interactions on long-term vegetation dynamics and to identify disturbance-driven changes in trait composition (tree seeder vs. tree resprouter prevalence) and ecosystem state (forest vs. non-forest).
3. Changes in tree seeder and the tree resprouter dominance show nonlinear, threshold-type trends over gradients of increasing compound disturbance frequency. Vegetation composition thresholds mostly occur in a narrow range of the compound fire–drought disturbance space. Additionally, trait compositional switches and the likelihood of sudden changes in ecosystem state are promoted by fire-drought interactions.
4. Distinct sequences of disturbance events cause vegetation transitions, disrupting ecosystem resilience, even under moderate recurrence of individual disturbances. An extreme drought year followed by one or two large fire events promotes shifts from resprouter- to seeder dominance. Contrastingly, a large crown fire followed by an extreme drought promotes changes from seeder to resprouter dominance. This disturbance sequence is also a mechanism strong enough to trigger sudden shifts in ecosystem state (from forest to non-forest).
5. *Synthesis*. Thresholds of change in vegetation composition occur over a narrow range of the modelled gradients of compound fire-drought recurrence, and the loss of ecosystem resilience is contingent on particular sequences of disturbance events. Overall, our findings highlight that disturbance interactions define the relative location of tipping points in ecosystem state, and that effects and feedbacks of compound disturbance regimes increase the long-term likelihood of sudden ecosystem shifts and, therefore, uncertainty in predicting vegetation state.

**KEYWORDS**
compound disturbance regimes, drought, fire, Mediterranean ecosystems, regeneration traits, resilience, sequence of events, state shift

## 1 | INTRODUCTION

Contemporary and palaeoecological observations suggest substantial ecosystem resilience to natural disturbance regimes (Johnstone et al., 2016; Lloret, Escudero, Iriondo, Martínez-Vilalta, & Valladares, 2012), highlighting the capacity of ecosystems to re-organize and recover their essential structure and function after disturbances (Holling, 1973). However, it is increasingly recognized that disturbances can also trigger persistent changes in ecosystems (e.g., Martínez-Vilalta & Lloret, 2016; McKenzie & Tinker, 2012; Scheffer, Carpenter, Foley, Folke, & Walker, 2001) and that disturbance regimes can maintain alternative vegetation and biome states (e.g., Batllori, Ackerly, & Moritz, 2015; Dantas, Hirota, Oliveira, & Pausas, 2016; Grady & Hoffmann, 2012; Staver, Archibald, & Levin, 2011). The response and resilience of ecosystems to disturbance regimes is modulated by their "ecological memory" (sensu Johnstone et al., 2016), which depends on the remnants of previous conditions or "ecosystem legacies" persisting after disturbances. Ongoing climatic changes and the predicted intensification of weather extremes (Jentsch, Kreyling, & Beierkuhnlein, 2007; Smith, 2011) are likely to trigger alterations in disturbance regimes (e.g., disturbance frequency, severity, size, timing) that could fundamentally alter "ecosystem legacies" and their dynamics and jeopardize ecosystem resilience (Johnstone et al., 2016). Assessing how, when, and where major ecological drivers such as disturbance can promote drastic ecosystem changes is a major research challenge (e.g., Trumbore, Brando, & Hartmann, 2015; Turner, 2010).

Recognizing the importance and prevalence of interactions among disturbance agents and their influence on ecosystem processes and structure is a key advance in disturbance theory and research (e.g., Buma, 2015; Crain, Kroeker, & Halpern, 2008; Paine, Tegner, & Johnson, 1998; Piggott, Townsend, & Matthaei, 2015; Turner, 2010). Interacting disturbances could disrupt stabilizing feedbacks that confer ecosystem resilience and amplify processes that may trigger state changes in forest ecosystems (e.g., Buma & Wessman, 2011; Clark et al., 2016; Kulakowski, Matthews, Jarvis, & Veblen, 2013). Additionally, limited experimental and empirical evidence indicates that species' responses and successional trajectories can be contingent on disturbance sequence (Frelich, 2002; Fukami, 2001; Gower, Fontaine, Birnbaum, & Enright, 2015; Miao, Zou, & Breshears, 2009; Zedler, 2010). The influence of a disturbance event on remnant ecosystem patterns and processes from a previous disturbance (i.e., on "ecosystem legacies") will thus shape the response of the system to that event and, in turn, to future disturbance events. Ecosystems' response to interacting disturbance regimes is thus not simply an additive result of the response to individual events.

The occurrence of exceptional periods of climatic water deficit (extreme drought) related to prolonged periods of high temperature and low precipitation has triggered vegetation mortality events worldwide (Allen, Breshears, & McDowell, 2015; Greenwood et al., 2017). Temperature and precipitation also modulate vegetation structure (fuel load and spatial distribution) and flammability, influencing the scale, frequency, and intensity of wildfires (Krawchuk & Moritz, 2011), as well as post-fire recovery (Wilson, Latimer, & Silander, 2015). Therefore, both fire and extreme drought are major determinants of species composition and ecosystem state (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015; Enright, Fontaine, Lamont, Miller, & Westcott, 2014; Moser, Temperli, Schneiter, & Wohlgemuth, 2010), particularly in semi-arid ecosystems.

Ecosystem shifts and/or alternative stable states have also been related to the existence of critical thresholds, altered system feedbacks, and stochastic disturbance–vegetation interactions related to these individual disturbance agents (e.g., Batllori et al., 2015; D'Odorico, Laio, & Ridolfi, 2006; Martínez-Vilalta & Lloret, 2016; McKenzie & Tinker, 2012; Staver et al., 2011). Moreover, simulation studies indicate that the cumulative effects of drought and fire disturbances modify vegetation composition when compared to their respective individual disturbance regimes (Batllori et al., 2017; Fyllas & Troumbis, 2009), promoting distinct landscape configurations that are otherwise only attained under high recurrence of fire or drought alone. However, given the inherent stochasticity of fire and drought regimes, in terms of frequency and severity, interactions between the two regimes are difficult to understand as observed time series will all be viewed as locally unique historical sequences. Understanding these interactions to anticipate ecosystem dynamics to climate change requires detailed studies of individual ecosystem histories, or, as in this paper, a reliance on models in which long time series can be examined and the effects of unique sequences of events evaluated through simulation replicates.

