

# Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes

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Projected effects of climate change across many ecosystems globally include more frequent disturbance by fire and reduced plant growth due to warmer (and especially drier) conditions. Such changes affect species – particularly fire-intolerant woody plants – by simultaneously reducing recruitment, growth, and survival. Collectively, these mechanisms may narrow the fire interval window compatible with population persistence, driving species to extirpation or extinction. We present a conceptual model of these combined effects, based on synthesis of the known impacts of climate change and altered fire regimes on plant demography, and describe a syndrome we term “interval squeeze”. This model predicts that interval squeeze will increase woody plant extinction risk and change ecosystem structure, composition, and carbon storage, especially in regions projected to become both warmer and drier. These predicted changes demand new approaches to fire management that will maximize the in situ adaptive capacity of species to respond to climate change and fire regime change.

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During this century, climate change is projected to cause profound plant species losses and migrations – and shifts in ecosystem structure and function – in many parts of the world (including several biodiversity hotspots; Malcolm *et al.* 2006). However, such assessments are based almost entirely on empirical niche (or climate envelope) models, which measure only one component of climate vulnerability (Dawson *et al.* 2011); published evidence points to more complex interaction

effects, suggesting that proximate causes such as altered disturbance frequencies are more important than direct climate impacts (Cahill *et al.* 2013; Grimm *et al.* 2013). Despite accumulating evidence of indirect effects, conceptual models offering broader, mechanistic views that facilitate prediction are lacking.

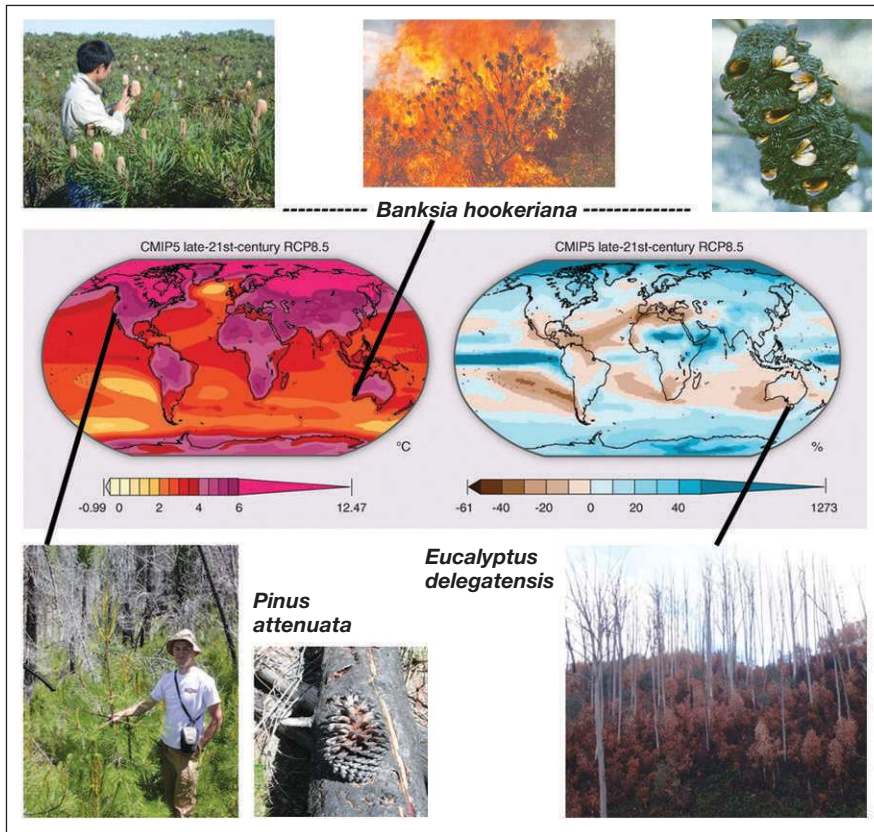
Fire is the dominant terrestrial, landscape-scale disturbance factor globally (Bowman *et al.* 2009), and recent studies using a range of global climate models project a more fire-prone future for most terrestrial ecosystems, especially in the middle and high latitudes (Moritz *et al.* 2012). Particularly vulnerable to the interactive effects of climate and fire-regime change are biomes where climate is projected to become both warmer and drier, a combination that will increase drought-related impacts and fire frequency (eg Mediterranean-type ecosystems; Figure 1).

