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How fire interacts with habitat loss and fragmentation

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Running head: How fire interacts with habitat fragmentation

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ABSTRACT

Biodiversity faces many threats and these can interact to produce outcomes that may not be predicted by considering their effects in isolation. Habitat loss and fragmentation (hereafter 'fragmentation') and altered fire regimes are important threats to biodiversity, but their interactions have not been systematically evaluated across the globe. In this comprehensive synthesis, including 162 papers which provided 274 cases, we offer a framework for

understanding how fire interacts with fragmentation. Fire and fragmentation interact in three main ways: (1) fire influences fragmentation (59% of 274 cases), where fire either destroys and fragments habitat or creates and connects habitat; (2) fragmentation influences fire (25% of cases) where, after habitat is reduced in area and fragmented, fire in the landscape is subsequently altered because people suppress or ignite fires, or there is increased edge flammability or increased obstruction to fire spread; and (3) where the two do not influence each other, but fire interacts with fragmentation to affect responses like species richness, abundance and extinction risk (16% of cases). Where fire and fragmentation do influence each other, feedback loops are possible that can lead to ecosystem conversion (e.g. forest to grassland). This is a well-documented threat in the tropics but with potential also to be important elsewhere. Fire interacts with fragmentation through scale-specific mechanisms: fire creates edges and drives edge effects; fire alters patch quality; and fire alters landscape-scale connectivity. We found only 12 cases in which studies reported the four essential strata for testing a full interaction, which were fragmented and unfragmented landscapes that both span contrasting fire histories, such as recently burnt and long unburnt vegetation. Simulation and empirical studies show that fire and fragmentation can interact synergistically, multiplicatively, antagonistically or additively. These cases highlight a key reason why understanding interactions is so important: when fire and fragmentation act together they can cause local extinctions, even when their separate effects are neutral. Whether fire–fragmentation interactions benefit or disadvantage species is often determined by the species' preferred successional stage. Adding fire to landscapes generally benefits early-successional plant and animal species, whereas it is detrimental to late-successional species. However, when fire interacts with fragmentation, the direction of effect of fire on a species could be reversed from the effect expected by successional preferences. Adding fire to fragmented landscapes can be detrimental for species that would normally co-exist with fire, because

species may no longer be able to disperse to their preferred successional stage. Further, animals may be attracted to particular successional stages leading to unexpected responses to fragmentation, such as higher abundance in more isolated unburnt patches. Growing human populations and increasing resource consumption suggest that fragmentation trends will worsen over coming years. Combined with increasing alteration of fire regimes due to climate change and human-caused ignitions, interactions of fire with fragmentation are likely to become more common. Our new framework paves the way for developing a better understanding of how fire interacts with fragmentation, and for conserving biodiversity in the face of these emerging challenges.

Key words: habitat fragmentation, habitat loss, fire, planned burn, wildfire, prescribed burning, interactions, succession, landscape, edge effect.

CONTENTS

I. INTRODUCTION

Biodiversity is in crisis (IPBES, 2019) and faces many direct threats instigated by the actions of people (Driscoll *et al.*, 2018). The current framework for classifying these threats uses a hierarchical classification of individual threats (IUCN, 2020). However, recent literature has placed growing emphasis on interactions between threats (Segan, Murray & Watson, 2016; Geary *et al.*, 2019). Threats to biodiversity can interact synergistically, leading to worse

conservation outcomes than the sum of individual effects (Brook, Sodhi & Bradshaw, 2008). For example, biodiversity loss can be accelerated by interactions of climate change with habitat loss (Mantyka-Pringle, Martin & Rhodes, 2012), pesticides with parasites (Coors & De Meester, 2008), and invasive predators with land-clearing, grazing and fire (Doherty *et al.*, 2015). However, other interactions are also possible, including potential beneficial outcomes (Regan *et al.*, 2011), additive outcomes that are the sum of separate effects, or antagonistic outcomes that are smaller than the largest independent effect (Cote, Darling & Brown, 2016). Understanding how and where multiple threats interact is important for identifying conservation risks and determining appropriate management actions (Segan *et al.*, 2016; Geary *et al.*, 2019).

Habitat loss and fragmentation (hereafter 'fragmentation') and altered fire regimes are major drivers of biodiversity decline (WWF, 2018). Fragmentation threatens more than 14,000 species on the International Union for Conservation of Nature's threatened species *Red List* (~80% of threatened species) (IUCN, 2020). Changes in fire regimes, such as too much fire, not enough fire, and inappropriate season or severity, are also major ecological and evolutionary disruptions (He, Lamont & Pausas, 2019; Kelly & Brotons, 2017; Bowman *et al.*, 2020) that threaten 14.6% of vulnerable, endangered and critically endangered species (4,407 species worldwide; IUCN, 2020). These two processes can interact to affect outcomes for species (Templeton, Brazeal & Neuwald, 2011; Tulloch *et al.*, 2016; Cochrane, 2003). For example, single habitat fragments may not offer a suitable post-fire environment for a population, such as an early- or late-successional plant species. If local extinctions occur in habitat patches that are too far apart for individuals or propagules to move between them, landscape-wide declines can result (Leach & Givnish, 1996; Nimmo *et al.*, 2019). This kind of synergy can occur, even if the site-level fire regime is not altered (Fenner & Bull, 2007). Furthermore, with many species adapted to particular successional stages after fire, fire can

also cause (Latta, Sondreal & Brown, 2000) or negate (Allen, Parrott & Kyle, 2016) fragmentation by creating habitat edges (Parkins, York & Di Stefano, 2018; Menezes, Cazetta & Dodonov, 2019) and altering the spatial arrangement of suitable habitat. Despite the potential importance of interactions between fire and fragmentation, there is no framework for evaluating their joint effects. Past reviews on this topic have been confined to specific ecosystems such as tropical rainforest or eucalypt forest (Gill & Williams, 1996; Cochrane *et al.*, 1999; Cochrane, 2003), limiting the range of mechanisms that have been documented and synthesised. We address this knowledge gap by asking: how does fragmentation interact with fire and how does the interaction influence biodiversity?

