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Summary

1. Increased incidence of landscape fire, and pollinator declines with co-extinctions of dependent plant species, are both globally significant. Fire can alter species distributions, but its effects on plant–pollinator interactions are poorly understood so its present and future role in coupled plant–pollinator declines cannot be assessed.

2. We develop a conceptual model of fire effects on plant–pollinator interactions. We review the empirical literature in the context of this model to identify important knowledge gaps regarding the processes underlying these effects and the phenotypic traits of flowering plants and pollinators mediating these effects. Fire generates, and plant–pollinator interactions respond to, heterogeneity at multiple spatial scales. There is evidence of local-scale fire effects on these interactions, but landscape-scale effects are poorly understood. Nest location and floral resource utilization primarily mediate pollinator survival during and after fire. Voltinism and mobility traits are potentially important but poorly studied. Plant traits mediating flowering responses to fire include growth form, phenology, and potentially bud location, seasonal changes in bud exposure, and response to bud damage.

3. *Synthesis and applications.* We suggest management actions and an agenda for future research to fill knowledge gaps currently inhibiting predictions of fire effects on plant–pollinator interactions. Fire regimes promoting floral diversity at local scales provide a surrogate means of managing pollinators and pollination while empirical research continues. Above-ground nesting, univoltine pollinators may be particularly vulnerable under expected fire regime changes. Improved knowledge of traits mediating exploitation of landscape heterogeneity could be used to enhance persistence of these species. Ultimately, our

conceptual framework could be used as a basis for understanding fire effects on aggregate network properties to inform fire management strategies buffering plant–pollinator networks against secondary species extinctions.

Key-words: conceptual model, fire regimes, flowering plants, phenotypic traits, plant–pollinator interactions, pollination, pollinators, fire management

Introduction

Fires occur regularly in most vegetation types (Mouillot & Field 2005) and are expected to become more widespread and prevalent under climate change (Jolly *et al.* 2015). The history of fire events occurring within a specific area and period of time defines the fire regime, which is characterized by the frequency (inter-fire interval), season, intensity, size, and spatial patterning of fires (Gill 1975; Keeley *et al.* 2011). Fire regimes can be manipulated by fire suppression and applying prescribed fire (e.g. Keeley *et al.* 2011), though the ability to control wildfire is expected to decrease as fire intensity increases across much of the globe under climate change (Stephens *et al.* 2012; Flannigan *et al.* 2013). Fire regimes can act as filters on biotic communities, determining relative abundances and species composition (e.g. Noble & Slatyer 1980; Keeley *et al.* 2011). Predicting the ecological consequences of altered prescribed and wildfire regimes requires knowledge of relationships between fire regimes and biota.

Predictions of fire effects on biodiversity are currently limited by substantial knowledge gaps, particularly (i) animal responses to fire, and (ii) interactions between fire and ecosystem processes such as herbivory and pollination that influence plant survival and reproduction (Driscoll *et al.* 2010). Here we focus on pollinating animals and animal-mediated pollination. Most flowering plants require animals to effect reproduction by transporting pollen to and from mates (Ollerton, Winfree & Tarrant 2011). While some animal-pollinated plants are able to self-pollinate in the absence of pollinator visitation, they may ultimately suffer

inbreeding depression and reduced genetic diversity (Wilcock & Neiland 2002; Eckert *et al.* 2010). Recent observations of pollinator declines in several countries are thus concerning (Potts *et al.* 2010; Vanbergen *et al.* 2013). While the role of altered fire regimes in these declines is unclear (Potts *et al.* 2010), fire management of pollinator habitat might help mitigate pollinator declines in regions where fire is an important ecological process (Willmer 2011). Moreover, a better understanding of fire effects on pollinators and their interactions with plants should improve predictions of plant population responses to fire. For instance, post-fire flowering (reproductive maturity) can precede recovery of pollinators and so pollination by several years (Ne'eman, Dafni & Potts 2000; Geerts, Malherbe & Pauw 2012); however, the rate of pollinator recovery can depend on fire characteristics such as size and patchiness (Watson *et al.* 2012). Thus the risk of subsequent fires occurring before significant reproduction – which can cause local plant extinctions (Keith 1996) – might be mediated by spatial patterns of fire, though this has not been tested. We identify similarly important knowledge gaps and possible management actions by (i) developing a conceptual model of coupled plant–pollinator population dynamics in fire-prone landscapes by synthesizing models of plant–pollinator interactions and fire-driven population dynamics currently available to managers, and (ii) reviewing empirical studies of fire's effects on plant–pollinator interactions, and the phenotypic traits mediating these effects, in the context of our model. We suggest future research directions for filling important knowledge gaps and developing our model to better inform biodiversity conservation in fire-prone landscapes.