Current conceptions of plant species responses to climate change in fire-prone ecosystems highlight the potential impacts either of climatic envelope shifts (where climate change leaves species stranded at sites no longer suitable for their growth; eg Fitzpatrick *et al.* 2008) or of shortened fire intervals, which increase “immaturity risk” (ie insufficient growing time before fire recurs; eg Westerling *et al.* 2011). Nevertheless, these impacts ignore – or at least conflate – multiple threatening processes acting together (Brook *et al.* 2008), which could produce markedly different outcomes for species and ecosystems, including notable shifts in composition and structure in response to comparatively small shifts in species climate envelopes (Scheffer *et al.* 2001; Bowman *et al.* 2014a). Furthermore, in light of the ongoing global trend of habitat fragmentation, plant species conserva-

## In a nutshell:

- Climate-change impacts on ecosystems occur via multiple interacting factors that may become most apparent after disturbances (eg fire); these disturbances are also subject to change as climate shifts
- Under warmer, and particularly drier, future climates, woody plants will on average produce fewer seeds and experience lower seedling survival; in increasingly fire-prone regions they will need longer fire-free periods to reach reproductive maturity and produce sufficient seeds to ensure self-replacement
- Warmer and drier conditions will increase fire frequency in many regions, shortening fire-free periods
- We present the combination of these demographic and fire-regime changes as the “interval squeeze” phenomenon, which describes the serious, interacting challenges faced by many woody plant species in fire-affected environments globally

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**Figure 1.** Projected changes in temperature (map on left) and precipitation (map on right) by the late 21st century based on global climate-change model ensembles (from Diffenbaugh and Field [2013]). Examples of woody species possessing life-history traits (fire-intolerance, high immaturity risk under increased fire, rapid fuel load accumulation systems) making them particularly vulnerable to interval squeeze include: *Banksia hookeriana* from southwestern Australia (three images at top showing a mature stand in flower [left], a burning individual with canopy-stored cones [center], and an open cone after fire [right]), *Pinus attenuata* from California/Oregon (two images at bottom left showing post-fire recruitment beneath fire-intolerant parents [left] and open cone after fire [center left]), and *Eucalyptus delegatensis* from southeastern Australia (image at bottom right highlighting immaturity risk, showing complete stand mortality of juveniles beneath dead parents after two fires at short intervals).

tion must inevitably focus primarily on species persistence in situ as climate changes, rather than on the notion that species can migrate in response to changing conditions (Aitken *et al.* 2008) or can be assisted to do so (Lawler and Olden 2011). Given this understanding, the management of synergistic fire–climate impacts is critical for biodiversity conservation.

We contend that three processes associated with a changing climate, and with climate–fire interactions, will combine to drive woody plant species losses and ecosystem state changes more quickly than is currently proposed based on climate envelope or fire-regime change alone. Plants wholly dependent on seeds for population recovery after fire are particularly vulnerable to such impacts, but species able to regrow vegetatively may also be at risk over longer timescales. The following interacting processes must be taken into account to more adequately assess the risk of species losses and ecosystem-state changes:

- (1) *Demographic shift* – altered rates of plant growth, reproduction, and survival in response to changed growing conditions;
- (2) *Post-fire recruitment shift* – altered levels of plant recruitment in the first year after fire, associated with increased frequency of years unfavorable for seedling establishment and survival; and
- (3) *Fire-interval shift* – altered mean time between successive fires due to changes in the drivers of ignition and fire spread.