II. EMERGENT FRAMEWORK

We structure our review around three main pathways by which fire and fragmentation can interact (Fig. 1). First, fire can influence fragmentation, such as when fire destroys or creates habitat. For example, wildfires in the Sierra Nevada, USA, destroyed the long-unburnt habitat of the fisher (*Martes pennanti*) increasing habitat fragmentation for this species (Scheller *et al.*, 2011). Second, fragmentation can influence fire, such as when habitat loss increases human access, which increases ignitions (e.g. Armenteras, Gonzalez & Retana, 2013). This is common in tropical forests, where people clearing land and moving into areas with new roads ignite many fires (Cochrane, 2001) that potentially spark a positive feedback of increasingly flammable vegetation (Cochrane *et al.*, 1999). Third, fire and fragmentation can also have interactive effects on a biotic response, such as abundance or species richness, even when fire and fragmentation do not directly influence each other (Hossack *et al.*, 2013; Alstad & Damschen, 2016). That is, fragmentation is primarily a result of clearing for agriculture or urbanisation, not fire, and this clearing has not changed the fire regime. However, when fire occurs in fragmented landscapes, the effect of fire on species can differ from when either

process acts alone, because succession within patches can drive local extinctions and patch isolation can prevent recolonisation (Nimmo *et al.*, 2019). We use these three broad ways that fire and fragmentation can interact as a framework for classifying interactions, and to synthesise empirical and modelling evidence of how they affect biodiversity.

III. APPROACH

We searched *Web of Science* for papers with titles, abstracts or key words ('topic' field) that included the terms (fire OR burn) AND (fragment* OR connectivity OR 'habitat patch' OR 'remnant patch' OR 'remnant vegetation' OR 'habitat amount'), and sourced additional papers from *Google Scholar*. We then searched for these key words and the words 'edge', 'isolation', 'dispersal' or 'movement', in the titles or abstracts. Papers with both a fire and a fragmentation term were retained (1,359 papers). We then followed eight rules for excluding papers related to relevance of the topic (e.g. excluding papers on 'bullet fragments' after 'firing weapons'), whether fire and fragmentation were considered together, and whether any interactions reported were supported by data or simulations (see online Supporting information, Appendix S1, Table S1). After this screening, 162 papers remained from which we collected data that guided our synthesis. All authors contributed to screening papers. Throughout, we use 'cases' to refer to individual responses. Where papers reported results for many species, we recorded only cases that represented different responses, rather than every case. For example, different species of the same taxon category (amphibian, reptile, etc.) that showed the same response to fire and fragmentation were recorded as a single case. On the other hand, a species showing a different response to others (regardless of taxon category), or responding to a different fire trait or fragmentation trait, was recorded as a separate case. Contrasting responses identified for the same species were also recorded as separate cases. We did this to limit the extent to which individual papers could dominate our summary tables

and to maintain the data-extraction process at a manageable level. Using this rule, we never recorded more than six cases per paper. An alternative approach would have been to extract every response and then use a resampling approach for analysis, but we deemed our approach the most efficient.

Cases described in the papers were classified into three categories of interaction: (1) fire influences fragmentation; (2) fragmentation influences fire; and (3) neither influences the other but they act together to influence a biotic response ('fire and fragmentation do not influence each other'). For some papers in the third category, fire did influence patch quality and so could potentially be reported in the first category. However, these studies had a focus on fragmentation traits that were unaffected by fire so were better classified in the third category [e.g. distribution of restored habitat or patches in urban landscapes (Conlisk *et al.*, 2014; Ramalho *et al.*, 2018)]. Data collected from each paper included fragmentation traits (e.g. edge condition, patch size, landscape connectivity), fire traits (e.g. frequency, extent, time since fire), biotic responses (e.g. abundance, richness, extinction rate, edge effect) and direction of effects (e.g. unchanged, decrease, increase; see Appendix S2 and S3). For each paper, we also recorded the experimental design, the ecosystem and region. After classification, we qualitatively synthesised the literature, using the classification as the framework to organise our ideas.

To standardise the way in which relationships between fire and fragmentation were recorded, we specified a direction of change for fire or fragmentation, depending on the type of interaction. For example, where increasing fire severity caused increased fragmentation, we could also have recorded that decreasing fire reduced fragmentation. Therefore, we always standardise to record how fragmentation and biotic responses changed in response to increasing fire, such as increasing severity, extent or frequency. This allows a logical next step to report how the fragmentation trait was influenced by an increase in the amount of fire,

and subsequently how those two together affected a biotic response. Similarly, when fragmentation led to reduced fire, we recorded the effect of increasing fragmentation, then noted the fire trait affected, such as fire frequency, and the direction of change, in this example, a decrease.

Considering the number of different fire traits, fragmentation traits and the 20 possible biotic response variables, there was an unmanageable number (>200,000) of potential joint categories. Thus, we further simplified the responses and only report summaries at higher levels. Simplified categories are defined below and detailed in Appendix S3, including classifying biotic responses to their level of biological organisation (individual, population, community) and fragmentation traits by scale (landscape, patch, edge). Although we collected data on when habitat loss *per se* and habitat fragmentation *per se* were reported (Fahrig, 2017), there were only four such cases from two simulation papers (Turner *et al.*, 1994; Pausas, 2006). For simplicity, we therefore refer to habitat loss acting together with the breaking apart of habitat as 'fragmentation', and use 'fragmentation *per se*' or 'habitat loss *per se*' when effects were reported separately.