Mediterranean-type ecosystems (MTEs) offer valuable insights into the interactions of fire and extreme drought events, as these disturbances shape their vegetation characteristics and landscape dynamics (Esler, Jacobsen, & Pratt, 2018; Keeley, Bond, Bradstock, Pausas, & Rundel, 2012). In such ecosystems, many species show regeneration traits (seeding, resprouting) that strongly determine their ability to respond and persist after disturbances: seeding species recruit from seeds stored in soil or canopy seed banks, whereas resprouting species recover their above-ground tissues from, in many cases, below-ground protected buds. The prevalence of these major regeneration strategies has been assessed in relation to fire regime (e.g., Enright et al., 2014), highlighting the importance of the match between fire and species' demographical growth rates. Regeneration strategies prevalence also varies along gradients of climatic aridity and the associated fire-productivity levels, with obligate seeders increasing on drier sites and resprouting species being better represented on wetter sites (e.g., Pausas & Bradstock, 2007). Additionally, regeneration niche partitioning in relation to drought conditions may explain the co-existence of seeding and resprouting species in MTEs (Vilagrosa, Hernández, Luis, Cochard, & Pausas, 2014). However, no systematic assessments have evaluated the effects of interacting fire and extreme drought – as opposed to chronic dryness – on the long-term prevalence of seeders and resprouters, particularly regarding the occurrence of shifts in the dominance of these major regeneration strategies.

We use a state-and-transition simulation model (STSM; Daniel, Frid, Sleeter, & Fortin, 2016) that incorporates regeneration traits and major vegetation characteristics (fuel load and flammability; Batllori et al., 2017) to systematically evaluate the long-term dynamics and response of MTEs vegetation under gradients of the frequency and sequence of events in compound fire-drought regimes. We define drought as extreme episodes of water deficit that promote vegetation mortality. Most forest species are adapted to on-site dryness levels, but the minimum water potentials they experience are close to their hydraulic safety margins (Choat et al., 2012). Drought as a disturbance thus occurs sporadically under relatively extreme water-stress conditions driven by climatic fluctuations. We use a series of modelling experiments to: (a) characterize the patterns of disturbance-driven compositional changes between major regenerative strategies (tree seeders vs. tree resprouters) along gradients of compound fire and drought, (b) determine the likelihood of sudden, disturbance-driven shifts in ecosystem state, from forest to non-forest vegetation, and (c) identify which specific sequences of fire and drought events are responsible for compositional and ecosystem state changes.

## 2 | MATERIALS AND METHODS

### 2.1 | Simulation model

The STSM used in this research incorporates six broad vegetation types (Supporting Information Figure S1 and Table S1) and associated, reliable ecological assumptions on their flammability, level of biomass (i.e., fuel load), and major regenerative traits (seeding vs. resprouting) of species in Mediterranean ecosystems: (1) sparse vegetation (e.g., herbaceous with occasional woody species), (2) shrublands, (3) and (4) two developmental forest stages (young vs. mature) of an obligate tree seeder-type (tree seeder, hereafter), and (5) and (6) two stages (young vs. mature) of an obligate tree resprouter-type (tree resprouter, hereafter). The tree seeder is considered a pioneer species and the tree resprouter a late successional species (Sheffer, 2012; Zavala, Espelta, & Retana, 2000). In both the tree seeder and tree resprouter, the respective young classes correspond to seedlings and saplings recently established (or regrowing in the case of resprouters) that are not yet able to produce seeds. Vegetation succession within the model is driven by a set of probabilities that define the rates of vegetation change among the different vegetation types (Supporting Information Table S1). In the absence of disturbances, the vegetation gradually transitions to resprouter-dominated forests, reflecting a major successional pathway across Mediterranean Basin MTEs (Capitanio & Carcaillet, 2008; Zavala et al., 2000).

Each vegetation type has associated distinct, fixed levels of biomass and flammability (Supporting Information Table S1), so that the proportion of each vegetation type in a cell determines the cell-level biomass and flammability values through time. Biomass level decreases from forest to sparse vegetation (mature forest > young forest > shrublands > sparse vegetation); flammability is higher in shrublands and the tree seeder-dominated vegetation than in tree resprouter-dominated forests (e.g., Barros & Pereira, 2014; Supporting Information Figure S2). The model simulates vegetation dynamics of a regional landscape composed of 400 cells affected by the same synoptic weather conditions (drought episodes, fire probability). Each cell is described by the proportion of the six vegetation types, its biomass and flammability levels, plus a cell-level counter of time since disturbance that modulates processes such as resprouting capacity and the amount of dead biomass. Each cell represents a large enough landscape area (e.g., 0.5–1 km$^2$) to encompass a mosaic of vegetation types with shared environmental conditions and capabilities to respond to the ecological processes incorporated in the model.

For this investigation, the late successional tree resprouter is considered less sensitive to both fire and sporadic, extreme drought than the pioneer tree seeder (Pausas et al., 2016). Both resprouting and seeding capabilities are modulated by time since the last disturbance (reserve accumulation for resprouting, e.g., Fairman, Bennett, & Nitschke, 2019; López, Gracia, Sabaté, & Keenan, 2009; maturation time in seeders, e.g., Moya, De las Heras, López-Serrano, & Leone, 2008) and, importantly, young tree seeders and resprouters are more sensitive (i.e., higher mortality levels) to both fire and drought than the corresponding mature classes (Supporting Information Table S1, Figure S2) (Enright et al., 2014; Pratt et al., 2014 but see Franklin, Spears-Lebrun, Deutschman, & Marsden, 2006). Regeneration traits are not specifically incorporated in shrublands, but this vegetation type is assumed to be highly persistent in the face of fire and drought (Keeley et al., 2012; Vilà-Cabrera, Saura-Mas, & Lloret, 2008). These basic vegetation types are representative of natural and semi-natural pine-oak systems that dominate extensive areas over the Mediterranean Basin MTEs (e.g., reprouters: *Quercus ilex*, *Quercus calliprinos*, *Quercus suber*, seeders: *Pinus halepensis*, *Pinus brutia*; Sheffer, 2012; Sheffer, Canham, Kigel, & Perevolotsky, 2013; Zavala et al., 2000).