Conceptual model

Choosing a fire management strategy that is most likely to achieve the general conservation objective of avoiding species extinction is difficult given the long timescales relevant to population persistence and alternative climate change scenarios. Simulation modelling based on observed responses of plants and animals to fire is advocated and increasingly used to predict the consequences (and effectiveness) of alternative fire management strategies and climatic change on fire regimes and, in turn, biodiversity (e.g. Bradstock *et al.* 1998; Franklin *et al.* 2001; Bradstock *et al.* 2005; Driscoll *et al.* 2010; Pacifici *et al.* 2015; Regos *et al.* 2015). The landscape is typically conceived of as a grid, with each cell having a fire age that either increases or returns to zero (is burnt) in each time-step, and an inter-fire interval across time-steps, depending on fire ignition (planned and unplanned) and spread between cells. The

fire history of each cell determines demographic characteristics of plant species such as survival, seed production, and seedling establishment, and habitat suitability for animal species (based on empirically-derived abundance–fire age relationships). As fire history changes across time-steps, cell occupancy changes according to demographic processes and habitat suitability, as well as dispersal from neighbouring occupied cells.

We believe the addition of plant–pollinator interactions could improve predictions of population persistence by improving parameter estimates and model structure. In the existing framework plant reproduction in each cell is typically assumed to occur when the cell reaches a certain fire age (e.g. when flowering commences) (e.g. Bradstock *et al.* 1998; Franklin *et al.* 2001). Pollinator visitation and seed set can vary with fire age (Ne'eman, Dafni & Potts 2000; Potts *et al.* 2006; Pauw 2007; Geerts, Malherbe & Pauw 2012; Van Nuland *et al.* 2013; Bourg, Gill & McShea 2014), suggesting a more accurate conceptualization of plant population dynamics would allow reproduction to vary as a function of pollination services provided to each cell. Pollinator abundance–fire age relationships have been observed (e.g. Potts *et al.* 2003a; Potts *et al.* 2003b; Chalmandrier *et al.* 2013; Rodríguez & Kouki 2015) and so might be used to derive a habitat suitability value for each cell according to its fire age. However, some animals require complementary resources (e.g. nests and forage) from contrasting fire age classes (Woinarski 2005). This has not been investigated in pollinators, but both pollinator nesting substrate and floral resources are known to vary with fire history (De Swardt 1993; Potts *et al.* 2003a; Potts *et al.* 2003b; Potts *et al.* 2005; Moretti *et al.* 2009; Chalmandrier *et al.* 2013; Rodríguez & Kouki 2015), and pollinators use other land-cover types in a complementary fashion (e.g. Westrich 1996). Moreover, many pollinators return to nest sites between foraging bouts to provision young, such that floral resources nearer to nests are of greater value. Lonsdorf *et al.* (2009) developed a grid-based model accounting for these pollinator characteristics and used it to predict pollinator abundance (the "pollinator source map"), and pollination services (the "pollination services map"), across heterogeneous landscapes. We integrate this with the existing conceptualization of population dynamics in fire-prone landscape to develop our conceptual model (Figure 1).

Pollinator source map

Lonsdorf *et al.* (2009) estimated the abundance of each pollinator species in each cell as the cell's nesting value multiplied by the sum of floral values in surrounding cells. A cell's floral value was a function of its distance from the nest cell relative to the pollinator's foraging

range and the land-cover types occupying it, with each type assigned a floral resource value. Fire alters the landscape distribution of pollinator floral and nesting resources (e.g. Potts *et al.* 2003b), but we are aware of only one study relating pollinator abundance to landscape fire age composition; Rubene, Schroeder and Ranius (2015) found bee and wasp species richness increased with the amount of early post-fire (and harvest) age classes in the landscape.