There were 28 combinations of fragmentation traits and direction of change among the fire influences fragmentation cases. We further simplified these into five categories (Appendix S4): worsen (e.g. fragmentation increases, patch condition decreases, edge length increases), improve (e.g. fragmentation decreases, patch size increases), non-linear (U or hump shaped), changed (direction cannot logically be applied), or unchanged. Increasing edge length does not always lead to worse biotic responses, and we note these exceptions in the results. There were 13 combinations of fire traits and direction among the cases of fragmentation influences fire, which we reduced to three categories (Appendix S5): more fire (e.g. increase in extent, severity, frequency, intensity, occurrence), less fire and non-linear change in fire.

There were 56 combinations of biotic response and direction of effect for the fire influences fragmentation interactions. We reclassified these to nine levels (Appendix S6): worsens, improves, non-linear, changed, unchanged, edge worsens (e.g. amount of edge increases), edge improves, edge unchanged, or no biotic response. For example, when biotic responses like abundance, richness and habitat use increased, the response was scored as 'improve'. When the response increased at an edge or into the burnt habitat, we scored the response as 'edge improves'. Similar simplifications were made for cases where fragmentation influences fire (Appendix S7) and fragmentation and fire do not influence each other (Appendix S8). Scoring was completed by K.B., and all scores reviewed by D.A.D., following Appendices S1–S8.

With cases showing that almost any response to any combination of fire and fragmentation interaction is possible, further insights might be obtained by defining responses that were contingent on other variables. For fire influences fragmentation cases, we used Fisher's exact tests to determine whether the number of cases that 'improve' or 'worsen' fragmentation and biotic responses depended on ecosystem, region, taxon, experimental design, or organisation level of the biotic response. Some papers reported multiple cases, but this test would be valid only with one case per paper providing independent data points. Using a permutation approach, we randomly removed cases for papers with multiple cases so that only one case was included per paper, and then performed Fisher's exact test. We repeated this procedure 100 times, interpreting differences among classes (ecosystem, region, etc.) using the distribution of the *P* values from these tests. For fragmentation influences fire cases, there were few biotic responses, precluding analogous tests to those applied in the fire influences fragmentation cases. We instead used the same permutation of Fisher's exact tests, but tested whether worsening landscape-scale fragmentation led to less or more fire, depending on ecosystem, region, and experimental design.

IV. OVERVIEW OF CASES REPORTED

We identified 274 cases from the 162 papers we reviewed. How fire influenced fragmentation was assessed in 162 cases (59% of all cases) from 96 papers, how fragmentation influenced fire was assessed in 69 cases (25% of all cases) from 41 papers, and how fire and fragmentation did not influence each other but acted together to influence a biotic response was assessed in 43 cases (16% of all cases) from 28 papers. In relation to fire traits, 133 of the 274 cases (49%) referred to fire occurrence (the impact of a single fire), with other attributes of the fire regime examined less often, such as frequency (21%), extent (12%) and time since fire (11%) (Table 1). Habitat fragmentation and loss were referred to together in 108 of 274 cases (39%), with other fragmentation traits examined less often, such as edges caused by fire (11%), patch condition (11%), edge condition (10%), landscape connectivity (9%) and patch size (9%) (Table 2).

V. FIRE INFLUENCES FRAGMENTATION

(1) How does increasing fire alter fragmentation and biotic responses?

There were similar numbers of cases where increased fire improved (36 cases) or worsened (40 cases) fragmentation traits and biotic responses (Table 3). Evidence that these outcomes depended on ecosystem or other covariates was weak (Table 4). For example, increasing fire was most often reported to reduce the severity of fragmentation traits and improve the biotic response in woodlands and savannah; whereas the reverse was more commonly reported for forests. However, when considering only one case from each paper in a permutation test, these differences had mean P values > 0.1 (Table 4).

(*a*) *Landscape scale*

Most cases where fire reduced the impacts of fragmentation occurred in landscapes in which there had been a history of sustained suppression or exclusion of fire by humans over past decades, particularly savannah woodlands (Table 4). These characteristically open plant communities, and the fauna dependent upon them, were often threatened by tree encroachment when fire was excluded [e.g. lesser prairie-chicken (*Tympanuchus pallidicinctus*) in North America (Boggie *et al.*, 2017)]. Several studies covering a range of taxa [e.g. birds, reptiles, amphibians and mammals from Australia and North America (Brown *et al.*, 2013; Smith *et al.*, 2016; Murphy, Evans & Storfer, 2010; Allen *et al.*, 2016)] indicated that more frequent fire in such landscapes improved connectivity between populations of the focal species. The species that benefitted from increased fire tended to be those that prefer early-successional vegetation [e.g. pyrophilous beetles in Canada (Saint-Germain, Drapeau & Hibbert, 2013), open-country birds in Spain (Zozaya, Brotons & Saura, 2012)]. Exploitation of such short-lived patches of suitable habitat requires regimes of frequent, highly connected disturbance to create new patches, or species that are highly mobile and can readily disperse to and colonise physically isolated, recently burnt patches [e.g. the beetle *Stephanopachys linearis* in Sweden (Ranius *et al.*, 2014)].

