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A framework linking biogeography and species traits to plant species vulnerability under global change in Mediterranean-type ecosystems

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Abstract

We review the roles that plant species traits and biogeography play in species' exposure and vulnerability to decline or extinction under global change, focusing on separate and combined impacts of multiple threats – climate change, land-use change, and altered disturbance regimes. We establish a conceptual framework and research agenda for identifying the spatial characteristics of species ranges, as well as the life history and functional traits, that are associated with extinction risk for plant species with functional attributes emblematic of fire-prone, winter-precipitation Mediterranean-type ecosystems (MTEs). MTEs worldwide are characterized by their high plant diversity and unique floras, historical and contemporary high rates of land use change, and strong interactions between climate, fire, and land use. We focus on the California Floristic Province (CFP), an MTE that is a global plant diversity hotspot, and show how our framework can be used to understand the relationships between vulnerability to multiple global change drivers, species traits, and biogeography. Vulnerability can be assessed across species using linked distribution and population models that forecast plant responses to global change scenarios. Our overarching hypothesis is that species-specific vulnerability to global change in MTEs is a function of interactions between species and spatial traits: the nature of this interaction will depend on the type of global change process.

Highlights

- Mediterranean-type ecosystems are winter-rain, water-limited, fire-prone biomes that have high human population densities and intensive human land use where climate change and land use change are expected to alter fire regimes as well as species distributions.
- We posit that species biogeography (range) is key to understanding species exposure to global change because drivers, and their potential interactions, are spatially structured.
- We expect that the plant traits associated with sensitivity (extinction risk) for a plant species emblematic of Mediterranean-type ecosystems include functional traits related to their carbon and water use strategies, and demographic traits related to disturbance response.
- We expect that species traits will be most strongly linked to vulnerability to climate change because of a functional relationship between traits and climate, while spatial traits will be most strongly linked to vulnerability to land use change.
- A linked modeling methodology can be applied to multiple species to assess both the exposure and sensitivity components of global change vulnerability in relation to traits.

Keywords: Biogeography, California Floristic Province, conservation, global change, Mediterranean-type ecosystem, plants, species range, species traits.

Introduction

As human-driven transformation of earth system processes rapidly increases, understanding how global change affects biological diversity is the greatest conservation challenge of our time (Rockstrom et al. 2009). For decades, habitat loss due to land use change has been the major threat to species persistence worldwide (Foley et al. 2005, Hansen et al. 2012,

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Newbold et al. 2015), but current and projected effects of climate change have become a serious global concern for the future of biodiversity and the ecosystem services it provides (Pereira et al. 2010, Dawson et al. 2011, Bellard et al. 2012, Urban et al. 2016, Pecl et al. 2017, Brondizio et al. 2019). Further, impacts from changes in disturbance regimes, such as fire, could rival or even exceed land use or climate change as primary biodiversity threats (Turner 2010, Bowman et al. 2011, Morris et al. 2020, Turner et al. 2020). As all of these threats increase in number and magnitude, there is a growing need to understand how they impact species directly and in combination. To identify which species will be most susceptible to decline or extinction, it is also important to understand the extent to which their traits and location enhance and enable the future projection of their vulnerability. In this way, it will be possible to design appropriate and effective strategies to conserve natural heritage.

Identifying traits associated with species decline has become the Holy Grail of conservation biology because of their potential as measurable surrogates for extinction risk, especially for poorly studied taxa (Lavorel and Garnier 2002, Foden et al. 2013). Plant life history traits are characteristics related to demography and reproductive strategy, while functional (structural, morphological, physiological) and dispersal traits also influence population resilience or vulnerability. Beyond understanding which traits mediate resilience versus vulnerability to global change is the need to understand the spatial attributes of species associated with high potential for extinction (e.g., Angert et al. 2011). Most global change threats have distinctive spatial and temporal signatures (Dwyer et al. 2000, Liu et al. 2015). Land use change drives biodiversity loss through direct habitat loss and fragmentation via agriculture, deforestation, or urban growth; this is often exacerbated by declining habitat quality resulting from other global change agents, e.g. climate change, altered disturbance regimes, and invasive species, as well as altered nitrogen cycle and increased atmospheric CO_2 (Sala et al. 2000). These agents of global change act in a spatially explicit manner, and their impacts show spatial dependence (following Tobler's first law of geography Tobler 1970)—they occur in specific geographic locations and across characteristic landscape configurations. They also interact, potentially causing synergistic impacts to population, community, and ecosystem processes (Tylianakis et al. 2008, França et al. 2020, Turner et al. 2020). The ways in which the geographies of species' distributions and agents of global change interact with species traits to influence extinction risk is an important, and generally overlooked, question.

Biodiversity in Mediterranean-type ecosystems (MTEs) is especially vulnerable to changes in climate, fire regime, and land use. MTEs are characterized by cool wet winters and warm dry summers and are found adjacent to cold ocean currents on the west coasts of continents at mid-latitudes. All five Mediterranean-climate regions are plant diversity hotspots of global significance (Myers et al. 2000), and their biological diversity is highly sensitive to rapid global change (Underwood et al. 2009, Keeley et al. 2011, Doblas-Miranda et al. 2015). Despite their relatively low percentage of land cover, MTEs world-wide are among the highest in plant species richness and endemism and include many species with restricted ranges (Cowling et al. 1996).

Changes in fire regimes have particularly significant consequences for plant species in fire-prone MTEs (Syphard et al. 2009, Keeley et al. 2011) because many plants have evolved traits that are responsive to a specific fire regime. Interacting global change drivers—climate change and land use change—may alter fire regimes in MTEs worldwide (Williams et al. 2001, Mouillot et al. 2002, Pausas et al. 2004, Keeley, Syphard 2016). Several recent analyses have shown important cumulative effects of these multiple and interacting threats on species persistence in MTEs (e.g. Keith et al. 2008, Bonebrake et al. 2014). MTEs share high biodiversity, habitat loss, an active and altered fire regime, and the onset of impacts due to climate change (Underwood et al. 2009, Doblas-Miranda et al. 2015).