Species in regions subject to a warming and drying climate will likely be most negatively affected if changes to all three processes result in synergistic impacts: that is, lower post-fire population densities, prolonged growth to reproductive stage, slower seed production and accumulation rates, and shortened fire intervals will combine to exacerbate immaturity risk and drive rapid population declines. We describe these three interacting processes, present evidence for each, and propose a conceptual model – the interval squeeze model – that predicts their consequences (Figure 2). These predictions provide a framework for understanding climate-change impacts, especially for woody species in ecosystems characterized by crown fires (fires that burn through all of the vegetation layers), and for adaptively managing such ecosystems.

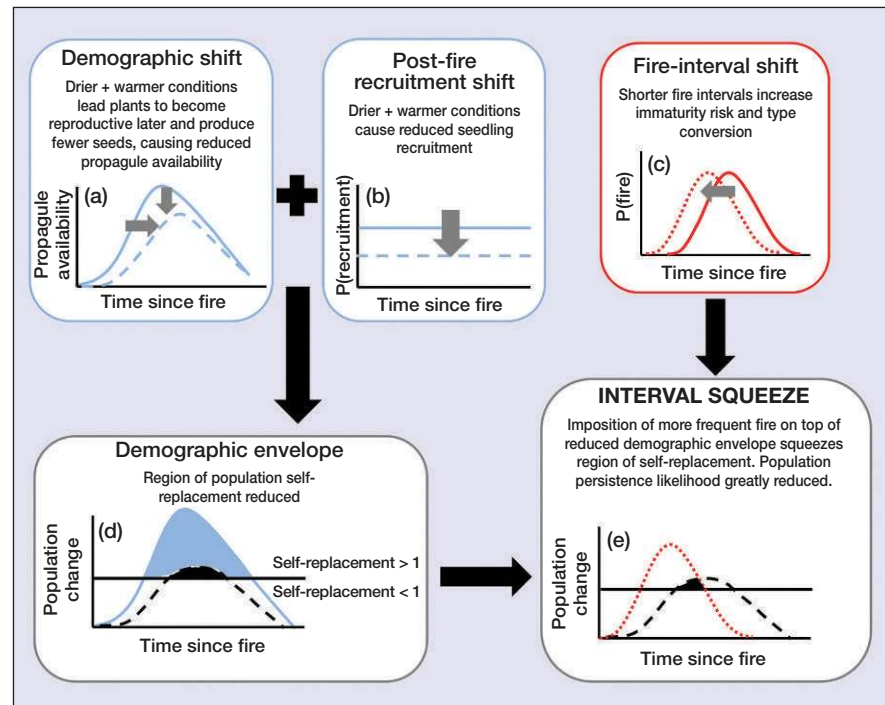
### ■ Demographic shift

Phenological adjustments to climate warming (eg earlier onset of flowering) are well documented for many plant species and regions (Parmesan 2006). However, the likely demographic effects – including lower rates of growth, survival, and fecundity – are even more profound, especially in areas affected both by warming and drying (eg Jump *et al.* 2006). Consequently, the minimum fire interval compatible with self-replacement will increase as climate warms. We refer to this process as “demographic shift”. Evidence for demographic shift ranges from direct to inferred, and is provided (1) by empirical and experimental climate-change studies, (2) by variations in demographic rates with annual fluctuations in climate (eg precipitation), and (3) within species over latitudinal and altitudinal gradients (see WebTable 1 and associated references).