Studies showing that fire increased habitat fragmentation tended to be of species that had known preferences for mid- to late-successional stages, such as the Hispaniolan white-winged crossbill (*Loxia leucoptera megaplaga*), from the Dominican Republic (Latta *et al.*, 2000); or species that had weak dispersal capabilities, including the tree *Allosyncarpia ternata* in Australia (Bowman & Dingle, 2006) and the arboreal red tree vole (*Arborimus longicaudus*) in the USA (Linnell *et al.*, 2017). Increased isolation caused by fire can result in increased inbreeding, as documented in the brown tree frog (*Litoria ewingii*), Victorian frog (*L.*

paraewingii) (Potvin *et al.*, 2017), and Utah juniper tree (*Juniperus osteosperma*) (Allphin, Hunt & Anderson, 2007).

A small passerine bird, the mallee emu-wren (*Stipiturus mallee*) (Brown *et al.*, 2013), illustrates the potential for transition from an interaction where fire influences fragmentation to a situation where fire no longer influences fragmentation but they interact to affect a biotic response (Fig. 2). Before habitat loss due to agricultural land-clearing, mallee emu-wren habitats were large enough to include a fire mosaic, with fire destroying sub-sets of habitat, which recovered subsequently. This spatial turnover led to low genetic structuring due to frequent population turnover (Brown *et al.*, 2013). However, when fragmentation was caused by land-clearing, land-clearing became the dominant spatial process and the effect of fire was reduced to one of habitat degradation where all or most of a habitat patch could be burnt at once; a situation that aligns with fire and fragmentation having independent effects that combine to drive the species towards extinction. Translocations are needed to counter these declining trends (Brown *et al.*, 2013).

(*b*) *Patch scale*

When fire affected patches, a similar number of cases reported improved (14 cases) and worsened outcomes (13 cases) for the biotic response (Table 3). For example, fire enhanced patch condition by increasing seed availability, leading to increased abundance of the early-successional Henslow's sparrow (*Ammodramus henslowii*), in the USA (Bechtoldt & Stouffer, 2005). Introducing fire to woodlands in the USA improved the size and quality of open glades by reducing woody cover, leading to increased population size of the eastern collared lizard (*Crotaphytus collaris collaris*) (Templeton *et al.*, 2011), and higher occupancy of savannah patches by the perennial herb *Penstemon grandiflorus* and the plains pocket gopher (*Geomys bursarius*) (Davis *et al.*, 1997).

Habitat condition was typically (11 of 13 cases) reduced when fire had a negative effect at the patch scale. Fire occurrence degraded patch quality for a reptile in Australian grasslands (Fenner & Bull, 2007), a bird in USA grasslands (Curnutt *et al.*, 1998), birds in Australian woodlands (Berry, Lindenmayer & Driscoll, 2015), birds in Mediterranean (Herrando & Brotons, 2002) and Australian forests (Catterall, Kingston & Park, 1997), and mammals in Amazonian forests (Mendes-Oliveira *et al.*, 2012). Effects of fire on patch quality can also influence the risk of local extinction. For example, under a regime of fire suppression, patch quality can decline for mid-successional forest species as the ecosystem transitions to rainforest, as found for the arboreal marsupial, the mahogany glider (*Petaurus gracilis*), in Australia (Jackson *et al.*, 2011). When threatened species already have reduced abundance in fragmented landscapes, the impacts of fire on patch quality can be detrimental, even when fire regimes are unchanged. The pygmy blue-tongue lizard (*Tiliqua adelaidensis*) was less able to forage in remnant, recently burnt, grasslands in Australia, reducing reproduction and body condition, potentially increasing the risk of local extinction and with no prospect of natural recolonisation (Fenner & Bull, 2007). In the case of prairie remnants in the USA, loss of biodiversity under fire suppression meant that reinstating fire was not enough to restore bird and plant species richness to habitat patches, and translocations were also needed (Van Dyke *et al.*, 2004).

(*c*) *Edge scale*

Fire-maintained edges ('unchanged' edge response, Table 3) could improve (10 cases) or worsen (15 cases) the biotic response, generally reflecting different species' preferences for unburnt or recently burnt habitat (also see Parkins *et al.*, 2018). For example, in Canadian spruce forests, species richness and abundance of spiders with a forest affiliation was higher on the unburnt side of the edge, while open-country species were most abundant in the fire-

maintained ecosystem (Larrivee, Drapeau & Fahrig, 2008). A similar response was reported across fire-maintained edges for plants in New Caledonia (Ibanez *et al.*, 2013). Edge studies involving fire-maintained edges often show an overall negative effect on biodiversity, with generalist species doing well in the fire-maintained ecosystem, and forest specialists declining [e.g. plants in the Mojave Desert, USA (Lybbert *et al.*, 2017); oribatid mites in Swedish pine forests (Zaitsev *et al.*, 2014); plants in Atlantic forests, Brazil (Menezes *et al.*, 2019)]. Fire-maintained edges also affect ecosystem processes, such as by limiting seed dispersal and reducing seed predation into early-successional habitat compared with unburnt rainforest in Colombia (Aide & Cavelier, 1994).

The edge patterns reported by most studies correspond to a 'spillover' edge effect (Villaseñor *et al.*, 2014), whereby there is a gradual transition from one side of the edge to the other. Edges caused by fire led to very few positive edge effects, where there are higher values at the edge and lower values on either side. Examples included log abundance, broadleaf regeneration and bryophyte species richness which were higher at boreal forest edges (Barbe, Fenton & Bergeron, 2017*b*; Harper *et al.*, 2015).