In this paper, we review the roles that the geographies of global change drivers and species traits play in terrestrial plant species' vulnerability to decline or extinction under global change in MTEs. We establish a conceptual framework and research agenda by identifying the spatial characteristics of species ranges as well as the traits associated with extinction risk for plant species emblematic of MTEs, focusing on the California Floristic Province (CFP). Based on this framework we predict relationships between biogeography, traits, and vulnerability, and describe a modeling methodology to test predictions using forecasts of global change impacts on CFP plant species.

The geographies of global change drivers in the California Floristic Province MTE

The California Floristic Province (324,000 km^2) is a MTE plant diversity hotspot (Fig. 1), with 20% of all vascular plant species found in the United States, 30% of which are endemic (Master et al. 2000). The region is topographically diverse (contributing to richness of biota) and its terrestrial ecosystems are, and will continue to be, fragmented by land use change. The CFP spans roughly 13 degrees of latitude and 4,000 m of elevation, and although it is defined by its MTE-rainfall seasonality throughout, a range of climatic conditions occur across this vast region. Terrestrial plant communities in the CFP experience some degree of summer dry period, but span strongly water-limited systems at lower elevations, latitudes, and farther inland, to light-limited forests at higher elevations and higher-latitude coastal areas (Barbour et al. 2007, Mooney and Zavaleta 2016). Species distributions among key plant functional types in the CFP are closely tied to climate, especially winter minimum temperatures (Ewers et al. 2003)

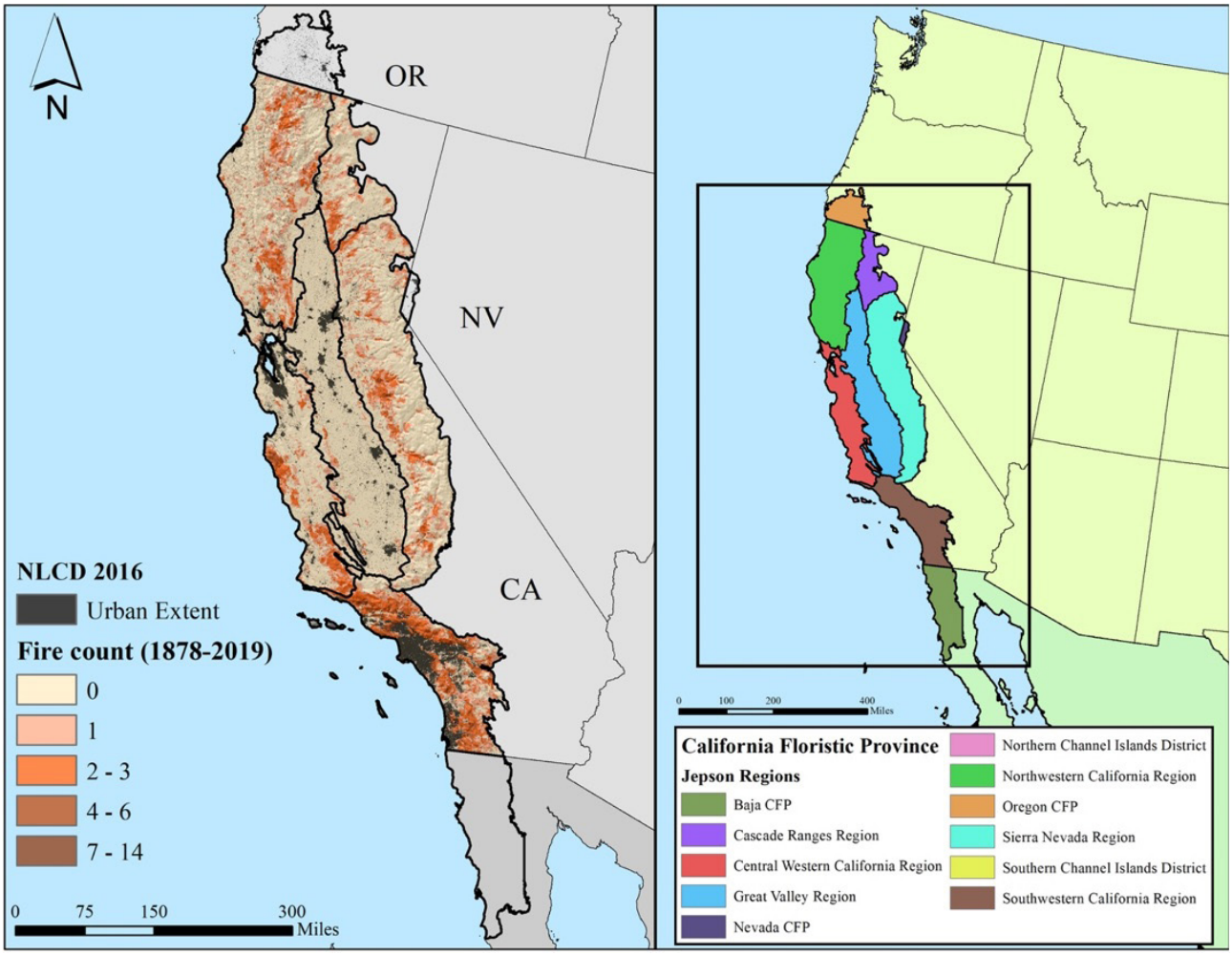

Figure 1. The California Floristic Province (CFP) in central western North America, showing urban extent (left from the U.S. Geological Survey Land Cover Database (www.usgs.gov), and historical fire frequency (left) calculated using data from California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (frap.fire.ca.gov), within the Jepson ecological regions shown on the right (from Hickman 1993).

and drought severity (Davis et al. 1999). California's climate has become warmer and effectively drier in the 20th century and is projected to change further in the future (Hayhoe et al. 2004, Cayan et al. 2008, Sun et al. 2015). Recent studies suggest that climate change has already had a measurable impact on plant species distributions (Rapacciuolo et al. 2014) and diversity (Harrison and LaForgia 2019, Harrison et al. 2020) in this region.