Within the model, fire and drought events occur as sporadic and stochastic mortality factors that can set back cells' vegetation to earlier successional stages (e.g., from forest to shrubland), depending on their vegetation properties at the time. The two disturbances are implemented through top-down disturbance regimes of a given recurrence (see description of Section 2.3). One model time-step represents 1 year, and in each time-step all cell properties are updated and tracked throughout the simulation run. The response parameters of the different vegetation types and the environmental conditions of the system (excepting disturbance stochasticity) are held constant over all cells and over simulation time (Supporting Information Table S1). The overall environment (top-down factors) determines drought frequency and severity and the climatic fire risk, as well as the rate of successional and compositional change among vegetation types. Vegetation processes are implemented cell by cell, but the dynamics of all cells are coupled by disturbances and by the influence of landscape properties (total biomass, abundance of mature tree classes) on the likelihood of fire and the rate of vegetation succession and replacement processes. Note that the rate of succession from shrubland to forest is faster (up to a maximum; Supporting Information Table S1) the higher the joint cell- and landscape-level proportion of mature vegetation classes, and shrublands no longer undergo succession to forest if the mature tree seeder and resprouter disappear completely from the landscape (Supporting Information Figure S3). Therefore, although regeneration is not directly parameterized, it is incorporated by the dependence of the post-disturbance occurrence of the young tree seeder and resprouter classes on the pre-disturbance occurrence of the respective mature classes (excepting resprouting).

## 2.2 | Drought, fire, and their interaction

Drought occurrence is implemented as die-off (change to another state) and dieback processes (defoliation or biomass mortality) only driven by climate (i.e., top-down specification). For a given event, drought-induced dieback is higher than die-off to incorporate into the model the capacity of MTEs species to endure drought. Die-off depends on the sensitivity level of each vegetation type (Supporting Information Figure S2c) and therefore, drought alters regeneration abilities of forest vegetation and succession trajectory indirectly through their higher influence on the mortality of young versus mature vegetation types. Biomass mortality corresponds to shoot dieback (i.e., fine, dead fuels). The levels of drought-induced dead biomass are updated through time on the basis of constant decomposition rates following a negative exponential function, being zero ~10–15 years after the drought event in the absence of subsequent disturbance (Supporting Information Table S1). For simplicity, it is assumed that post-drought recovery (vegetation regreening) occurs rapidly after the event (Supporting Information Figure S4); live biomass is always computed on the basis of cells' vegetation proportion whereas dead biomass is generated (and decomposed subsequently) when drought occurs.

Fire probability is jointly determined by climate (a top-down component of the fire regime) plus the modulating effects (increasing fire probability) of the landscape-level fuel load and flammability (live and dead biomass) and the effects of drought on drying fuels (i.e., allowing feedbacks between disturbances via fuel and vegetation changes to be captured by the model, Supporting Information Figure S5). When it occurs, fire burns all live and dead vegetation within the affected cells (i.e., crown, intense fire) and propagates through the landscape, from a random ignition point, on the basis of each cell's fuel load and flammability. During a drought year, the effects of extreme drought on fire probability (via drying fuels) are low in our framework as the typical seasonal dryness in MTEs translates into conditions suitable to the regular occurrence of fire independent of severe episodes of water deficit. Longer term effects of fire–drought interactions are incorporated in the model through drought-induced vegetation dieback (levels of dead biomass) and die-off (change to a different vegetation type) which influences landscape flammability and fuel load and thus modulates the probability of fire (Supporting Information Figure S5). Additional details regarding the model structure and processes are given in Batllori et al. (2017).

## 2.3 | Simulation scenarios

We analysed different disturbance scenarios resulting from the combination of multiple individual regimes of fire and drought. Individual fire and drought regimes were defined by disturbance recurrence whereas the rest of properties (i.e., fire sizes, drought severity) were held constant. We examined 20 different fire and drought regimes ($N$ = 400 compound disturbance scenarios) in which disturbance frequency increased at 5-year intervals within the 15–100 years frequency-range, plus two low frequency disturbance regimes of 150 and 200 years.

Within each tested fire regime, disturbance frequency would correspond to the climatic fire risk or baseline probability of fire occurrence. The effective, stochastic fire frequency within each simulation run depends, however, on how the landscape-level fuel load (live and dead biomass) and flammability modulate the top-down aspects of fire recurrence throughout the simulation; for example, a high proportion of the tree seeder in the landscape or high levels of drought-induced dead biomass increases the probability of fire due to its higher flammability. Fire regimes are characterized by the occurrence of small frequent and large infrequent fires (probability of occurrence 80% and 20%, respectively), simulating the mixed fire regimes described in MTEs (San-Miguel-Ayanz, Moreno, & Camia, 2013). Small fires burn 5%–25% of cells in the landscape whereas large fires burn 80%–100% of cells. In our simplified approach, drought increases the likelihood of fire through its effects on drying fuels, vegetation composition, and the levels of dead biomass but it does not influence the likelihood of small or large fire events.

Drought regimes result from the combination of the frequency of drought occurrence, the duration in years of the drought events (drawn for each event from a Poisson distribution with $\lambda$ = 1 year), plus a stochastically defined severity of the events that promote 10%–25% of vegetation die-off (change to another state) and vegetation dieback (defoliation or biomass mortality) across all cells (severity follows a uniform distribution on the interval 10%–25%); events causing >30% of vegetation die-off are rare in MTEs (Allen et al., 2010). The intensity of drought events and their direct effect on biomass mortality (dieback) is equal for all cells to reproduce homogeneity in weather conditions over the entire landscape, but the actual levels of a cell's vegetation die-off (i.e., drought-induced change to another vegetation state) depend on the vegetation composition of each cell, as mediated by their sensitivity levels to drought (Supporting Information Figure S2c).