(*d*) *Unexpected responses*

In a few cases, when fire led to improved landscape or patch metrics, biotic responses worsened. For example, the beetle *Stephanopachys linearis* only breeds in burnt trees, but surprisingly, its extinction probability increased when fire increased connectivity in Sweden (Ranius *et al.*, 2014). This may have occurred due to higher predation at more connected sites, or faster depletion of resources at more connected sites due to higher immigration. There were several cases where fire worsened a landscape or patch metric, but the biotic response was positive: typically, this was due to increases in species that prefer disturbed habitat such as invasive species (e.g. Litton & Santelices, 2002; Peeler & Smithwick, 2018),

or ‘open-country’ specialists (Barbe, Fenton & Bergeron, 2017*a*). In an unexpected result, the abundance of eight bird species increased as isolation of unburnt patches increased within large burnt areas in Australian mallee woodlands (Berry *et al.*, 2015). Only one of the eight species was typical of open country, but all species were also common in the surrounding five-year-old burnt habitat. It appeared that unburnt habitat was providing important resources to which birds were willing to travel, with more birds accumulating in unburnt patches when these were more isolated and, therefore, rare in the landscape (Berry *et al.*, 2015). A similar response has been suggested for salamanders concentrating in recently burnt patches (Hossack *et al.*, 2013). A case illustrating another mechanism comes from fire-mediated mosaics on the Iberian Peninsula, where patches with a higher edge-to-area ratio nevertheless had higher bird species richness because birds were attracted to edges (Herrando & Brotons, 2002).

(2) Effects of fire traits

All fire traits with more than one case, including extent, frequency, occurrence and time since fire, had examples in which increasing incidence of fire in the landscape improved fragmentation traits, as well as the opposite, in which increasing fire worsened fragmentation traits (Table 5). The directions of these effects depended on whether the study had a focus on early-successional habitats, where more fire improved outcomes, or late-successional habitats, where fire was detrimental. Thus, increasing fire extent improved connectivity of open habitat used by open-country birds (Zozaya *et al.*, 2012), increasing fire frequency increased connectivity for early-successional reptiles (Smith *et al.*, 2016), and decreasing time since fire increased occurrence and colonisation of a beetle that breeds in burnt trees (Ranius *et al.*, 2014). On the other hand, increasing fire extent worsened fragmentation and loss of tropical rainforest (Cumming *et al.*, 2012), increasing fire frequency threatened

rainforest refuges of the Carpentarian rock rat (*Zyzomys palatialis*) (Brook, Griffiths & Puckey, 2002), and decreasing time since fire increased habitat fragmentation for bark beetles that depend on mature trees (Seidl *et al.*, 2016).

There were more cases of fire extent, frequency and occurrence influencing landscape-scale metrics than patch metrics (extent: 10 landscape, one patch; frequency: 9, 5; occurrence: 52, 24; Table 5). By contrast, for time since fire there were nine cases at a landscape scale and 12 at a patch scale. This likely reflects the utility of time since fire in measuring habitat quality within patches. For example, time since fire was used as a patch-level predictor of black pine snake (*Pituophis melanoleucus lodingi*) habitat in the USA (Baxley, Lipps & Qualls, 2011), with patch quality and occupancy higher at shorter times since fire. Similarly, short times since fire increased patch size and condition, increasing eastern collared lizard abundance in the USA (Templeton *et al.*, 2011). In both cases, short times since fire also had landscape-scale effects, reducing fragmentation and increasing connectivity (Baxley *et al.*, 2011; Templeton *et al.*, 2011), emphasising the general point that the effects of fire traits can be measured across scales. Further, in the few papers where the biotic effects of fire were measured at multiple scales, the direction of the effect was the same. We found only three papers, from Canada and the USA, which reported how a particular biotic response was affected by fire occurrence or time since fire at multiple scales. All found that more fire led to improved outcomes at both patch and landscape scales (Barbe *et al.*, 2017*a*; Baxley *et al.*, 2011; Davis *et al.*, 1997).

VI. FRAGMENTATION INFLUENCES FIRE

(1) How does worsening fragmentation affect fire and biotic responses?

When fragmentation traits worsened, such as increased habitat fragmentation, reduced patch size, or increased edge, fire increased in 40 cases but decreased in 24 cases (Table 6).

Examples spanned an increase in fire occurrence, frequency, extent, intensity and correlation among fires (Costafreda-Aumedes, Comas & Vega-Garcia, 2016; Benchimol & Peres, 2015*a*; Alencar *et al.*, 2015; Silva *et al.*, 2018; Cochrane & Laurance, 2002). There were two main ways that worsening fragmentation traits caused fire to increase, reported from Europe and the Americas: by increasing anthropogenic ignitions (Armenteras *et al.*, 2013; Salvati & Ferrara, 2014; da Silva *et al.*, 2018) and increasing edge flammability (Benchimol & Peres, 2015*a*; Brudvig, Wagner & Damschen, 2012; Roman-Cuesta, Gracia & Retana, 2009). Among the 24 cases reporting reduced fire as a consequence of worsening fragmentation traits, cases from Europe and North America reported that fire was reduced when fragmentation impeded fire spread. Fire spread was limited by expansion of non-flammable vegetation types or physical obstruction by infrastructure (Wirth *et al.*, 1999; Azevedo *et al.*, 2013; Breininger *et al.*, 2006). Worsening fragmentation was also associated with anthropogenic fire suppression in cases in Australia and North America (Leach & Givnish, 1996; Yates & Broadhurst, 2002).

Whether worsening fragmentation led to more or less fire was significantly related to ecosystem type and geographic region (Table 7). In Central and South America, worsening fragmentation always led to more fire. In these tropical forest and savannah ecosystems, fragmentation caused edges to become more susceptible to fire (Benchimol & Peres, 2015*a*; Armenteras *et al.*, 2013; Durigan, De Siqueira & Franco, 2007) and typically there was more fire in the landscape because cattle ranchers use fire to clear forest and improve forage (Armenteras *et al.*, 2013). Consequently, forest fires always increased in response to fragmentation in cases from Central and South America (e.g. Roman-Cuesta, Gracia & Retana, 2003). Although we did not sample studies that reported less fire with fragmentation in South America, reduced fire occurrence has recently been reported from Chilean agricultural land (McWethy *et al.*, 2018). The geographic bias also likely explains the

significant effect of ecosystem type on whether fragmentation led to more or less fire (Table 7). Fragmentation of forest ecosystems was most commonly reported to lead to more fire, and 30 of 37 forest cases with more fire were from Central and South America.