Land Use Change

Expanding urban and agricultural land use associated with human population growth has increased in MTEs worldwide in recent decades and continues to be a major driver of biodiversity loss (Doblas-Miranda et al. 2015, Peñuelas et al. 2017). The location and spatial arrangement of habitat loss and fragmentation can have differential effects on extinction risk. Non-random contiguous habitat loss commonly associated with urban growth, deforestation, or agricultural conversion, is more likely to cause extinction in biodiversity hotspots than random habitat loss because endemic species' ranges are typically small, and disturbance is more likely to affect the entire range of small-range species (Brooks et al. 2002, Seabloom et al. 2002, Staude et al. 2020). Furthermore, not only the spatial configuration of habitat patches but the geographical location of species drives exposure to spatially explicit threats. Numerous studies have demonstrated an overlap of high biodiversity and human impacts, particularly in the form of land use change (Myers et al. 2000, Ricketts and Imhoff 2003, Allan et al. 2019)—the concept of biodiversity hotspots for conservation prioritization, i.e. areas of high species richness and high habitat loss, is predicated on this overlap (Myers et al. 2000). In the CFP, a correlation between plant species richness and habitat loss rates has been attributed to underlying habitat characteristics that influence species distributions such as rainfall, soil quality, and elevation which also influence the rate of conversion to human-dominated

land uses (Seabloom et al. 2002), highlighting the importance of spatial patterns of land use change in species vulnerability. In Southern California, areas of high species richness are also spatially congruent with area of high fire hazard (Syphard et al. 2016).

Climate Change

While habitat loss and fragmentation affect species' distributions and population dynamics directly, rapidly changing climatic conditions affect species' geographies indirectly and dynamically because of physiological limitations and the shifting of suitable habitat. Species' range-characteristics arise from biogeographical history (Soberón 2007), ecological tolerances, and environmental factors that are spatially structured (Elith and Franklin 2013). Almost two decades ago, Parmesan and Yohe documented (and titled their paper) "a globally coherent footprint of anthropogenic climate change impacts across natural systems" (Parmesan and Yohe 2003), finding that the majority of species examined (in groups ranging from plants to amphibians) showed advancing spring phenological events (see also Root et al. 2003), and of the almost 50% of species showing range shifts, 80% of those shifts matched unique 20th century rising global temperatures—poleward or to higher elevations (see also Walther et al. 2002). These effects were seen across terrestrial, marine and aquatic ecosystems with the greatest negative effects for range-restricted species, polar and mountain-top species, coral reef species and amphibians (Parmesan 2006). More recent global studies document lags between the velocity at which species ranges and isotherms are shifting in recent decades (Chen et al. 2011, Pecl et al. 2017), and attribute range shifts to other global change drivers in addition to climate change (Lenoir et al. 2020). Climate change is also causing changes in plant community dynamics (reviewed in Franklin et al. 2016). In the CFP, the fingerprint of anthropogenic climate change on species' biogeography (elevational range shifts) cannot be explained simply by shifts "uphill" and to higher latitudes in response to temperature warming, but rather must be understood in terms of multiple aspects of climate in this water-limited biome, as well as other contemporaneous global change factors (Rapacciuolo et al. 2014).

Plant communities in water-limited ecosystems, including MTEs, respond differently to climate change than those in energy-(heat- and light-) limited ecosystems (Boisvenue, Running 2006). Rising temperatures increase climatic water deficit by increasing evapotranspiration, even if precipitation is unchanged (Stephenson 1998). Increasing water stress in water-limited terrestrial ecosystems is linked to plant mortality and recruitment failure, as well as changes in fire and other disturbance regimes (insect outbreaks) (Breshears et al. 2005, Allen et al. 2010, Das et al. 2013), which can interact to result in broad scale extirpation of plant communities and replacement with species with better-adapted traits.

Terrestrial species geographies that overlap with areas of rapid climate change, e.g., with higher climate change velocity (Loarie et al. 2009, Serra-Diaz et al. 2014), may be more susceptible to extirpation or extinction given the lack of time available to adapt or disperse into areas with more suitable habitat, especially when habitat is fragmented.

Altered Fire Regimes

Fire and other natural disturbances are important drivers of ecosystem dynamics, and wildfire has played a key evolutionary role for MTE biota (Pausas and Keeley 2009). A disturbance regime comprises the typical frequency, severity, size/magnitude, timing, and so forth of a periodic natural disturbance (Pickett and White 1985), and fire regimes develop in response to long-term biotic, abiotic, and human characteristics of a region, primarily climate, vegetation, and location and frequency of ignition source (Syphard and Keeley 2020).

Fire regimes have been altered by human actions that have both decreased and increased fire in different places and times (Bistinas et al. 2013), and altered fire regimes are a significant driver of global change. Human causes that alter fire regimes include other global change drivers, notably land use change, climate change, and introduction of non-native species (D'Antonio and Vitousek 1992, Fusco et al. 2019, Syphard et al. 2019a). Urban/exurban growth and land use/land cover change not only drive direct habitat loss and fragmentation but also affect fire patterns via the extent and intensity of agriculture (Andela et al. 2017) and from changes to patterns of housing development and land cover. These changes affect fire by altering vegetation (i.e., fuel) and the distribution of human-caused ignitions (Syphard et al. 2007, Syphard et al. 2008, Mann et al. 2014, Radeloff et al. 2018, Syphard et al. 2019b).