For each of the 400 disturbance scenarios of compound fire-drought regimes, we performed 100 simulation replicates to account for stochasticity in disturbance events. Each replicate consisted of 1,500 model steps (years), the first 300 of which were discarded for output analysis to allow the system to adjust to the modelled disturbance regimes.

## 2.4 | Model output analysis

First, the mean abundance of each vegetation type (tree resprouters, tree seeders, shrublands, and sparse vegetation) across cells and years was computed for each simulation replicate; young and mature classes were pooled together in analyses. Then, results from the 100 individual replicates were averaged over each implemented scenario of compound disturbances. This served to assess the overall dominance of each vegetation type under the 400 compound disturbance scenarios examined here.

Second, temporal fluctuations in landscape-level forest abundance (including tree resprouters and seeders) were characterized. We assessed the variance in forest abundance within 25-year moving windows across time (i.e., across model steps) in each model replicate (`rollapply` function in `zoo` package; Zeileis & Grothendieck, 2005). A 98% quantile threshold in variance values, defined from the distribution of variances in each replicate, was then used to identify variance peaks and, therefore, large and sudden fluctuations in forest abundance induced by disturbances. Such forest abundance fluctuations were then used to assess the disturbance-driven occurrence of both compositional changes (tree resprouter- vs. tree seeder-dominated landscapes) and changes in ecosystem state (from forest to non-forest dominated landscapes).

To assess disturbance-driven compositional changes, we assessed whether the tree resprouter or tree seeder dominance at the landscape level (abundance ≥50%) was maintained after large disturbance-induced fluctuations in forest abundance. We thus used a 50% landscape-level dominance of pre- and post-disturbance forest abundance to identify compositional shifts between the two regeneration strategies (Supporting Information Figure S6). Note that within this definition, compositional seeder-resprouter shifts are not constrained to any timeframe (e.g., certain years after a forest variance peak) and, therefore, they may reflect changes related to different post-disturbance rates of forest recovery and potentially include phases in which shrublands dominate before landscape-level dominance of any of the two regeneration strategies is attained.

Sudden changes in ecosystem state induced by disturbances (from forest to non-forest-dominated landscapes) were defined as rapid and major forest abundance declines (variance peaks that implied changes from >50% to <25% in the landscape-level forest abundance) that persisted through time (>150 years), and thus that were decoupled from typical rates of vegetation succession and disturbance magnitude (Supporting Information Figure S7). Therefore, we assess long-transient non-forest states induced by compound fire-drought regimes that derive from a disruption of the recovery capacity of the system and that, given its temporal persistence, could have significant ecological (and management) implications.

Finally, 10-year windows around each variance peak that promoted a compositional shift or a sudden change in ecosystem state were used to assess the specific fire-drought (or drought-fire) sequences causing them. Disturbance sequences were thus identified retrospectively, emerging from stochastic specification of the disturbance regimes. All analyses were conducted in R (R version 3.3.2; R Core Team, 2016).

## 3 | RESULTS

Simulation results show that changes in the overall dominance of the tree resprouter and the tree seeder follow nonlinear, and occasionally non-monotonic, trends over gradients of increasing disturbance frequency (Figure 1). As expected from our modelling assumptions, the late-successional tree resprouter dominates under low and moderate regimes of compound fire and drought (fire and drought return intervals – mFRI and mDRI – longer than 50 years), whereas the abundance of the pioneer tree seeder increases under higher disturbance rates (mFRI 20–30 years when mDRI is longer than ~50 years, or up to mFRI 100 years when mDRI is low, ~15–20 years; Figure 1). However, substantial changes in the dominance of the two regeneration strategies occur over small variations in compound disturbance regimes (Figure 1a,b), pointing to the existence of disturbance frequency thresholds for vegetation composition. Shrubland dominance also increases under relatively high frequencies of compound fire and drought (joint mDRI and mFRI <15–20 years) that exceed the regeneration ability of tree seeders (Figure 1c). Finally, the abundance of sparse vegetation also shows nonlinear increasing trends under the highest frequencies of compound fire and drought implemented in this study (Figure 1d).

Within a given disturbance regime and simulation replicate, temporal fluctuations in forest abundance (i.e., variance peaks associated with disturbances) are related to compositional shifts in the landscape-level dominance of the two regeneration strategies. Such changes mostly occur over a limited range of compound fire-drought regimes, under relatively high disturbance frequencies (e.g., mFRI <25–30 years; Figure 2). Directional disturbance-induced shifts from tree resprouter- to tree seeder-dominated landscapes prevail, although compositional shifts in both directions can occur. Gradual transitions from tree seeder- to tree resprouter dominance occur in the model as a result of the defined successional processes, but disturbance events may also trigger abrupt declines in tree seeder abundance that result in the subsequent dominance of the tree resprouter at the landscape scale. The likelihood of compositional shifts between the two regeneration strategies displays nonlinear and varying relationships with compound fire-drought regimes