Fifty of 67 cases (75%) that reported how fragmentation influences fire did not report a biotic response (Table 6). That is, three quarters of research into ecosystems where fragmentation influences fire had a narrow focus on the fragmentation and fire aspects, rather than also considering the consequences for the biota. This contrasts with the fire influences fragmentation cases, where only 10.5% (17 of 162) did not report a biotic response (Table 3).

(*a*) *Landscape scale*

Worsening fragmentation at a landscape scale was reported by 18 cases to increase fire and by 16 cases to reduce fire (Table 6). When worsening landscape fragmentation altered fire, four cases reported an improvement and five a worsening of the biotic response (Table 6). For example, more fire associated with tropical forest edges increased the mortality of Amazonian trees with thin bark and low wood density (Brando *et al.*, 2012, 2014). Conversely, less fire resulting from expanding wetlands and roads that impeded fire spread increased the growth of Siberian Scots pine (*Pinus sylvestris*) (Wirth *et al.*, 1999). However, for fire-affiliated species, fragmentation that led to less fire was detrimental, including for North American prairie species such as the herb *Ceanothus americana* (Leach & Givnish, 1996) or the tree *Pinus palustri*s (Loudermilk & Cropper, 2007). Similarly, in the Florida Scrub, USA, fire suppression in fragmented farming landscapes reduced habitat quality and consequently reduced survival of the Florida scrub jay (*Aphelocoma coerulescens*) (Breininger *et al.*, 2006).

(*b*) *Patch scale*

Two cases showed that worsening conditions at the patch level led to less fire, and reported biotic responses (Table 6). Using structural equation modelling, Ramalho *et al*. (2014) showed that smaller patches of Australian *Banksia* woodlands had reduced fire frequency, which was significantly associated with a decline in richness of woody plant species. Similarly, in northern Sweden, small islands had longer times since the most recent fire than large islands, and this decreased the genetic variation of Norway spruce (*Picea abies*) because clonal growth was more common on small islands (Wang *et al.*, 2003). In the Australian example, fire was reduced due to anthropogenic fire suppression, whereas in the Swedish example, small islands were less likely to be struck by lightning.

(*c*) *Edge scale*

Altered edge conditions typically led to more fire (Table 6) due to fuel accumulation (Benchimol & Peres, 2015*a*), drying (Brando *et al.*, 2014), and more ignitions by people (Armenteras *et al.*, 2013). In two cases where a biotic response was reported, this led to increased Amazonian tree mortality (Brando *et al.*, 2014). By contrast, in holm oak (*Quercus ilex*) woodlands in Portugal, edges reduced fire because fires burnt through shrublands and typically stopped at the damp woodland edges (Azevedo *et al.*, 2013). In these cases, plant abundance and species richness increased on the burnt side of the edge, the only cases of improved biotic responses at edges (Azevedo *et al.*, 2013).

(2) Which fragmentation traits influence fire?

Considering the effect of specific fragmentation traits on fire, rather than just considering the scale, changes in edge condition and increases in edge length were most often reported to lead to more fire (Table 8). Thirteen of 17 cases reporting an association between edge

condition and fire were from Central or South America, particularly tropical forests (e.g. Silva *et al.*, 2018; Cochrane, 2001; Armenteras *et al.*, 2013). They reported higher occurrence of fire close to edges (Cochrane, 2001), and greater fire frequency and intensity (Silva *et al.*, 2018). For other fragmentation traits there were no strong trends; worsening fragmentation can lead to both less or more fire, and occasionally non-linear fire responses.

VII. FIRE AND FRAGMENTATION DO NOT INFLUENCE EACH OTHER, BUT THERE IS A BIOTIC RESPONSE

There were 43 cases (25 simulation models with data, 18 empirical) in which fire and fragmentation did not influence each other but acted together to influence a biotic response (Table 9). For most cases, this scenario transpired in landscapes where fragmentation arose due to clearing for agriculture, urbanisation or infrastructure development, and fire occurred in that already fragmented landscape. There was a high proportion of simulation studies in this category (58%), compared with 18% in the fire influences fragmentation category and 12% in the fragmentation influences fire category. In simulations, fire and fragmentation could be implemented independently, even though in the real-life landscapes that were being modelled fragmentation often served to increase (Tierney, 2018) or decrease (Regan *et al.*, 2010) fire. The high number of simulation cases in this category reflects, in part, that simulations typically implement fire and fragmentation independently, and not that simulations more often focus on systems in which fire is actually independent of fragmentation.

(1) Landscape scale

Most cases (28 of 43, 65%, including 10 empirical cases) examined fragmentation traits at a landscape scale. Half of these (14, including 11 simulations) reported that the interaction with

fire worsened the biotic response (Table 9). More fire in increasingly fragmented landscapes led to decreased population abundance across taxa, including simulation studies on mammals (Ramalho *et al.*, 2018), plants (Conlisk *et al.*, 2012), and fish (Falke *et al.*, 2015), and empirical studies on amphibians (Hossack *et al.*, 2013) and insects (Marschalek *et al.*, 2016). It also decreased the simulated occurrence of birds in remaining habitat patches [e.g. San Diego cactus wren (*Campylorhynchus brunneicapillus sandiegensis*) in coastal sage scrub, USA (Conlisk *et al.*, 2014)], and increased simulated extinction risk for mammals in peri-urban landscapes [southern brown bandicoot (*Isoodon obesulus*) in Australia (Ramalho *et al.*, 2018)]. In most cases, fire reduced population size in habitat patches, and fragmentation reduced colonisation (except Hossack *et al.*, 2013), which together led to worse outcomes for biodiversity.