A major predicted impact of anthropogenic climate change in fire-prone ecosystems is an altered fire regime, and while many projections suggest that fire activity could skyrocket in upcoming decades due to warmer temperatures and drier fuels (Westerling et al. 2006, Flannigan et al. 2016), the trends and responses are much more nuanced (Keeley and Syphard 2016) with recent global net declines in fire activity (Doerr and Santín 2016). The reason for these nuances is that different climatic and other factors limit fire behavior in different places and at different times (Pausas and Ribeiro 2013); in many areas, human influence may override the effect of climate on fire regimes (Syphard et al. 2017b, Radeloff et al. 2018). In short, the future of fire regimes under climate change is highly uncertain.

While the CFP is a MTE biome, it is not homogenous with respect to fire regime. Climate may play an important but varying role in modifying fuel abundance, contiguity, or flammability, and therefore fire regime. In wetter regions of the CFP with generally higher biomass, climate may significantly increase fire likelihood via limits to fuel moisture; in drier ecoregions, fires may be more limited by fuel abundance and contiguity (Krawchuk and Moritz 2011). In more developed areas, climate is generally

not as significant as land use or ignitions (Syphard and Keeley 2015, Keeley and Syphard 2017). This geographical complexity is particularly characteristic of the CFP due to its widely varying natural plant communities, topographic conditions, and resulting fire regimes (Keeley and Syphard 2015, Keeley and Syphard 2016, Keeley and Syphard 2017). Humans also dramatically alter fire regimes (Syphard et al. 2009, Parisien et al. 2016, Balch et al. 2017), and in most of the CFP 95% of fire ignitions are caused by humans (Syphard et al. 2007, Syphard et al. 2017a).

Plant traits mediate response to global change drivers

If extinction is correlated with species' life history or functional traits, as many researchers contend (Davies et al. 2000, Henle et al. 2004, Pereira et al. 2004), then specific traits will be important factors in understanding species vulnerability to global change-driven decline and disappearance (Foden and Young 2016). Recent research has made valuable headway in shedding light on such traits and the challenges of identifying them (Jiguet et al. 2007, Angert et al. 2011, Dawson et al. 2011, Foden et al. 2013, Garcia et al. 2014, Pearson et al. 2014, Estrada et al. 2015, Chichorro et al. 2019). Knowing which species' traits determine the resilience of natural populations to multiple, sometimes interacting, threats remains, however, a fundamental unanswered question in ecology because of cryptic, cumulative, synergistic or counteracting effects (Sutherland et al. 2013).

Plant traits mediate the functional response of plant species to climate, and therefore species' distributions, across environmental gradients and biogeographical range (Stahl et al. 2014, Violle et al. 2014, Skelton et al. 2021). Plants possess suites or syndromes of coordinated, quantitatively measurable traits (Westoby et al. 2002). *Functional traits* are broadly defined as measurable attributes affecting fitness via their effects on growth, survival, and reproduction (organismal performance) (McGill et al. 2006, Violle et al. 2007, Albert et al. 2010). Functional traits include structural, morphological, phenological, and physiological characteristics (e.g., seed mass, deciduousness, growth form, photosynthetic rate) that affect fitness (Violle et al. 2007) and are strongly associated with variation in the biotic and abiotic environment (Salguero-Gómez et al. 2016). *Response traits* are those that govern responses to changing environmental conditions, including along resource gradients and those caused by disturbances (Violle et al. 2007, Gillison 2013). Particularly relevant to fire-prone MTEs, *disturbance response traits* include those traits related to reproductive strategy and population dynamics (growth form, height, demographic parameters, and dispersal strategies) that mediate how a species may recover following fire (Lavorel and Garnier 2002). We propose that three groups of plant traits that are relevant to explaining plant species vulnerability to global change in fire-prone, seasonally water-stressed, MTEs: life history strategy, leaf economic strategies, and hydraulic strategies.

Species with "slow" life histories (characterized by low adult mortality, low growth rates, low fecundities, and late reproduction) tend to be more prone to extinction than species with "fast" life histories (characterized by high adult mortality, high growth rates, high fecundity, and early age at first reproduction) (Purvis et al. 2000, Rueda-Cediel et al. 2018). Species demographic and dispersal-related traits that govern individual or population-level responses to disturbance may lead to predictable population declines (e.g. frequent fires increase extinction risk in obligate seeding plants because they prevent the seed bank from accruing (Regan et al. 2010)). Plant species demography can be captured in traits such as: longevity (dictated by survival rates); timing and form of reproduction (vegetative versus seed germination); the number of seeds produced; and whether they are stored in a seed bank. Seed size and plant height (Westoby 1998) are also related to dispersal strategy (Vittoz and Engler 2007) as well as to resource acquisition. Plant species defined in terms of these and other demographic traits tend to show predictable changes along environmental and disturbance gradients (Noble and Gitay 1996, Pausas 1999, Rusch et al. 2003).

The leaf economics spectrum describes carbon (and nitrogen) use strategies in terms of leaf traits (Wright et al. 2004) although Reich (2014) argued that the framework can be extended to water use by including root and stem traits related to water acquisition. This fast-slow plant economic spectrum describes the relationship between functional traits and the acquisition of resources – carbon, nutrients, and water. Key traits that have been related to carbon and water acquisition strategies are specific leaf area (SLA) and percent leaf nitrogen by mass (%N), as well as others (leaf phosphorus, photosynthetic rate, dark respiration rate, leaf phenology, stomatal conductance, specific leaf weight, photosynthetic pathway) (Wright et al. 2004, Gillison 2013, Reich 2014).