To link pollinators more explicitly to plant fire responses, we suggest an alternative to land-cover type as the basis for estimating floral values. A plant may be absent from a cell due to cumulative effects of the antecedent fire regime (e.g. local extinction following inter-fire intervals shorter than the time required to replenish propagule stores (Keith 1996; Gill & McCarthy 1998)) and failure to recolonize from neighbouring cells (Bradstock *et al.* 2005). A plant may be present but not flowering due to inappropriate fire history conditions (see 'Traits' section). The value of each cell for each pollinator species then depends on the floral resource quality (e.g. nectar sugar content, pollen) of each plant species they interact with in the cell. Determinants of interactions are discussed in the '*Cell networks*' section below.

Lonsdorf *et al.*'s model was developed for relatively static landscapes so further additions are necessary for fire-prone landscapes. Adult pollinators active in a given season developed on the resources of the previous season so there should be a time-lag between fire-driven changes in floral resources in one time-step and changes in pollinator abundance in the next (Potts *et al.* 2003b). In addition to the indirect effects of fire on pollinators through habitat alteration, exposure to heat and smoke can cause direct effects (Whelan *et al.* 2002; Dafni, Izhaki & Ne'eman 2012). Rates of post-fire recovery depend on within-cell recruitment, or recolonization through dispersal from neighbouring cells (Watson *et al.* 2012). Thus a cell's nesting and floral values need to be multiplied by its pollinator abundance in each time-step to allow modelling of the cumulative effects of changing resources, direct effects, and dispersal across time-steps. These are poorly understood for pollinators in any frequently disturbed landscape, though Le Féon *et al.* (2013) found bee abundance and species richness were related to the previous five years of crop rotations in the landscape surrounding sites.

Pollination services map

Lonsdorf *et al.* (2009) used their pollinator source map to derive a "pollination services map" predicting the numbers of each pollinator species arriving in each cell as a function of the abundances of pollinators residing in and distance (relative to pollinator flight ranges) to surrounding cells. The value of each pollinator species to each plant species in the cell then

determines overall visitation. Due to the time-lags and direct fire effects described in the previous section, the pollination services map of a particular time-step should be based on the pollinator source map of the previous time-step minus direct effects occurring during the transition to the current time-step. This accounts for effects on pollination resulting from fire-driven changes in pollinator populations, such as observed lags between the post-fire return to flowering of species and recolonization by their pollinators (Ne'eman, Dafni & Potts 2000). However, it does not account for the plant–plant and pollinator–pollinator interactions that can occur between co-occurring species. These are relevant to both pollination and floral resource intake by pollinators and enter our conceptual model as determinants of the plant–pollinator interaction network that forms in each cell in the pollination services map.

Cell networks

In our model the plant species flowering, and the pollinators residing or arriving, in a given cell in a given time-step form an interaction network described by the presence/absence or frequency of interaction between each plant–pollinator species pair (Jordano 1987; Schleuning, Fründ & García 2015). Pair-wise interaction probabilities vary with matching traits (e.g. tongue length vs. nectar tube depth, phenological overlap (Stang *et al.* 2009; Junker *et al.* 2013)) and spatio-temporal variation in plant and pollinator abundance (Carstensen *et al.* 2014; Kaiser-Bunbury *et al.* 2014; Schleuning, Fründ & García 2015; Trøjelsgaard *et al.* 2015). Since fire can drive variation in flower and pollinator abundances (e.g. Potts *et al.* 2003a) we focus on this aspect of network formation.