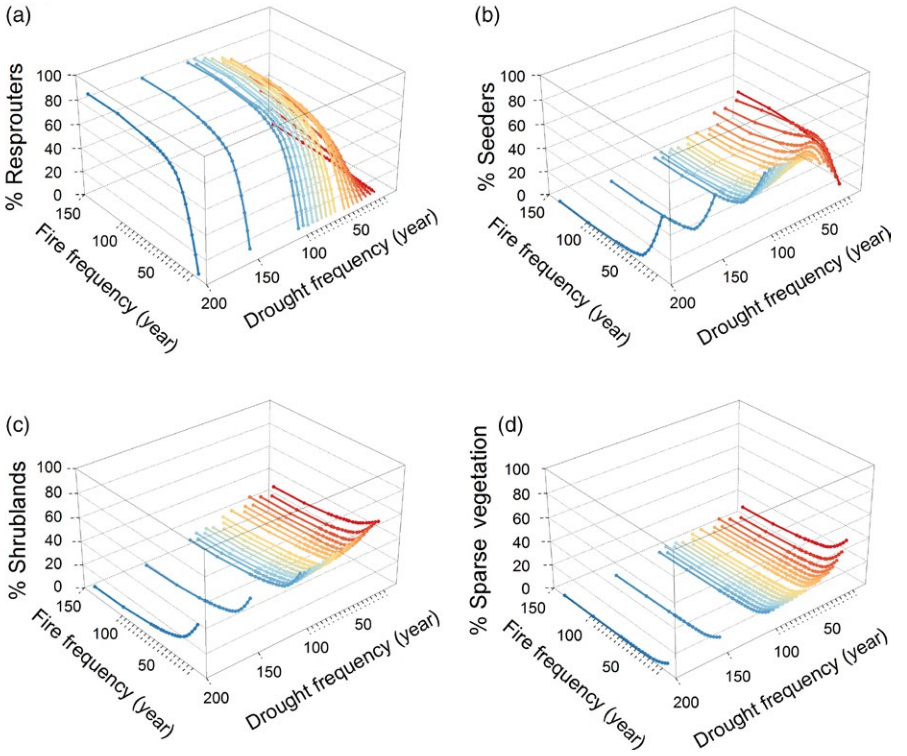


**FIGURE 1** Proportion of major vegetation types in relation to compound fire–drought regimes. Each plot corresponds to the average abundance of a vegetation type over the 100 model replicates performed under each compound disturbance scenario: (a) tree resprouters, (b) tree seeders, (c) shrublands, and (d) sparse vegetation. Line colour depicts drought frequency: reds – high recurrence and blues – low recurrence

(Figure 2 and Supporting Information Figure S8). Also, regeneration trait compositional shifts are more likely to occur under mixed vegetation with similar abundance of the tree seeder, the tree resprouter, and shrubland formations (Supporting Information Figure S9d–f). In general, for a given intermediate recurrence in one of the disturbance regimes (e.g., fire or drought) the likelihood of occurrence of compositional shifts increases with increasing recurrence of the other disturbance (e.g., drought or fire, respectively) up to a maximum. Then, the number of compositional shifts decreases at high disturbance recurrence as forest abundance declines and shrubland dominance increases.

Importantly, our simulations indicate that different sequences of disturbance events drive compositional shifts in the two directions (from tree resprouter to tree seeder vs. from tree seeder to tree resprouter). A drought year followed by a large fire, or two large fire events in a short interval (<10 years), promotes most of the compositional shifts from tree resprouter- to tree seeder dominance (Figure 2a). In contrast, an extreme drought event (lasting 2 or 3 years), a large fire followed by a drought event, and in some cases a large fire event alone promote most of the compositional shifts from tree seeder- to tree resprouter dominance (Figure 2b).

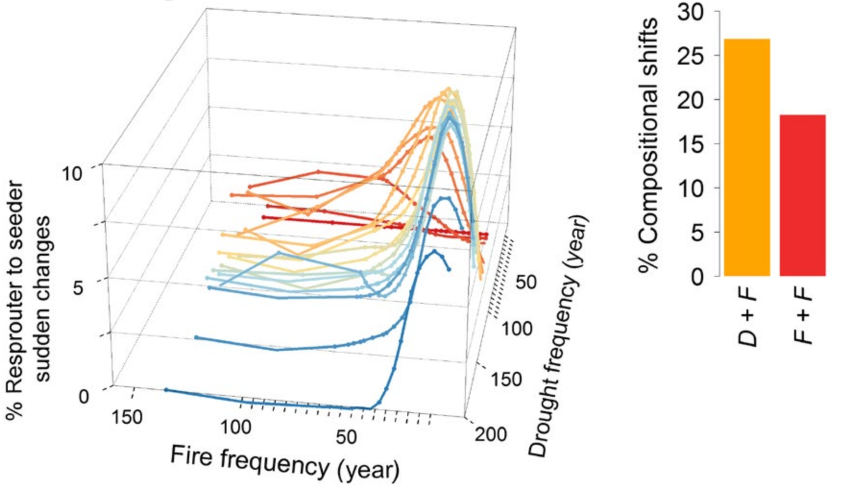
Irrespective of regeneration trait dominance (tree resprouter vs. tree seeder), when the disturbance-driven change in landscape-level forest abundance is large (from >50% to <25%) and shrublands dominate over a long period of time after such abrupt forest abundance decline (>150 years), we consider that a sudden change in ecosystem state occurs (Supporting Information Figure S7). The likelihood of such sudden ecosystem shifts, from forest (tree seeder + tree resprouter) to non-forest (shrubland + sparse vegetation)-dominated landscapes, shows a nonlinear relationship with forest abundance and with disturbance frequency (Figure 3a and Supporting Information Figure S10). Sudden changes in ecosystem state are highest in landscapes with intermediate forest cover and moderate to high frequencies of fire and drought (mFRI up to 40 years and mDRI of 20–40 years, and mDRI up to 70 years when mFRI is high). The vast majority of sudden shifts in ecosystem state from forest to non-forest are triggered by disturbance sequences including a large fire event (in a drought year or not) followed by, at least, one extreme drought year (81.2%; Figure 3b). Fire alone (e.g., two large fires in a short interval of time, <10 years), can also promote sudden changes from forest to non-forest in some cases (2.6% of the detected shifts). In contrast, our simulations indicate that at the predetermined frequency and intensity values we used, drought alone does not trigger sudden changes in ecosystem state. This is consistent with other studies assessing the interacting effects of drought with other disturbance-types (e.g., fire and grazing; Koerner & Collins, 2014). Finally, a substantial portion of sudden ecosystem shifts (16.76%) are triggered by extreme sequences including the occurrence of a drought episode and several large fires (at least two) within a short period of time (<10 years, Figure 3b).