A great range of hydraulic strategies are found in plants in water-limited MTEs. Traits associated with hydraulic strategies for maintaining high leaf water supply under high evaporative demand (resistance to wilting, death, and drought-induced xylem cavitation) in the CFP (Bhaskar et al. 2007) include deciduousness (Mooney and Dunn 1970), leaf life span (Ackerly 2004a), low SLA (Ackerly 2004b), seed size (Baker 1972, Ackerly and Nyffeler 2004), photosynthetic stems, deep roots, sapwood capacitance, photosynthetic responses to leaf water potential, and hydraulic architecture (Pivovaroff et al. 2016). Morphological and anatomical traits related to water acquisition that may be easily measured include stem wood density, rooting depth, stomatal density, and guard cell length (Sack et al. 2003, Gillison 2013, Pivovaroff et al. 2016).

Tradeoffs in resource acquisition and disturbance response strategies lead to correlations of traits and

environmental gradients in the CFP (Ackerly and Cornwell 2007, Cornwell and Ackerly 2009). In CFP woody plant communities, leaf, wood, and whole-plant (height) traits are correlated with gradients of soil moisture availability (Ackerly et al. 2002) and there are trade-offs among leaf-economic traits related to light acquisition and those related to hydraulic strategy (rooting depth); in taller forest plant communities, light acquisition strategies are more important than in shorter shrublands (Ackerly and Cornwell 2007). These traits are also related to vulnerability to environmental change, especially to climate warming and drying (Pezner et al. 2020).

While carbon and water-use strategies are directly linked at the leaf level, it is unclear if they may be decoupled at the whole plant level, something important to consider in a changing climate (Pappas et al. 2016, Grossiord et al. 2020). The physiological tolerance hypothesis posits that a greater range of functional strategies can be supported in a benign (warm and wet) climate than a harsh (dry, cold or both) climate (Currie et al. 2004). Accordingly, within the CFP, plant height, seed mass, foliar nutrient concentration, and SLA tend to show more functional diversity in more benign MTE climates; as water stress increases across a climate gradient, taller species with higher SLA, leaf N, and seed mass are selectively lost from the community, resulting in lower functional trait diversity (Harrison et al. 2020). This suggests that in a warming and drying CFP predicted under 21st century anthropogenic climate change scenarios, functional diversity and plants with faster resource acquisition strategies may be lost from plant communities.

Here, we have described trait variation along three axes of life history, leaf economic, and hydraulic strategies. However, these axes may in fact not be orthogonal when considering plant species throughout the CFP; some traits that covary with broad-scale climatic gradients have been shown to be uncorrelated within local plant communities in the CFP (Ackerly 2004a). Environmental tolerances and physiological adaptations tend to covary with plant life form (Raunkiaer 1934), life history, and fire response strategies (Chapman and Crow 1981, Keeley 1981, Keeley 1998, Ackerly et al. 2002), largely due to resource allocation and life history tradeoffs (Austin 1987, McGill et al. 2006). Owing to these tradeoffs, correlated traits have been grouped together into plant functional types, a useful framework for analysis and prediction in community and evolutionary ecology (Gillison and Carpenter 1997, Smith et al. 1997, Diaz et al. 1998, Ackerly 2003, Pausas and Lavorel 2003, McGill et al. 2006, Rüger et al. 2020). So, while we describe a framework based on continuous trait variation along three axes, in fact it may be that variation among CFP plants is captured by clusters of trait values representing plant functional types.

Framework

Species and Spatial Traits and Global Change Vulnerability

Summarizing the literature reviewed in the previous sections, we identify some functional and response traits that are often measured in plant trait studies and that we hypothesize mediate global change effects on MTE plant population dynamics along the dimensions of life history strategy, leaf economic strategy, and hydraulic strategy (Table 1). These include traits related to stress tolerance as well as fire disturbance response that are important in shaping MTE plant species and community distributions. We also describe spatial attributes of species distributions that we predict will be correlated with vulnerability to non-random patterns of global change in the CFP (Table 2). We expect that range size, range topography, and range location (biogeography) will be related to global change exposure.

By applying a methodology that can predict the effects of global change projections on plant species to many species with a range of trait values and spatial attributes, we can implement this framework to test hypotheses (Tables 1, 2) and make predictions about

Table 1. Plant species traits related to three dimensions of environmental response determining organismal performance, and hypotheses about how those traits are related to the global change drivers of climate change, land use change, and altered disturbance regimes in the California Floristic Province (CFP), a Mediterranean (climate) Type Ecosystem (MTE) as well as other MTEs.

Dimension	Traits	Hypotheses
Life history strategy and disturbance response	Longevity; age of first flowering; fecundity; seed longevity; seed size; plant height; dispersal vector	Species with 'slow' life histories (long lived, later maturing, especially if they are poor dispersers) are more vulnerable to losses of suitable habitat (from any global change driver) than 'fast' species that can disperse longer distances
Leaf economic strategy	SLA; leaf %N	Species with 'fast' resource acquisition strategies (high SLA, high %N) are more vulnerable to climate change (trending effectively drier in the CFP) than slow ones
Hydraulic strategy	wood density; sapwood capacitance; deciduousness	Species with adaptations for water stress (high wood density, drought deciduousness, low SLA) are less vulnerable to climate change (trending warmer and drier)

Table 2. Spatial attributes (based on Pearson et al. 2014, and Costanza et al. 2019) of species distributions (ranges) that may be related to exposure to global change drivers (climate change, land use change and altered fire regimes), and hypotheses about how those traits are related to the global change drivers in the California Floristic Province (CFP) and other Mediterranean (climate) Type Ecosystems (MTEs).