The probability that a plant–pollinator species pair interacts in a network may increase with the plant's floral abundance as it becomes more likely the pollinator will encounter the plant, but also because the plant becomes more attractive to and so influences the foraging decisions of the pollinator (Carstensen *et al.* 2014). The latter process extends to situations where pollinators perceive different plant species as equivalent when evaluating densities of flower patches such that plants with shared pollinators jointly attract visits (Thomson 1981). However, increasing the abundance of one plant species in a network can increase visitation, but also heterospecific pollen transfer (reduced quality), to other plant species in the network (Lopezaraiza–Mikel *et al.* 2007) unless there is divergence in pollen placement on pollinators (Armbruster, Edwards & Debevec 1994). Moreover, the effects of floral abundance (conspecific or heterospecific) on visitation to a target plant varies with spatial scale; greater floral abundance at local scales often enhances visitation by concentrating pollinators in the

target plant's patch, but at larger scales reduces visitation by diluting pollinators across neighbouring patches (Veddeler, Klein & Tscharntke 2006; Holzschuh *et al.* 2011; Hegland 2014; Schmid *et al.* 2015). Empirical studies of the scales at which pollinators respond to floral densities (e.g. Thomson 1981) might be used to define cell sizes in our model such that plant–plant facilitation occurs within cells, but competition occurs between cells. Within-cell competition is also possible when pollinators shared by plant species are able to distinguish between them and preferentially visit the more rewarding/attractive species (Thomson 1981; Rathcke 1988).

The probability that a plant–pollinator species pair interacts can also increase with the pollinator's abundance as it expands its foraging niche (increases the range of species visited) to reduce intraspecific competition (Fründ *et al.* 2013; Trøjelsgaard *et al.* 2015). Similarly, when pollinator species richness increases a greater range of plant species may be visited, though as a result of pollinator species shifting and *contracting* their foraging niches to avoid *interspecific* competition (Brosi & Briggs 2013; Fründ *et al.* 2013). Thus, heterospecific pollen transfer, and so seed set, increases in the case of intraspecific, but decreases in the case of interspecific pollinator–pollinator competition (Brosi & Briggs 2013). Less abundant or rewarding plant species or patches (cells) may nonetheless benefit from both forms of pollinator–pollinator competition as pollinators are forced to visit less attractive resources, though this would reduce cell floral values for competitively inferior pollinators that are more likely to be displaced (Bronstein 1995; Tylianakis *et al.* 2008; Essenberg 2013).

There is some evidence of fire-driven variation in plant–plant and pollinator–pollinator interactions. Four studies reported variation in pollination associated with fire-driven changes in conspecific and/or heterospecific floral abundance (Potts *et al.* 2006; Pauw 2007; Van Nuland *et al.* 2013; Bourg, Gill & McShea 2014). However, only Van Nuland *et al.* (2013) considered the spatial and temporal scales at which these effects occurred by manipulating floral densities at local scales, finding immediate increased visitation with increased local conspecific floral abundance (which was greater in early age classes). Potts, Dafni and Ne'eman (2001) found evidence that a shrub species differed in reward status, flower visitor species composition, but not pollination services between recently burnt and long unburnt sites because competitively inferior pollinator species were displaced to less rewarding individuals.

Traits

Here we discuss phenotypic traits for use in parameterizing our conceptual model. A trait-based approach is justified because there is intraspecific variation in both fire response traits (e.g. Moreira, Tormo & Pausas 2012) and matching traits (e.g. Poisot, Stouffer & Gravel 2015) such that trait rather than species information should be used in applying the grid-based model to a particular management area. Trait-based models have been developed to predict the consequences of environmental change for plant–pollinator interactions, though fire regimes have not been addressed (Lavorel *et al.* 2013; Schleuning, Fründ & García 2015). We extend these by identifying traits mediating direct responses to fire and indirect responses through mutualistic partners, in the context of our spatially explicit conceptual model. For pollinators we attempt to cover the full range of parameters required to simulate population dynamics, but for plants we limit discussion to traits relevant to pollination since other variables have been addressed elsewhere (e.g. Noble & Slatyer 1980).