Several studies of tree species' range limits (both altitudinal and latitudinal) in the Northern Hemisphere reported decreased growth and increased mortality at the southern limit of species' ranges (due to the negative impact of increasing drought and warming), and faster growth and increased seed production at the northern limit. For example, Jump *et al.* (2006) documented a 49% reduction in tree growth over the past 30 years at the southern range limit of European beech (*Fagus sylvatica*) in Spain (WebTable 1). Biotic interactions, including weakened resistance to insect outbreaks and altered herbivory patterns, may further exacerbate species declines as ecosystem stresses increase (WebTable 1). Demographic rates also vary along climate gradients. For instance, within their respective geographic ranges in southwestern Australia, selected woody plant species in relatively drier areas were smaller in size and had longer juvenile stages than in less dry areas (Burrows 2008); likewise, in eastern Australia (spanning 23–43°S latitude), *Eucalyptus* species exhibited reduced growth rates when subjected to increased temperatures (Bowman *et al.* 2014b). These lines of evidence point toward direct impacts of climate change on rates of growth, survival, and fecundity in woody plants; vital rates are generally diminished under warmer conditions, as plant water-use increases (eg Bowman *et al.* 2014b), and these rates will be even more strongly affected where both warmer and drier conditions prevail (eg reduced seed production in the piñon pine [*Pinus edulis*]; Redmond *et al.* 2012).

■ **Post-fire recruitment shift**

In fire-affected vegetation types, especially those characterized by stand-replacing crown fires, recruitment occurs predominantly in the first year after fire from seeds that persisted within the burned stand in canopy or soil seed banks, or were dispersed from adjacent unburned populations (Keeley *et al.* 2006). If such years are markedly drier than average, then seedling recruitment may be poor or may fail completely (Enright *et al.* 1996, 2014). We refer to this as “post-fire recruitment shift”. A decrease in mean precipitation guarantees an increase in the fre-



**Figure 2.** Conceptual model showing how changes to demographic rate, post-fire recruitment rate, and fire interval combine to reduce the fire-interval envelope compatible with post-fire self-replacement (ie leads to interval squeeze) for a fire-intolerant perennial plant species as climate warms and dries (as projected for all of the world's high biodiversity, Mediterranean-type ecosystems). (a) Demographic shift is represented by the relationship between propagule availability and stand/cohort age. The solid curve depicts the pre-change distribution of age-related propagule availability, and the dashed curve represents the changed distribution as climate dries. (b) Probability of post-fire recruitment shift is shown as a uniform decrease (dashed line) in recruitment in response to an increased incidence of drought after fire. (c)  $P(\text{fire})$  represents the probability that a stand will have burned by a given age (ie the probability density form of the fire-interval distribution, including age dependency; after Moritz [2003]). The solid curve and the dotted curve depict the pre-change distribution of fire intervals and the changed distribution as climate dries, respectively. (d) Combined demographic shifts (a and b, above) slow the rate of propagule production, and thus availability at time of fire, while reduced post-fire recruitment levels decrease stand density and seed availability after fire, shortening the range of fire intervals for which self-replacement is possible (indicated by the width of the area filled in black). (e) Interval squeeze resulting from fire-interval shift (c) and combined demographic shifts (d) further constricts the envelope of fire intervals compatible with stand self-replacement (width of the area filled in black), reflecting the intersection of the fire (dotted) and demographic (dashed) curves and the self-replacement (solid horizontal) line.

quency of dry years, so the probability of recruitment following fire must decrease.

Surprisingly few studies report the effects of post-fire weather conditions on recruitment, and empirical data are sparse (WebTable 1). Enright and Lamont (1992) reported lower post-fire recruitment in the southwestern Australian shrub *Banksia hookeriana* in dry years after fire, and Enright *et al.* (1996, 2014) estimated that reduced levels of post-fire recruitment increased the fire interval required for stand self-replacement. Yet most studies report other factors influencing post-fire regeneration and do not consider climate change; Maia *et al.* (2012),



for instance, identified fire severity and topographic variation as major factors influencing post-fire recruitment levels for *Pinus halepensis* and *Pinus pinaster* in the Iberian Peninsula, Spain.

Post-fire recruitment levels will also be reduced in relation to projected increases in fire severity and fire size as climate warms (Buma *et al.* 2013); higher severity fires are lethal to a larger proportion of on-site seed banks, and larger fires reduce the probability of recovery due to dispersal limitation among species dependent on wind dispersal (Donato *et al.* 2009; Holz *et al.* 2015).