Attribute	Metrics	Hypotheses
Range size	occupied area; largest patch; habitat breadth;	Species with larger ranges are less vulnerable to habitat loss or shift from all global change drivers
Range topography	slope; aspect; topographic heterogeneity	Species in flatter regions are more vulnerable to climate change owing to greater climate velocities; species in topographically heterogeneous regions are less vulnerable due to presence of topoclimatic refugia; species at high elevations in mountains are more vulnerable to climate warming due to lack of available habitat
Range location	ecoregion(s) in range	Species in regions projected to undergo urban growth (coastal, and central valley) and those projected to undergo great changes in fire regime (uncertain) are more vulnerable to land use and fire regime change that climate change

the relationship between traits, space and vulnerability. Those hypotheses, summarized in the tables, are discussed further here.

Overall, we expect that species traits will be strongly linked to climate change vulnerability because of a functional relationship between traits and climate, while spatial traits as well as species traits will be strongly linked to land use change vulnerability. Both life history traits (especially dispersal and longevity) and range distribution may determine sensitivity to fire regime change which is affected by both climate change and land use change.

Longer-lived species with slow life histories will likely be most vulnerable to all global change drivers of habitat loss or habitat displacement (Table 1). Species with dispersal traits and syndromes that support only short-distance dispersal will be vulnerable to large habitat shifts, losses, and fragmentation driven by any global change driver. Furthermore, altered fire regimes characterized by increased fire frequency may be more detrimental to populations of species with 'slow' life histories—especially those dependent on a minimum time between fires for seed bank development—than to habitat contractions resulting from climate change and land use change (Keith et al. 2008, Regan et al. 2010, Regan et al. 2012, Syphard et al. 2013, Bonebrake et al. 2014).

Species whose range is confined by natural barriers and/or overlaps the most with spatially-explicit threats will be most vulnerable to global change, regardless of their traits (Table 2). Distribution shifts induced by climate change may ultimately result in disproportionate habitat reduction or fragmentation for plant populations abutting coastlines, or urbanized areas, or shifting to higher elevations where there is less land area (Thuiller et al. 2005, Hijmans and Graham 2006, Kelly and Goulden 2008, Preston et al. 2008, Kuhn et al. 2016).

A Linked Modeling Methodology for Analyzing Global Change Vulnerability

Implementing the proposed framework requires a methodology that can predict the response of plant species to global change; that response then serves as a dependent variable in order to test the effect of traits and spatial attributes across species. In 2008, Williams et al. developed a powerful integrated conceptual model for assessing species vulnerability to climate change; this has been widely applied to assess extinction risks and conservation action for biodiversity vulnerable to climate change (e.g., Dawson et al. 2011). This model differentiates *exposure* and *sensitivity* as factors determining vulnerability, and *adaptive capacity* as a factor that can ameliorate sensitivity. Exposure to climate change is defined as the degree to which climate experienced by organisms changes within a species range, and therefore is affected by range traits. Sensitivity is a function of species' ecology, physiology and genetic diversity, whereby sensitivity is determined by species life history traits, dispersal ability, and population dynamics, as well as adaptive capacity (genetic diversity and plasticity). Species vary in their degree of intrinsic sensitivity and capacity to adapt to exposure (Williams et al. 2008, Chevin et al. 2010), and traits can capture this variation.

Assessing species vulnerability to future global change projections is typically addressed using change scenarios and predictive modeling (e.g., Thomas et al. 2004, Keith et al. 2008, Merow et al. 2014,

Warren et al. 2018); scenario-based modeling is the approach we describe here. Species distribution models (SDM) (Franklin 2010), and climate change projections, have been widely used to assess the climate change exposure of species (Pearson and Dawson 2003, Thomas et al. 2004, Dawson et al. 2011, Warren et al. 2018). Keith et al. (2008) linked projected species' ranges under climate change scenarios predicted using SDMs with single species population models (Akcakaya et al. 2004) to assess both the exposure and sensitivity components of MTE plant species vulnerability to climate change and altered fire regimes.

We have described an integrated or linked modeling methodology previously in detail (Franklin et al. 2014). Future climate change projections are linked to a species distribution model to make dynamic projections of climatically suitable habitat for a species under different scenarios. Combining these with land use projections yields dynamic maps of habitat that is both climatically suitable and intact (or "available" as habitat); overlaying these with projected future fire regimes (Keeley and Syphard 2016, Syphard et al. 2019b) indicates available habitat that is also projected to have a suitable disturbance regime for a species. Dynamic suitable habitat maps are linked to a spatially explicit population model constructed using demographic and fire response data. The linked modeling methodology (Fig. 2) incorporates the impacts of habitat shifts, loss, and fragmentation,