Pollinators – cell fire history

Fire history of the cell can be linked directly to pollinator occupancy/abundance through mortality associated with the fire event. While highly mobile adult pollinators may typically evade fire, most species have a relatively immobile immature life stage that may be vulnerable when in exposed locations during fire events. Below-ground nesting pollinators may experience less mortality than above-ground nesting pollinators during fire because of insulation by soil (Williams *et al.* 2010; Cane & Neff 2011). Fire severity might moderate these effects since high severity fires can kill below-ground bee eggs and pupae (Cane & Neff 2011). Low severity fires can leave patches of vegetation – and their animal occupants – unburnt (Robinson *et al.* 2013), such that above-ground nesting species may survive such fires. Species with non-overlapping generations (e.g. univoltine species with short-lived adults) are presumably particularly vulnerable to fires that occur in the season during which the population comprises only immobile immatures. Finally, the number of time-steps taken for abundance of species experiencing direct effects to reach pre-fire levels may be less for multivoltine (and to a lesser extent bivoltine) species, since this trait may assist rapid reproduction and population recovery following disturbance (e.g. Draney & Crossley Jr 1999). Moretti *et al.* (2009) found early fire age classes dominated by multivoltine bees, though early post-fire conditions might simply be more suitable for mutlivoltinism (e.g. longer flowering periods).

Cell fire history can also be linked to nesting and floral suitability. Associations between early sere and below-ground nesting bees are often attributed to greater amounts of exposed soil, and associations between early sere and above-ground nesting bees to the greater amount of dead wood (nesting substrate) when low severity fire damages rather than consumes vegetation (Potts *et al.* 2005; Moretti *et al.* 2009; Williams *et al.* 2010; Rodríguez & Kouki 2015; Rubene, Schroeder & Ranius 2015). However, these associations could equally be explained by direct effects (see previous paragraph). Floral resources would be linked to fire history when plant traits determining their flowering response to fire (see 'Plant – cell fire history' section) were also (or were correlated with) matching traits (i.e. the response–effect framework extended to multi-trophic interactions (Lavorel *et al.* 2013)). There is some evidence of this in the Mediterranean where early age classes are dominated by open access flowers with concentrated nectar and short-tongued pollinators that are more efficient at extracting this resource, whereas later age classes are dominated by long nectar tube flowers with dilute nectar and long-tongued pollinators that are capable of exploiting these flowers (Potts *et al.* 2003a; Moretti *et al.* 2009). Finally, a given reward level (e.g. nectar sugar content) may represent a lower floral value for large-bodied pollinators with greater energetic requirements (e.g. Schmid *et al.* 2015).

Pollinators – cell composition and configuration

An important variable in the grid-based model is foraging range, which increases with pollinator body size (e.g. Greenleaf *et al.* 2007; Benjamin, Reilly & Winfree 2014). There is evidence this trait mediates responses to landscape composition and configuration. Large pollinators are often less sensitive to habitat patch size (clumped vs. dispersed habitat configuration) presumably because they are capable of utilizing small habitat fragments (isolated cells) (Jauker *et al.* 2013; Hopfenmueller, Steffan-Dewenter & Holzschuh 2014), though more sensitive to the amount of habitat (number of suitable cells) in the landscape (composition) presumably due to their greater energy requirements (Larsen, Williams & Kremen 2005).

Dispersal is important for recolonization following direct fire effects or a cell's return to habitat suitability, but is poorly understood for pollinators. A rough distinction might be made between species that return to nesting sites to provision young (many bees and birds) and species that oviposit freely as they move through the landscape (many pollinating flies),

304 the latter being less constrained in their dispersal movements (Jauker *et al.* 2009; Parsche,
305 Fründ & Tscharntke 2011).

306 *Plants – cell fire history*

307 The time taken to reach reproductive maturity after fire, following either germination or
308 vegetative regrowth (for resprouting species), and subsequently return to a vegetative or
309 dormant (seed or adult) state, determines the relationships between flowering and fire age.
310 Interspecific differences in the onset and cessation of flowering can correspond
311 approximately to growth form. Trees take longer than shrubs, which take longer than herbs,
312 to reach reproductive maturity following fire (Burrows, Wardell-Johnson & Ward 2008), and
313 taller-stature plants can inhibit flowering of lower-stature plants through competition for light
314 and other resources as their canopies recover from fire (Coates & Duncan 2009; Keeley *et al.*
315 2011). For taller-stature plants, flowering capacity may cease with adult senescence, bud
316 bank attrition, or due to a lack of environmental cues associated with fire (Enright *et al.* 2011;
317 Lamont & Downes 2011).