## 4 | DISCUSSION

### 4.1 | Ecosystem shifts

The general vegetation patterns observed in our investigation are consistent with the typical dynamics observed in many Mediterranean Basin MTEs (Figure 1) (Carnicer et al., 2014; Pausas

(a) Tree resprouter to tree seeder



(b) Tree seeder to tree resprouter

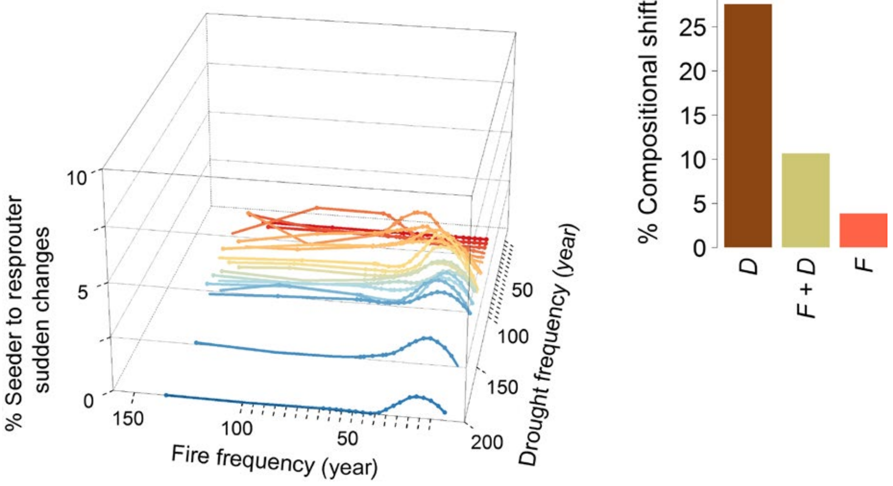


**FIGURE 2** Proportion of disturbance-driven forest compositional changes over the assessed compound fire-drought regimes. The top row (a) depicts shifts from tree resprouter- to tree seeder-dominated landscapes, and the bottom row (b) shows shifts from tree seeder- to tree resprouter-dominated landscapes. In both cases, the proportion of compositional shifts relative to the 100 replicate runs under each compound fire-drought scenario is depicted. The bar plots to the right of each 3D surface plot depict the proportion of landscape-level compositional changes between the two regeneration strategies driven by specific sequences of fire and drought events; *F* – large fire (burning 80%–100% of the landscape), *D* – drought episode. Only sequences generating >2% of the observed regenerative traits compositional shifts are depicted

& Lloret, 2007; Sheffer, 2012; Zavala et al., 2000): late-successional, resprouting tree species (e.g., *Q. ilex*, *Q. calliprinos*) dominate under lower disturbance frequencies whereas pioneer, fast-growing tree seeders (e.g., *P. halepensis*, *P. brutia*) are more abundant at intermediate disturbance recurrences. Inter-disturbance periods that are too short limit the ability of tree seeding species in this system to persist (e.g., seed production constraints) and shrubland communities increase (Keeley et al., 2012). More generally, our results also conform to regeneration trait dominance reported in other Mediterranean ecosystems in relation to gradients of disturbance (e.g., Clarke, Bell, & Lawes, 2015; Enright et al., 2014). Even so, the simulations presented here strongly indicate that variation in compound disturbance regimes has the potential to promote threshold-type changes in ecosystem state (forest vs. non-forest) and, therefore, that substantial ecosystem changes may occur under small shifts in fire or extreme drought regimes. Given the tight link between climate and fire and drought, such patterns reinforce the idea that, despite the often assumed resilience of Mediterranean ecosystems to disturbances, such ecosystems may sometimes lie close to tipping points that could lead to substantial vegetation changes under relatively small climatic changes.

## 4.2 | Sequence of events

In our framework, following Jõgiste et al. (2017) and Johnstone et al. (2016) and from an ecosystem recovery perspective, surviving adult trees and recruits (either from resprouting or seeding) would constitute the "material legacies" whereas plant regeneration traits (resprouter vs. seeder) and other traits such as their sensitivity to disturbances would correspond to the "information legacies." The interplay and totality of material and information legacies comprise "ecological memory" and modulate the response and resilience of the system to disturbance regimes. Regeneration traits such as seeding and resprouting presumably confer increased resilience to the system. However, our assessment strongly suggests that, similar to short-interval events of individual disturbances (Buma, Brown, Donato, Fontaine, & Johnstone, 2013; Syphard, Franklin, & Keeley, 2006), resilience mechanisms may fail under certain sequences of