Improvements in biotic responses were infrequently documented (1 empirical and 4 simulation cases at the landscape scale) and all were for plants (Table 9). For the threatened Australian shrub tranquillity mintbush (*Prostanthera askania*) in fragmented agricultural landscapes, simulations suggested an increase in fire frequency was associated with decreased extinction risk and increased abundance (Tierney, 2018). In longleaf pine (*Pinus palustris*) woodlands, USA, higher fire frequency also increased plant species richness in sites that were species poor due to historical land clearing (Brudvig & Damschen, 2011). The three cases reporting non-linear biotic responses were from simulation studies of plants and indicated that intermediate fire frequency was beneficial, but the magnitude of the effect depended on the amount of fragmentation. For example, the simulated abundance of the obligate-seeding shrub *Ceanothus greggii* from the USA was highest at 40 year fire-return intervals and intermediate to high fragmentation levels, provided that fire was spatially uncorrelated (Regan *et al.*, 2010). However, if fires were correlated and burnt across the

whole landscape, then fragmentation reduced the benefits of intermediate fire-return intervals, decreasing abundance (Regan *et al.*, 2010).

There were a further five empirical cases at the landscape scale where fire and fragmentation did not influence each other, and their combined effect did not influence the biotic response (unchanged response; Table 9). For example, using occurrence data for 44 plant species from rosemary scrub, USA, Miller *et al.* (2012) found weak effects of fire on extinction rates and no effects of patch size, connectivity or their interaction with fire on extinction rates. Persistent seed banks may have contributed to these muted responses (Miller *et al.*, 2012). That these null responses were all empirical studies suggests that in some cases, ecological processes intervene to prevent fire–fragmentation interactions, and such effects are typically not incorporated in simulations.

(2) Patch scale

At the patch scale, effects of patch connectivity and patch size were reported (Table 9). Reducing patch connectivity in combination with increasing fire had similar effects to landscape-scale fragmentation and loss (4 simulation, 1 data case). For example, Tulloch *et al*. (2016) simulated *Banksia* tree dynamics in Australia and found that most species had positive population growth rates at mid-level fire intervals (40–80 years, *cf.* <20 or >80 years), with greater sensitivity to fire interval when connectivity was low.

When decreasing patch size interacted with more fire it led to worse outcomes for biodiversity in four of eight cases, two of which were simulations. For example, Brooker & Brooker (1994) simulated the effects of patch size, fire extent and frequency on extinction risk of the splendid fairy-wren (*Malurus splendens*), in fragmented Australian farmlands. When patch size was large (2000 ha), only annual burning over the entire patch led to a 100% extinction rate. However, as patch size declined, the range of fire frequency and extent that

led to 100% extinction rate expanded, so that in 40-ha patches, fire every 1.6 years and with ~60% of the patch area burnt led to a 100% extinction rate.

In two empirical examples, patch size influenced the effect of fire within the patch, but in opposite directions. On large islands in a hydro-electric dam in Brazil, vertebrate species richness was unaffected by fire, but on small islands, severe fire caused richness to decline by approximately four species more than the effect of small patch size alone (Benchimol & Peres, 2015*b*). By contrast, fire in small patches of prairie in the USA did not cause species to decline, because disturbance-sensitive birds typically did not occur on small patches (Herkert, 1994). However, species that prefer longer times since fire could be found in large patches, so would be at risk if large patches were entirely burnt (Herkert, 1994).

(3) Edge scale

We found only two cases examining edge effects, where fire and fragmentation did not influence each other (Table 9). Fire had an important influence on forest regeneration in Panamanian pastures (Hooper, Legendre & Condit, 2004). Wind-dispersed, light-dependent species were most abundant near the forest edge in recently burnt grassland, but there was no edge effect when experimental plots remained unburnt (Hooper *et al.*, 2004). In a second empirical case, examining an invasive grass (*Avena barbata*) in Australia, Gosper *et al.* (2011) found that fire did not significantly increase its biomass or density at remnant woodland edges beyond the edge effect itself.

VIII. FEEDBACK LOOPS: FIRE AND FRAGMENTATION INFLUENCE EACH OTHER

Because fire can influence fragmentation and *vice versa*, there is the potential for feedbacks between these two processes (Fig. 2B). Some studies described feedbacks in a system but

very few studies demonstrated closure of feedback loops. For example, large fires in less-fragmented Canadian forests resulted in more, small unburnt forest patches (Gralewicz, Nelson & Wulder, 2012). These small forest patches were subsequently burnt more often than large patches, but without fire, they could recover over a 20-year period. The study did not clarify whether burning within that 20-year time period led to further fragmentation and subsequently greater fire susceptibility of remaining patches (i.e. a closed feedback loop) (Gralewicz *et al.*, 2012). A feedback loop was demonstrated in Amazonian forests, where forest fragmentation led to increased anthropogenic fire ignitions as a pasture-management tool. The increased fire ignitions increased the incidences of fire 'escaping' into remaining fragmented forest, which in turn promoted further forest loss through burning and post-fire logging (da Silva *et al.*, 2018; Cumming *et al.*, 2012). A similar situation has been described for Australian forests (Lindenmayer *et al.*, 2011).