318 A fire's impact on flowering can depend on its intensity in relation to the plant's
319 requirements for elevated temperatures and responses to tissue damage. Seeds requiring heat
320 shock to germinate can experience greater germination after more intense fires (Knox &
321 Clarke 2006). Similarly, adult fire-stimulated flowering species might increase flowering
322 with fire intensity where temperature is the flowering cue (Lamont & Downes 2011). Lower-
323 stature (competitively inferior) adults may enhance growth and flowering after more severe
324 fires that increase light (through canopy removal) and nutrient availability (e.g. Bowen &
325 Pate 2004; Knox & Clarke 2006; Lamont & Downes 2011). Flowering of evergreen adults
326 may initially increase with fire severity because of greater damage to dominant apical buds
327 (Bowen & Pate 2004), but excessive damage from high severity fires may reduce flowering
328 in species resprouting from poorly protected above-ground or shallow below-ground buds
329 (Clarke *et al.* 2013).

330 The effects of a fire on flowering can also depend on the season in which it occurs. Flowering
331 may be reduced in seeds germinating immediately after fire if the time available for growth
332 between fire/germination and the flowering season is short (Hiers, Wyatt & Mitchell 2000).
333 Conversely, seeds germinating in the first appropriate season (e.g. cued by seasonal
334 temperature regimes) after fire may experience reduced survival and growth, and delay

flowering for one or more years, as the time between fire and the appropriate season increases (Knox & Clarke 2006; Ooi 2010). Resprouting species that flower before producing foliage can do so within weeks of fire regardless of season (provided resource reserves have been replenished since the previous fire), such that fire season determines flowering season (Le Maitre & Brown 1992). Resprouting adults needing to produce foliage before or with flowers typically bloom during the growing/flowering season after fire and the effects of fire timing may depend on whether plants are evergreen or deciduous and capable of producing multiple stems. For deciduous, single-stemmed plants (e.g. many geophytes) and evergreen resprouters, the flowering response often increases with the length of time between fire and the flowering season (Le Maitre & Brown 1992; Bowen & Pate 2004; Lamont, Wittkuhn & Korczynskyj 2004). This may occur because there is more time for regrowth and bud maturation prior to flowering (Bowen & Pate 2004), and in the case of dormant geophytes (particularly those that store only enough resources for one season's growth) greater resource allocation to flowering by avoiding fire damage to foliage (Le Maitre & Brown 1992). For deciduous plants capable of producing multiple stems (e.g. rhizomatous herbs), flowering can be enhanced by fires closer to the flowering season, presumably because exposure of apical stems creates opportunities for release of supressed buds (Platt, Evans & Davis 1988; Hiers, Wyatt & Mitchell 2000). Finally, co-occurring species can flower in different months such that phenological period influences the effects of fire season on flowering (Pavlovic, Leicht-Young & Grundel 2011) and therefore the effects of fire in a given season will vary between species with different phenologies.

Management recommendations and future research

Immediate actions

Since fire effects on plant–pollinator interactions are poorly understood, few management recommendations can be given. Perhaps the most widely applicable is to manage for flower diversity because it has great potential for conservation benefits and at least rudimentary knowledge of flowering responses to fire is widespread. Floral diversity is positively associated with pollinator diversity because a greater range of foraging niche requirements are met and floral resource availability is stabilized across pollinator activity periods (Blüthgen & Klein 2011; Bennett & Gratton 2013; Dorado & Vázquez 2014). In turn, greater pollinator diversity can enhance and stabilize pollination services through pollinator–

pollinator interactions and complementarity due to interspecific variation in traits such as flower height preferences (Hoehn *et al.* 2008; Blüthgen & Klein 2011; Ebeling, Klein & Tscharntke 2011; Brosi & Briggs 2013).