### ■ Fire-interval shift

Warmer conditions are projected to promote fire activity in many regions globally by lengthening fire seasons, increasing the annual number of extreme fire weather days (typically characterized by a combination of high temperature, low relative humidity, and high wind speed), and increasing the abundance of dry fuels, which will result in larger and more severe fires (Westerling *et al.* 2006; Moritz *et al.* 2012). The net effect of these changes will be to shorten fire intervals, reducing the time available to plants for seed accumulation, selecting for more flammable species (D'Antonio and Vitousek 1992), and elevating the probability of local extirpation of slow growing and slowly maturing species after fire events (Westerling *et al.* 2011). We refer to this process as “fire-interval shift”. Fire-interval shift has already occurred for many species as a result of fires associated with intentional burning to reduce fire risk to people and infrastructure assets (fuel load management), and increases in unplanned anthropogenic fires linked to human population and infrastructure growth (Syphard *et al.* 2009). Empirical evidence of the impacts of fire-interval shift on plant populations and ecosystem properties has been found from boreal Canada to California, tropical North and South America, and Australia (WebTable 1). Although studies have highlighted the potential deleterious impacts of changing fire regimes on woody plant species persistence and key ecosystem properties as the climate changes, the direct effects of climate change on demographic rates have not been considered. These studies may therefore underestimate the extent of immaturity risk and resilience among such species and systems.

We predict that interval squeeze has the potential to initiate a long-term, nonlinear trajectory of change in fire frequency in many communities that are dominated by woody plants. The immediate prospect for shortened fire intervals in response to increased frequency of extreme fire weather days and drought is particularly high in these communities because standing biomass (fuel sources) has accumulated under historically moister climates. Thus, interval squeeze is a proximal, and transitional, consequence of changing fire–climate regimes, with many fire-intolerant species at risk of extirpation, and many resprouting species slowly declining in density. In the

longer term, changes to woody species composition and structure might lead to lower fuel loads and longer fire intervals. However, such a mechanism of stabilizing feedback may be offset by stand-type conversion (eg where woody species are replaced by grasses, including invasive species; Keeley and Brennan 2012), maintaining the potential to support short-interval fire regimes.

The consequences of fire-interval shift are exemplified in a study by Bowman *et al.* (2014a), who described widespread losses of, and ecosystem state conversion for, mountain ash (*Eucalyptus delegatensis*) forests after extensive wildfires that have burned 87% of the species range in Victoria, southeast Australia, since 2002. Some stands regenerating after fires in 2003 and 2007 were reburned in subsequent wildfires in 2009 and 2013 while the stands were still immature, leading to complete regeneration failure and conversion of some sites to dominance by shrubs and grasses – a phenomenon similar to that reported for wet Mediterranean-type forests in western North America (Odion *et al.* 2010).

Taken together, these lines of evidence show how shifts in post-fire recruitment rates will interact with climate-driven demographic rates and fire-interval shifts to drive stand-level responses to altered fire regimes in many plant species. Under a warming climate, many species in fire-affected ecosystems will show reduced rates of growth, reproduction, and recruitment. Combined with an increased frequency of fire, many species will experience a marked narrowing – interval squeeze – of the range of fire intervals (the fire-interval envelope) compatible with stand replacement.

### ■ The conceptual model

Together, the three processes – demographic shift, post-fire recruitment shift, and fire-interval shift – will act as a strong biodiversity and ecosystem filter, threatening species with decline or loss and threatening ecosystems with state changes in vegetation structure and composition as a result of interval squeeze. Here we present a conceptual model of their potential combined impacts under a changing climate, focusing on systems where climate is projected to become both warmer and drier (Figure 2).