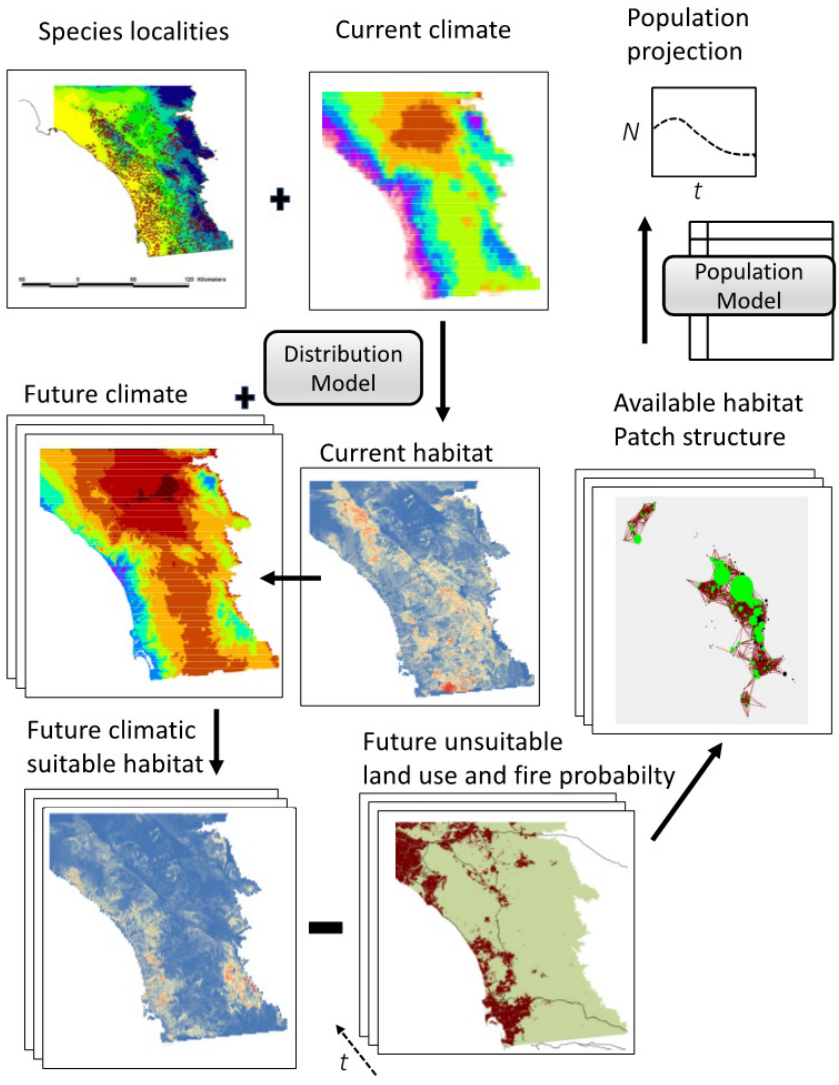

Figure 2. Linked modeling methodology for assessing species vulnerability to global change. Future climate represents a climate change scenario based on combinations of climate model and emission scenarios. The figure is simplified because current climate and each future climate scenario is represented by a single map whereas it is actually described by multiple climate variables (not shown), some of which are used for species distribution modeling. Furthermore, there are multiple future climate scenarios. Future unsuitable land use and fire represents projections of land use change or highly altered fire regimes (and again there may be multiple scenarios, so this entire workflow would be carried out for each scenario combination). The resulting dynamic maps of a habitat patch network are linked to a spatially-explicit metapopulation model. Stacks of maps represent multiple time periods (*t*).

fires, and aspects of species life history and ecology determining population dynamics. Exposure can be quantified by spatial attributes of the projections of future habitat, such as changes in area, fragmentation or spatial shifts, while sensitivity can be described by metrics based on population projections, such as population growth rate, expected minimum abundance or extinction risk, under habitat change scenarios.

Future fire regimes, or fire regime characteristics, can be predicted using scenarios of climate, vegetation, and/or land use change in models based on historical relationships (Krawchuk et al. 2009, Davis et al. 2017, Syphard et al. 2017b). Predictive maps of future fire regime attributes can be used to determine if projected fire regimes diverge from historic fire patterns within a species range—comparing past versus future fire regime. This is analogous to the comparisons often made to assess if *current* fire regimes are within the historic range of variability for a landscape—past versus present (Morgan et al. 1994, Veblen 2003).

The Linked Modeling Approach Applied to CFP Species

We have previously applied this linked modeling methodology (Fig. 2) to assess individual plant species' vulnerability to three major global change drivers in the CFP—climate change, altered fire regime, and land use change (Franklin et al. 2014). We propose that by applying this linked modeling approach to many species in a region (tens or hundreds) the resulting estimates of exposure and sensitivity can be compared to species traits and spatial characteristics of occupied habitat; this strategy would thus implement the framework proposed in this paper, testing our hypotheses about how traits contribute to vulnerability or resilience in particular contexts across species.

Our previous research (Franklin et al. 2014) has revealed some of the relationships between global change threats and some plant functional and spatial traits in relation to threats for individual species in the CFP by applying the linked modeling approach to single-species case studies (Fig. 3). Species fall into one of four main modes of disturbance response reproductive strategies in MTEs as described by demographic traits: obligate seeders (fire-cued germination and post-fire recruitment from a seed bank); resprouters (post-fire vegetative recovery); facultative seeders; and non-resprouting plants not stimulated to germinate by fire (Keeley et al. 2011). For a long-lived obligate seeding shrub (dependent on infrequent crown fire to stimulate seed germination), habitat loss due to land use change or climate change unintuitively increased population abundance under