How floral diversity is enhanced may vary between regions depending on knowledge and management approaches. For instance, in North American prairies knowledge of interspecific differences in flowering response to fire season could be used to generate floral diversity through mixed fire season regimes (Hiers, Wyatt & Mitchell 2000). In southern Australia knowledge of the fire ages in which different species flower could be incorporated into existing optimization procedures that determine fire age mosaic compositions maximizing species diversity (Di Stefano *et al.* 2013; Kelly *et al.* 2015). In any case, the aim should be to create floral diversity within pollinator foraging range (while being cognisant of pollinator habitat area requirements) which in turn should generate the local pollinator diversity required for enhancement of pollination services (Tscharntke *et al.* 2012).

Future research

The landscape ecology approach to empirical research (Wagner & Fortin 2005) is required to understand the effects of fire-generated spatial heterogeneity on pollinator populations and foraging behaviour. Space has so far been considered only as a substitute for time in studies of fire effects on pollinators and pollination, despite the fact that pollinators and pollination respond to landscape heterogeneity (Kennedy *et al.* 2013; Vanbergen 2014) and these responses are an important component of our conceptual model.

Prioritizing species for empirical research might be based on vulnerability under future fire regimes predicted from species traits. Fires are expected to be larger, more severe, more frequent, and occur throughout more of the year across much of the globe under climate change (e.g. Flannigan *et al.* 2013). This would increase the probability of overlap between severe fire and immobile life stages, reducing abundances particularly of above-ground nesting pollinators with non-overlapping generations, and reduce the amount of time for on-site post-fire population recovery, reducing univoltine pollinators most dramatically.

Consequences of pollination failure for plant persistence can also help prioritize plant species. Bond (1994) suggested these consequences will depend on the plant's reproductive dependence on pollination (e.g. self-incompatibility) and demographic dependence on seeds (e.g. non-clonality). Carpenter and Recher (1979) suggested a link between reproductive and

fire-related traits, whereby non-sprouters are self-compatible in order to ensure high rates of seed set before the next fire. However, some non-sprouters abort all self-sired seeds and instead enhance seed set by successfully attracting pollinators (Lamont, Olesen & Briffa 1998). Resprouters depend less on seed (Bond 1994), but can still be driven to extinction through pollinator decline particularly if non-clonal (Pauw & Bond 2011; Pauw & Hawkins 2011). Simple dichotomies between the consequences of pollination failure for non-sprouters versus resprouters are untenable – reproductive traits need to be considered in addition to fire-response traits.

Ultimately, to guard against extinctions resulting from loss of mutualistic partners (Pauw & Bond 2011), the conceptual framework presented here might be expanded to predict aggregate metrics of plant–pollinator interactions networks such as nestedness (the degree to which specialists interact with generalists) and connectance (number of interactions relative to the number of species). These properties have been linked to the probability of co-extinctions of dependent species (though the nature of the relationships is still being debated (e.g. Vieira & Almeida-Neto 2015)) and so may be used in addition to or in place of traditional biodiversity measures such as species diversity (Tylianakis *et al.* 2010; Kaiser-Bunbury & Blüthgen 2015). Moreira, Boscolo and Viana (2015) found both local conditions and landscape heterogeneity within foraging range enhanced nestedness and the number of interactions by enhancing local hymenopteran pollinator diversity. Vanbergen *et al.* (2014) found that regular site disturbance (grazing) increased floral diversity and connectance, but lowered nestedness. Landscape context had little effect on network properties, potentially due to the dominance of flies which may be less constrained in their dispersal movements (see 'Traits' section above). These initial findings suggest a spatially-explicit grid-based model with organism responses to fire mediated by phenotypic traits might be developed to predict network properties under alternative fire regimes. Further research aimed at understanding these dynamics could thus enhance the capacity of fire managers to promote ecosystem resilience in the face of diverse environmental changes.

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Data accessibility

Data have not been archived because this article does not contain data.