The conceptual model demonstrates how slowed demographic rates, lower post-fire recruitment rate, and shortened fire interval combine to reduce the fire-interval envelope compatible with population persistence for a fire-intolerant woody plant species in a warming and drying climate. Demographic rates (Figure 2a) are described by propagule availability, representing the pattern of seed production (and accumulation for species with seed banks) in relation to time since fire (ie the age of the stand/cohort) and availability of sufficient seeds for self-replacement under average climate conditions. Seed availability declines in the long-term absence of fire (Figure 2a) as a result of ongoing mortality and senescence of individual plants and reduced seed production as

**Panel 1. Case study: interval squeeze in *Banksia hookeriana***

*Banksia hookeriana* (Proteaceae) is a fire-intolerant shrub of Mediterranean-type shrublands near Eneabba, southwestern Australia (29°51'S, 115°16'E). Individuals recruit in the first winter after fire from seeds released from a canopy-stored (serotinous) seed bank, producing an even-aged cohort (such that stand age is equal to the time since last fire). The plants reach reproductive maturity at an age of ~5 years, accumulate an increasing store of seeds in closed cones in their canopy to ~25 years, and die by 40 years (Enright *et al.* 1996). Previous studies indicate that the species is best adapted (with highest estimated rate of population increase,  $\lambda$ ) to a fire interval of 15–20 years, with intervals less than 10 years and greater than 30 years likely to lead to population decline or loss (Enright *et al.* 1996). Seed production and plant survival are both strongly correlated with total rainfall in the previous winter–spring, with a 20% reduction in rainfall leading to a 50% reduction in annual seed production and an age-standardized annual survival rate reduced by 6% (Keith *et al.* 2013). Mean annual rainfall in the center of the species' geographic range has declined by more than 20% since the mid-1960s, during which time temperature has increased by 0.15°C per decade (Eneabba Climate Station No 08225; Australian Bureau of Meteorology). *B. hookeriana* shows direct evidence of demographic envelope shift, with estimated seed stores for successive post-fire cohorts of the same age in the same site declining by more than one-half from 1971 to 2012 (Table 1). Current fire management in *B. hookeriana* shrublands prescribes fire intervals of 12–20 years to reduce fuel loads to protect human lives and infrastructure and to promote biodiversity conservation outcomes. While a 12–20-year fire interval was likely compatible with the ecological requirements of the species based on historical rainfall and plant demography (Enright *et al.* 1996), this is no longer true given slowed seed bank accumulation rates under a drying climate. If fire interval decreases as projected (Moritz *et al.* 2012), then the temporal mismatch between demographic rates and disturbance regime will be exacerbated, resulting in interval squeeze and consequent population decline for this species. Similar scenarios will apply to many other fire-intolerant species; for instance, Redmond *et al.* (2012) reported a marked decline in recent seed production and storage for piñon pine (*Pinus edulis*) in North America relative to levels recorded in the 1970s.

**Table 1. Comparison of plant height and serotinous seed bank size (mean  $\pm$  standard error) in *Banksia hookeriana* after stand-replacing fires in 1971, 1987, and 2005 at the same site near Eneabba, southwestern Australia**

Attribute	Year			
	1987	1994	2004	2012
Plant age (yrs)	16	7	17	7
Plant height (cm)	141 $\pm$ 3	81 $\pm$ 2	111 $\pm$ 4	87 $\pm$ 2
Total cones plant <sup>-1</sup>	42.1 $\pm$ 7.2	4.1 $\pm$ 0.3	14.9 $\pm$ 1.5	1.9 $\pm$ 0.1
Estimated seeds plant <sup>-1</sup>	371	50	153	24

**Notes:** Data span plant growth and reproduction from 1971 to 2012 and are associated with a significant trend of decreasing rainfall. Table modified from Keith *et al.* (2013).

resource allocation for maintenance and repair increases in large, old plants (Harper and White 1974). The shape of the demographic curve at longer fire intervals may vary between species – depending on the timing and speed of senescence, the effects of declining stand density on total seed production and storage, and age-related patterns of seed production – but changes in the curve's shape make little difference to model predictions.