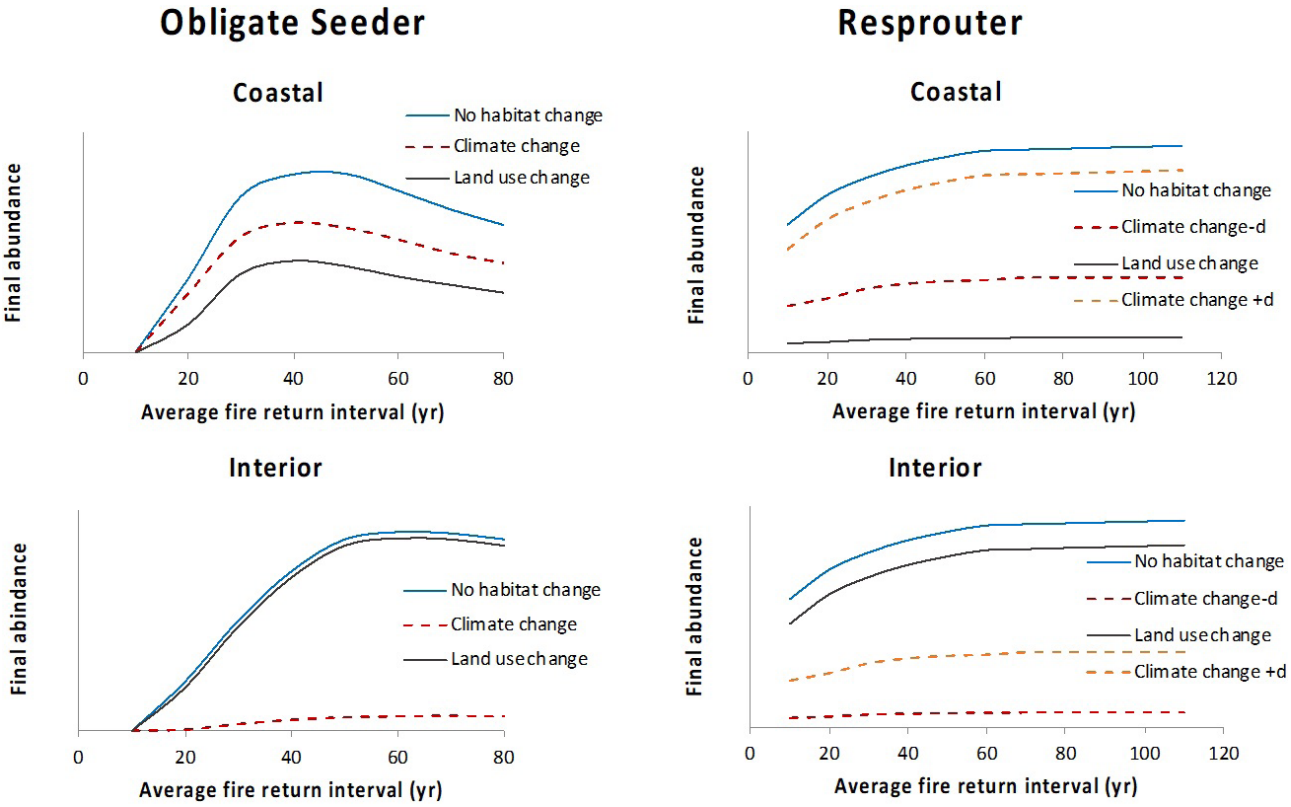

Figure 3. Population trajectories distributed across a range of fire return intervals for two fire disturbance response functional types (obligate seeder, resprouter) with different biogeographical distributions (Coastal, where land use change is concentrated, and the less-developed Interior where climate change interacts with topography) in the California Floristic Province (CFP). Note that +/-d is with or without large potential dispersal distance. These trends reflect results from previous studies employing the linked modeling framework.

a regime of frequent fires. This functional type is highly vulnerable to short-interval fires, and habitat fragmentation decoupled fires across the landscape (Regan et al. 2010). This result held up despite overall habitat loss, but only up to a point. Once habitat loss surpassed a threshold, the negative effects of reduced habitat outweighed the beneficial effects of risk spreading of frequent fire.

For a different species of the same disturbance response type, the ranking of threats when fire occurred periodically depended both on the driver of habitat change (urban growth or climate change) and where the species occurred (biogeographical range) relative to the distribution of the threat (Syphard et al. 2013). Nevertheless, very frequent fire caused populations to decline to a greater extent than habitat loss under land use change and climate change scenarios, highlighting that species traits can strongly influence vulnerability in the face of particular threats.

Conversely, in other cases, species traits appeared to play a lesser role in population persistence under scenarios of frequent fire and habitat loss. For a narrowly distributed obligate-seeding shrub, embedded in a coastal, urban landscape, model projections suggested that habitat contractions due to climate change would play a larger role in risk of decline than more frequent fires, largely because few, if any, opportunities exist for the species to shift its range in response to climate change due to surrounding land use (Lawson et al. 2010). And for a restricted-range resprouting tree found in valley foothills, realistic dispersal rates and distances were insufficient to track future shifts in suitable habitat due to projected climate change (Conlisk et al. 2012).

These previous results illustrate how the relative role of intrinsic (e.g. species traits) versus extrinsic (e.g. multiple threats and spatial context) factors in plant species' vulnerability to extinction can be assessed in the linked modeling framework for individual species (Fig. 3). Evaluating a much greater number of species across a more comprehensive range of traits and trait values (Table 1) and spatial contexts (Table 2) will allow our hypotheses regarding traits and geography in the CFP to be tested. We are not aware of studies that comprehensively consider a range of spatial traits in conjunction with species traits in the context of multiple interacting threats.

Conclusion

Our framework linking plants traits, species biogeography, and the spatial context of multiple global change threats that render plant species vulnerable to extinction, is particularly applicable to MTEs owing to their high plant diversity and unique floras, historical and contemporary high rates of land use change, and strong interactions between climate, fire, and land use. Based on our review of the relationship between plant traits, plant geographies, and global change, our proposed framework can be applied to make a range of predictions falling under an overarching hypothesis, which is that species-specific vulnerability to global change in MTEs is a function of interactions between species and spatial traits; the nature of this interaction will depend on the type and number of global change processes. The proposed methodology based on forecasting under global change scenarios provides a tool by which to estimate future vulnerability.

All MTE floras comprise plant species with similar disturbance responses and functional traits. Thus, the identification of species traits, spatial context, and threats that deem plant species vulnerable to extinction is relevant across MTEs (e.g. to California, southeastern Australia, South African Cape, Eurasian Mediterranean, Chile). Our framework, and the methodology to test hypotheses, addresses exposure and vulnerability, but not the adaptive capacity component of species sensitivity to global change (because it does not account for genetic and phylogeographic diversity, and plasticity); nonetheless, it is a useful approach for forecasting global change impacts on biodiversity in fire-prone ecosystems where climate change and land use change are expected to alter fire regimes as well as affect species distributions.

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