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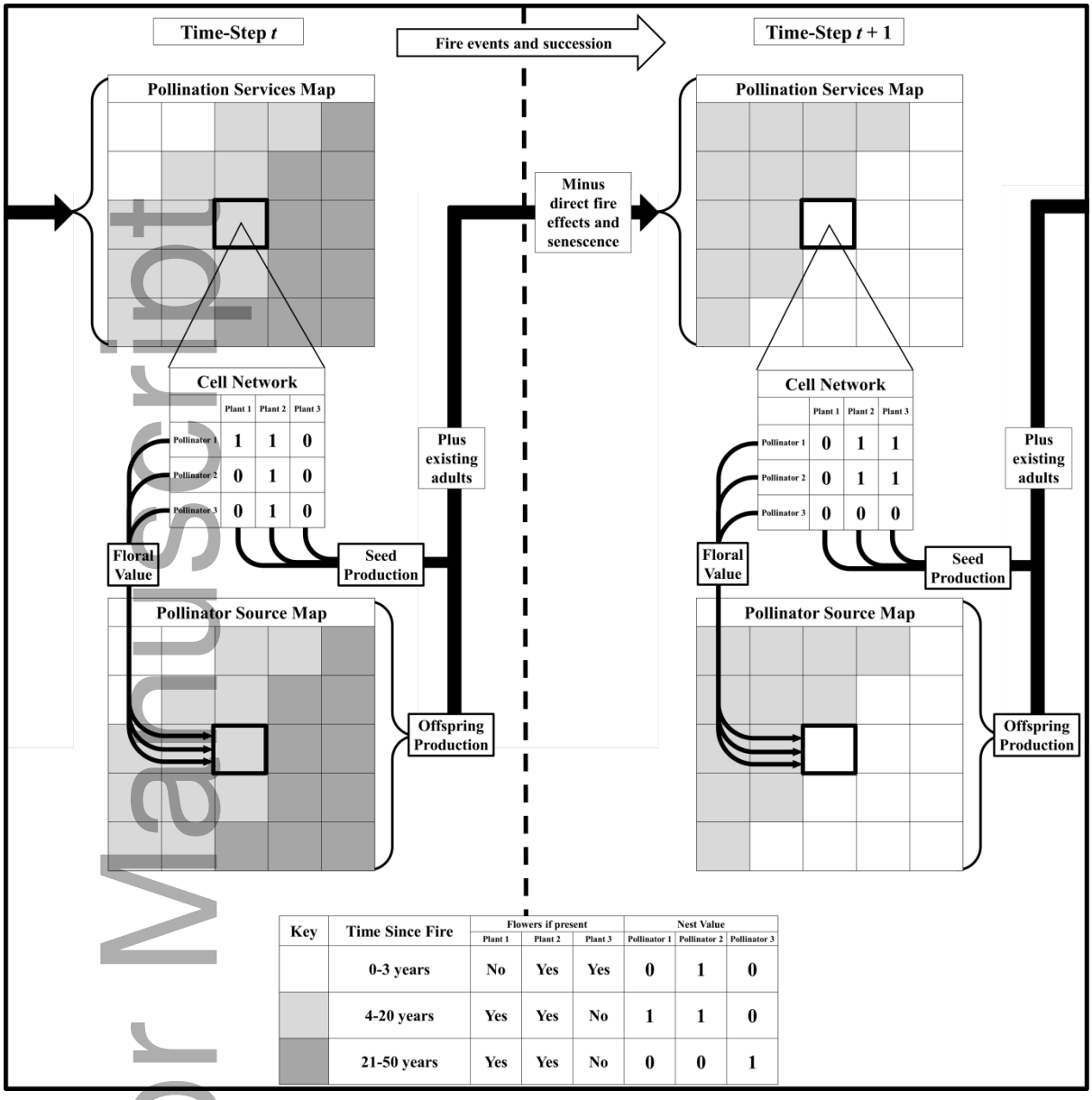

Figure 1: Temporal change in our conceptual landscape model. The pollination services map contains a plant–pollinator interaction network in each cell (only one cell shown) based on the abundance of each pollinator species arriving in the cell and each plant species flowering in the cell. The outcome of each cell's interaction network (in conjunction with the quality of each interaction partner) for that time-step is: (i) seed production for each resident plant species; and (ii) the floral value for each pollinator species, which is used in conjunction with the nesting value of each cell to calculate offspring production in the pollinator source map. Before the pollination services map is calculated in the next time-step, seeds, offspring, and adults remain dormant, transition to different life stages (e.g. plant 3 commences flowering), senesce, or are killed by fire (direct effects: e.g. plant 1 and pollinator 3), and nest availability changes with fire age.