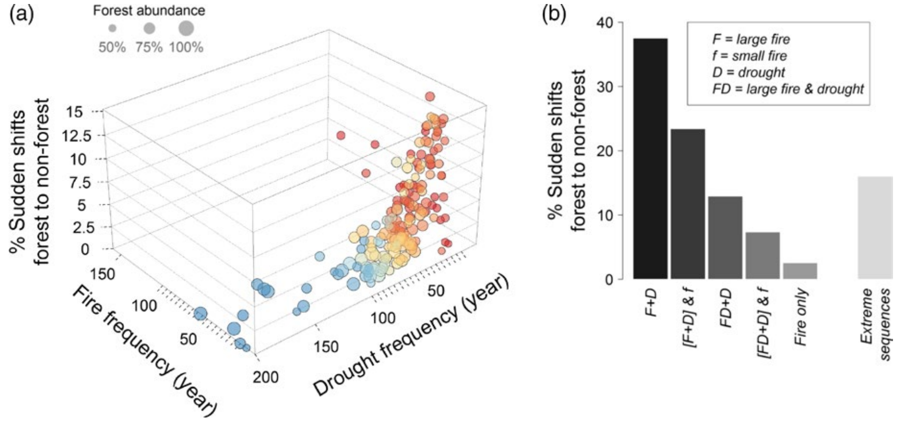


**FIGURE 3** Proportion of sudden, long-transient ecosystem shifts from forest to non-forest landscape dominance (a) and sequences of fire-drought events triggering such changes (b). In (a), dots show the proportion of sudden shifts relative to the 100 replicate runs under each compound fire-drought scenario; dot colour depicts drought frequency (reds – high recurrence and blues – low recurrence) and dot size is proportional to the mean landscape-level forest abundance right before the shifts in ecosystem state under each disturbance scenario. In (b), the proportion of sudden shifts associated to specific sequences of fire and drought events is shown. The symbol "+" denotes the sequence of disturbance events (e.g., *F* + *D* = large fire followed by extreme drought) whereas *FD* corresponds a large fire and extreme drought occurring in the same year. Note that *D* corresponds to extreme drought episodes of one or more years of duration, and that the & *f* notation corresponds to small fires occurring before or after the sequence of events specified within the brackets. *Extreme sequences* refer to those conditions in which at least two large fires and a drought episode (irrespective of its duration) occurred within the assessed 10 years windows. Please see Section 2.4 for details on disturbance sequence assessment

consecutive fire-drought events, leading to sudden changes in vegetation trait composition (seeder vs. resprouter dominance) or in the state of the system (forest vs. non-forest).

We found that the sequence of a large crown fire followed by an extreme drought year is a strong enough mechanism to disrupt "ecological memory" in MTE forests. This sequence of fire-drought disturbance events accounted for most of the sudden changes in ecosystem state (from forest to non-forest) in our simulations. Although the intense crown fires characteristic of MTEs have a profound impact on post-disturbance "material legacies," in mature MTE forests regeneration traits ("information legacies") should allow the recovery of populations through recruitment of new individuals after fire. However, extreme drought conditions in the years following fire may disrupt mechanisms of ecosystem resilience due to the increased sensitivity of recruits (i.e., higher mortality) to water-stress. Limited survival of recruits could therefore lead to sudden and potentially long-lasting changes in ecosystem state if extreme climatic conditions occur right after a fire year. Long-term experimental studies in other ecosystems have also emphasized the potential effects of post-fire environments and their complex interplay with ecological memory to vegetation dynamics (e.g., Blackhall et al., 2017). Shifts in ecosystem state may be maintained through time by climate-fire-vegetation feedbacks and the lack of succession towards forested states as a result of recruitment constraints derived from the lack of in-site seed sources (Mack & D'Antonio, 1998; Santana, Baeza, Marrs, & Vallejo, 2010; Tepley et al., 2018).

The occurrence of a fire after an extreme drought year does not appear, in the majority of cases, as a mechanism strong enough to promote sudden ecosystem state changes, from forest to non-forest vegetation. Nevertheless, this sequence of events was responsible for the majority of regeneration traits compositional shifts of the system (i.e., from tree resprouter to tree seeder-dominated forests). Such compositional shifts mostly occurred under mixed vegetation (Supporting Information Figure S9). We suggest that the effects of a single pre-fire extreme drought year, at the severity levels implemented here (10%–25% vegetation die-off), are not strong enough to significantly alter "ecological memory" in mature forests to promote a shift to a shrubland state after fire. However, the influence of this mechanism cannot be ruled out under the climate change context as the forecasted increase in climatic extremes in the coming decades could lead to higher levels of drought-induced forest mortality and, therefore, to greater impacts of drought events on "ecological memory" (Allen et al., 2015; IPCC, 2014).

The strong effect of a post-drought crown fire in "material legacies," along with the pioneer and fast-growing character of the tree seeder in our approach, would favour their expansion in relation to the tree resprouter (a late successional species), potentially leading to a trait compositional shift. Such a pattern is consistent with post-fire conversion from mixed forests to tree seeder-dominated systems in some MTEs (Rodrigo, Retana, & Picó, 2004). Alternatively, the influence of consecutive, extreme drought years, potentially promoting shifts from tree seeder- to tree resprouter dominance is also consistent with recent mortality patterns observed in pine-oak systems in southern Mediterranean Basin MTEs (Esteve, Martínez, Hernández, Robledano, & Lloret, 2016). The influence of the specific sequences of fire-drought events discussed here may have different impacts in other MTE regions (e.g., California) and environments where regeneration traits (seeding vs. resprouting) are correlated differently to other life-history traits (e.g., pioneer vs. late successional species) or fire adaptations (e.g., thick bark to survive fire).

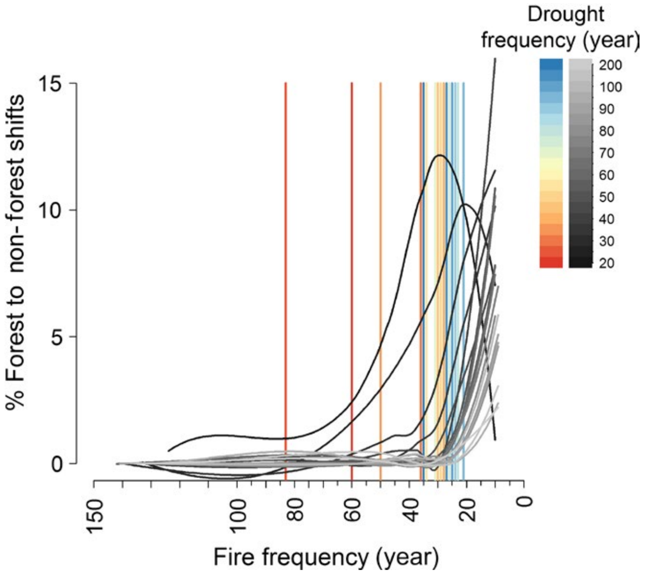


**FIGURE 4** Proportion of sudden shifts between forest and non-forest-dominated landscapes along a fire regime gradient. The solid grey curves correspond to the result of local polynomial regression fitting (`loess` function; R Core Team, 2016) on the proportion of sudden shifts detected in the 100 model replicates performed under each compound fire-drought scenario. Note that the dark-light grey colour scale corresponds to a gradient of drought recurrence (from high to low drought frequency, respectively).The coloured vertical lines illustrate the turning points, as inferred by automated, iterative break detection procedures to characterize changes within time series (R package `bfast`; Verbesselt, Hyndman, Newnham, & Culvenor, 2010), at which the likelihood of sudden changes in vegetation state increases markedly under each compound fire-drought regime