Slowed growth and reproduction shift the demographic envelope to the right (prolonged time to maturity and to sufficient propagule availability; Figure 2a). Increased frequency of drought, and thus of fire followed by drought, leads to a projected lowering of the post-fire recruitment rate, independent of time since last fire (Figure 2b). Longer fire seasons and more frequent extreme fire weather days increase the probability of fire in younger stands, driving the fire envelope to the left (shortened fire interval; Figure 2c), so that a larger proportion of fires occur before adequate propagules are available for self-replacement. Combined demographic and post-fire recruitment shifts (Figure 2d) slow the rate of seed production and reduce stand density and total size of the seed pool available after fire, thereby reducing the range of fire intervals for which self-replacement is possible. Intersection of the altered fire-interval curve with the combined demographic and post-fire recruitment-shift curve defines the fire-interval “envelope” (ie range of stand ages) within which self-replacement after fire will

occur. The resulting stand self-replacement envelope (Figure 2e) is then constricted to a much narrower band, representing a marked increase in the probability of decline or loss of populations and species.

### Scope and implications

The scope of the interval squeeze model is best defined based on functional traits related to disturbance (fire-intolerant at greater risk than [ $>$ ] fire-tolerant), seed dispersal (on-site seed bank or wind dispersed  $>$  other mechanisms such as animal vectors), seedling recruitment (episodic after disturbance  $>$  continuous), and plant longevity (lifespan longer than mean fire interval  $>$  lifespan shorter than mean fire interval). From an ecosystem perspective, communities dominated by fire-intolerant woody plants and with crown or mixed-severity fire regimes are more vulnerable to interval squeeze. At greatest risk are Mediterranean-climatic regions with high biodiversity and projected warmer and drier climates (see Panel 1 for evidence of interval squeeze for *Banksia hookeriana*). Interval squeeze is most likely to show its strongest impacts in these areas, with rainfall projected to decline by 20–40% and temperatures to rise by up to 6°C by the end of the 21st century (Diffenbaugh and Field 2013). In these biodiversity hotspots, species with vulnerable life histories (fire-intolerant species dependent on post-fire recruitment) are expected to decline in response

to these interacting impacts, possibly leading to multiple extinctions.

From an organismal perspective, species with restricted distributions are the most susceptible to interval squeeze, with single large fire events capable of affecting the majority of extant populations (eg Bowman *et al.* 2014a). Particularly vulnerable will be fire-intolerant species of fire-prone shrublands, woodlands, and forests, including many shrub and conifer species in Australia and South Africa (eg members of the Proteaceae, Cupressaceae, Ericaceae, Myrtaceae, Fabaceae), western North America (Rhamnaceae, Pinaceae, Cupressaceae, Ericaceae), and southern Europe and the boreal zone (Pinaceae, Ericaceae), which rely on seeds for regeneration after fire (Buma *et al.* 2013). Temperate and boreal woodlands and forests are also highly vulnerable due to the dominance of fire-intolerant tree species (eg Brown and Johnstone 2012). Grassy woodlands characterized by surface fires (including many tropical and temperate savannas) might be affected more gradually; while mature trees may be slower to respond to changing climate, the probability of favorable conditions for recruitment is likely to decline (Weltzin and McPherson 1999; Hoffmann *et al.* 2012). Least affected may be non-woody ecosystems such as grasslands and prairies, as well as arid regions without sufficient biomass to propagate frequent fires.

Mediterranean-type woodlands, temperate mixed conifer forests, and boreal forests could experience a loss of overstory species, leading to major changes in ecosystem states – such as conversion of forest to shrubland or tundra – and carbon stores (Odion *et al.* 2010; Grimm *et al.* 2013). Such outcomes would come with a loss of biodiversity and ecosystem services as well as increased costs associated with adaptive management, including enhanced levels of fire exclusion and suppression. As ecosystems change in response to interval squeeze, feedback effects may become increasingly important, further escalating the rate of change, such as conversion from woody to grassy dominance and increased vulnerability to pests and pathogens. Projected increases in fire size and severity may further exacerbate shifts in species composition and carbon stores.