The potential disruption of "ecological memory" as a result of specific sequences of events emphasizes that the effects of interacting disturbance regimes, even if only occurring sporadically over time, can exert a strong influence on the dynamics of vegetation (Kreyling, Jentsch, & Beierkuhnlein, 2011). Although some of the disturbance sequences assessed in our approach have a low likelihood of occurrence in most landscapes (e.g., two large fires occurring within a short period of time, <10 years), they could be relevant at local scales (Harvey, Donato, & Turner, 2016). In this sense, our framework does not conform to the reported dominance of resprouting species as a result of consecutive, high-intensity fire events (Enright et al., 2014); this could be seen as an artefact of the model related to the higher capacity attributed to the tree seeder to re-colonize the landscape from small remnants (e.g., after two large fire events) and the substantial loss of the resprouting capacity of young resprouters under consecutive fire events (Fairman et al., 2019; Karavani et al., 2018).

Our modelling approach does not allow for additional feedbacks between fire occurrence and drought through changes in vegetation productivity which could also affect the probability of vegetation shifts in the system (Williams et al., 2013). Similarly, factors such as climatic fluctuations (e.g., dryness levels as opposed to extreme drought) or fire severity that can modulate system resilience by influencing seed production or resprouting capability (Enright et al., 2015; Nicholson, Prior, Perry, & Bowman, 2017) are not incorporated in our framework. Regardless, our results emphasize that the effects of disturbance interactions can be of paramount importance in the context of ongoing global change as the frequency and intensity of extreme episodes of water deficit are projected to increase globally, and specifically in MTEs (IPCC, 2014), with the consequent increases in the likelihood of successive fire-drought events. The inherently stochastic nature of fire and drought makes it difficult, however, to anticipate disturbance-driven tipping points (Reyer et al., 2015). The integration of recent advances towards characterization of disturbance thresholds such as drought-induced mortality thresholds (Martínez-Vilalta, Poyatos, Aguadé, Retana, & Mencuccini, 2014) and fire weather indices (Bedia et al., 2015) may help, however, in assessing ecosystem vulnerability to rapid, disturbance-induced changes in relation to major plant traits such as regeneration strategies.

### 4.3 | Implications for ecosystem resilience

Across the space of compound fire-drought regimes examined here, we find that the interacting effects of the two disturbance regimes define the relative location of tipping points in ecosystem state (Figure 4). Our simulations suggest that fire frequency thresholds may exist (20–40 years recurrence) under which the likelihood of sudden ecosystem changes as a result of fire–drought interactions increases significantly irrespective of the frequency of extreme droughts. Fire–drought interactions could thus have a more limited influence on ecosystem state across a large portion of disturbance frequency gradients, especially at low disturbance recurrence. However, under high extreme drought recurrences (<20–25 years) the fire frequency threshold of sudden ecosystem shifts is displaced beyond fire return intervals over 50–60 years (and as high as 80 years). In such longer fire intervals, however, the increase in the likelihood of sudden ecosystem shifts is more gradual than at higher fire frequencies, pointing to both the possibility and rarity of ecosystem shifts within this range of the disturbance space. The implications of these findings are twofold. On one hand, it strongly suggests that even in places where fire recurrence is low, increased recurrence of extreme droughts under climate change will increase the likelihood of sudden shifts in ecosystem state. Similarly, in places where extreme droughts occur infrequently, sudden shifts may have an increased probability of occurrence if fire frequency approaches recurrence thresholds. These patterns agree with recent observation of forest resilience to extreme drought events that suggest that co-drivers (other disturbances such as fire or insect outbreaks) may play a key role in determining tipping points of ecosystem change (e.g., Clark et al., 2016). On the other hand, we propose that thresholds of ecosystem resilience are not only contingent on "ecological memory" ("material legacies" and "information legacies") but also on the regimes of interacting disturbances. Therefore, aside from accurate description of current ecosystem state, increased characterization of past, current, and future compound disturbance regimes will be required to perform meaningful predictions of ecosystem change under changing climates.

### 4.4 | Synthesis

It is increasingly recognized that ecosystem assessments based on the impact of individual disturbance regimes will not capture potential alterations caused by the interacting effects of multiple stressors (e.g., Batllori et al., 2017; Buma & Wessman, 2011; Enright et al., 2014; Johnstone et al., 2016). Among these alterations, our analysis emphasizes that the effects and feedbacks of compound disturbance regimes increase the long-term likelihood of sudden ecosystem shifts and, therefore, uncertainty in predicting vegetation state. Extreme disturbance events or short inter-disturbance periods have been related to loss of resilience and sudden changes in ecosystem state (e.g., Buma et al., 2013; Martínez-Vilalta & Lloret, 2016). Our approach highlights that specific sequences of events, even under moderate recurrence of individual disturbances, are a strong enough mechanism to promote shifts in ecosystem state. The joint influence of consecutive disturbance events on "material legacies" can constrain the effects of "information legacies" and lead to loss of ecosystem resilience. We suggest that the locations of disturbance-driven tipping points are contingent on the interacting effects of disturbance regimes and, therefore, cannot be inferred from analysis or prediction of individual disturbance regimes. Integration of current ecosystem state, thresholds of disturbance, and models of compound disturbance effects will be required to assess ecosystem vulnerability and the likelihood of sudden shifts in ecosystem state under changing climates.

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## AUTHORS' CONTRIBUTIONS

E.B. conceived the idea; all authors designed methodology; E.B. and M.d.C. developed the model; E.B. performed model simulations and output analysis; E.B. led the writing; all authors contributed to results interpretation and discussion. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

This manuscript does not use original data.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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