In regions where precipitation is projected to increase or remain unchanged, woody species responses will vary depending on the interplay of biotic and abiotic drivers. For example, long-term monitoring of Scots pine (*Pinus sylvestris*) at treeline sites in Scandinavia revealed increased recruitment over recent decades, with warmer summers improving seed viability and warmer winters increasing survival (Kullman and Kjällgren 2006). Although Hoffmann *et al.* (2012) found increased frequency of fire associated with more rapid surface fuel accumulation rates to be the main threat to the tree layer in neotropical savanna woodlands, Murphy and Bowman (2012) contend that increasing tree growth rates (due to higher atmospheric carbon dioxide concentrations) may be facilitating seedling escape from the fire-trap zone

close to the ground in northern Australian savanna woodlands, leading to increased tree density.

Ultimately, plant species will respond to climate change in one of three possible ways: (1) migrate to keep pace with climate change, (2) adapt in situ through selection of tolerance traits, or (3) go extinct (Aitken *et al.* 2008). Given the myriad of potential problems associated with both natural and assisted species migration, in situ adaptive management approaches to conservation of biodiversity will be critical to species persistence (Fitzpatrick *et al.* 2008) and will remain the primary focus of conservation efforts into the foreseeable future. We show that climate change will cause demographic as well as fire-regime shifts, but such demographic shifts have not been recognized explicitly in current scholarly debates concerning fire–climate interactions and their potential impacts on the viability of plant species in the world's many fire-affected ecosystems. The conceptual model presented here reveals how demographic and fire-interval factors interact and must be taken into account when projecting climate-change impacts on plants and plant communities.

Adaptive approaches to fire management could slow population declines and losses projected under climate change and fire-regime change, allowing more time for in situ selection of traits favoring tolerance in organisms. For example, Franks *et al.* (2007) found evidence for rapid selection of increased tolerance to a shortened growing season in the annual *Brassica rapa* plants from seeds produced during drought years with shorter time to reach maturity. Several measures that may increase resilience for fire-intolerant woody species at risk of climate- and fire-regime-driven declines include increasing inter-fire intervals to provide more time for propagule production, using weather forecasting to match time (year and/or season) of management fires to projected post-fire conditions favorable for recruitment (eg projected average or above-average rainfall), and assessing the adequacy of seed availability for key species through monitoring before burning. Ex situ seed banking may also become more important as a restoration resource where increases in fire frequency, size, and severity lead to serious post-fire seed limitation.

Our model provides a framework for identifying potential fire–climate interaction impacts on woody plant species in fire-prone ecosystems and is readily testable using empirical data to establish its validity and utility. The interval squeeze model offers opportunities for further research exploring the relative strength of and interactions between drivers across gradients of climate, management, and fire types (Table 2). Sensitivity of populations to the three drivers of change proposed here may be explored through simulation modeling based on plant demographic and climate data (including projected climate changes), to identify the relative importance of each driver and to determine how this sensitivity may vary among species and ecosystems.

**Table 2. Potential directions of future research investigating the scope and validation of the interval squeeze model**

Topic	Data/future study
Fire frequency and fuel limitation	Incorporate fuel limitation into modeling of future fire activity and demographic age of reproduction
Growth rate	Empirically quantify plant growth under varying conditions; conduct meta-analysis of existing data for species possessing key traits
Reproductive rate	Empirically measure flowering and seed production; synthesize datasets across keystone species and functional types
Seed limitation	Determine levels at which species become propagule limited given growth and fire frequency and seedling survival; develop predictive models of landscape-level seed availability
Seed bank size	For species with seed banks, model seed longevity and seed bank size over time
Interaction strength	Perform simulation modeling to quantify strength of interaction versus additive effects among fire and demography with changing climate
Fire size and severity	Determine changes to fire size and severity in relation to dispersal distance for species without seed banks (see Buma <i>et al.</i> 2013)

Given the broad geographic distribution of ecosystems vulnerable to interval squeeze, this is an issue of global environmental importance.

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