It is possible that more examples of feedback loops exist, given the number of studies that identified possible feedback scenarios [e.g. where fire influenced fragmentation (98 cases), or where fragmentation influenced fire (41 cases had possible feedbacks)]. Moreover, there is a substantial literature showing that conversion of wooded ecosystems to grassy or similarly open ecosystems involves a positive feedback with fire (Staver, Archibald & Levin, 2011). These feedbacks favour expansion of open, more flammable ecosystems under topographic and climatic conditions that permit fires to occur (Hoffmann *et al.*, 2012; Tepley *et al.*, 2018). Limited evidence for feedback loops to date is probably because few studies run long enough to detect a mutually reinforcing loop or because feedback loops are not explicitly studied in a fragmentation context.

IX. TYPES OF INTERACTIONS

At its simplest, four classes of results are needed to evaluate a fire–fragmentation interaction fully: (1) a baseline effect in unfragmented, unburnt habitat; (2) the effect of fire in unfragmented habitat; (3) the effect of fragmentation in unburnt habitat; and (4) the effects of fire and fragmentation together (Fig. 3A). There were only 12 cases from 10 papers for which we were able to extract the independent and interactive effects of fire and fragmentation traits.

Of the 12 cases reporting independent and interactive effects of fire and fragmentation, six were empirical, and four of those reported synergies, where the combined effect was greater than their summed independent effects. For example, wetlands in fragmented landscapes in the USA had similar-sized populations of the long-toed salamander (*Ambystoma macrodactylum*) as wetlands in protected landscapes (Fig. 3B) (Hossack *et al.*, 2013). Population size was reduced as the area of high-severity fire within 2 km of wetlands increased, but the reduction was higher in fragmented landscapes reflecting a positive synergy (Fig. 3B). Fires in protected landscapes reduced population size by a factor of seven, but in fragmented landscapes, fire eliminated populations. While fire creates a matrix that is hostile to the desiccation-prone salamander, the authors did not offer an explanation for this synergy.

In a contrasting example, plant species richness in prairie remnants in the USA was positively associated with connectivity in sites that had been recently burnt, but was unrelated to connectivity in unburnt sites (Fig. 3C). Fire promoted germination and establishment, while connectivity allowed propagules to arrive, with both needed to increase species richness (Alstad & Damschen, 2016). The reduced benefit of fire in fragmented landscapes suggests a multiplicative interaction (smaller than summed effects but larger than largest individual effect; Fig. 3C). Gorissen *et al*. (2015) provide an example where both fire and fragmentation

had negative effects on abundance of the Blue Mountains water skink (*Eulamprus leuraensis*) in perched swamps in Australia, but when acting together resulted in population extinction (Fig. 3D). The large independent effects of fragmentation and fire make it difficult to identify if the effect was additive (summed effects), multiplicative or synergistic in this case.

In one of two papers that examine fragmentation *per se*, Pausas (2006) simulated the proportion of the landscape occupied by the tree genus *Pinus* in the Mediterranean, for five levels of forest configuration and six levels of fire frequency. Fire interacted with fragmentation to more than offset the benefits of fragmentation, in a strong synergy (Fig. 3E). One other study based on simulations also reported synergistic interactions (Rodriguez-Buritica & Suding, 2013), although other simulation studies reported additive (Lindenmayer & Possingham, 1996) or multiplicative interactions (Tulloch *et al.*, 2016; Conlisk *et al.*, 2012).

X. DISCUSSION

A significant challenge in understanding, and responding to, global threats to biodiversity is that threats can interact in complex ways (Segan *et al.*, 2016; Geary *et al.*, 2019). Understanding interactions between threatening processes can be critical; some threats acting alone can have limited or no negative effects, but acting together can drive populations to extinction (Figs. 3D, E). This also suggests a need to recognise interactions in IUCN threat classifications (IUCN, 2020) because, acting alone, some processes might not be threatening but in situations where they act together, may need recognition and action. Here, we reviewed the global literature to assess potential interactions between two major threats to biodiversity, altered fire regimes and habitat fragmentation. We synthesised 162 studies using a framework that highlights three broad categories of interactions: fire influences fragmentation;

fragmentation influences fire; and neither influences each other directly but they act together to influence biotic responses.

Conceptually, the same ecological processes take place in all three categories of our framework (Fig. 1), such as changes in edge effects and the effects of condition, amount and spatial arrangement of habitat. However, the papers reporting that fragmentation influences fire, or that neither influences the other, include landscapes that have incurred habitat conversion for agricultural or other human uses. In these situations, the level of fragmentation is primarily determined by land-use change and fragmentation dynamics are linked to the rate of land clearing and land abandonment. If land is abandoned, the landscape may recover through revegetation (Jonson, 2010), transition through succession (Hooper *et al.*, 2004), or remain locked in a cleared stable state (Standish *et al.*, 2007). By contrast, when fire influences fragmentation, fragmentation dynamics are typically associated with mosaics of fire in extensive natural systems, with dynamics dominated by succession. From a conservation and management perspective, instances of fire influencing fragmentation can be addressed primarily by changes to fire management, and reintroductions if poorly dispersing species are lost (Rickards, 2016). However, for the other fire–fragmentation interactions, the underlying causes and consequences of land clearing, abandonment, and changes to the fire regime must be addressed.

A common theme emerging across our three categories of interaction was that the direction of the effect of the fire–fragmentation interaction was frequently determined by the successional preferences of species. Adding fire to landscapes where fire has been suppressed benefitted early-successional species, whereas increasing the amount of fire was detrimental to late-successional species. This was generally true regardless of scale, the aspect of the fire regime examined, or the fragmentation traits considered. It was also true across a wide range of ecosystems. For example, fire has caused patch-quality decline in grasslands (Fenner & Bull,

2007; Curnutt *et al.*, 1998), woodlands (Berry *et al.*, 2015), Mediterranean forests (Herrando & Brotons, 2002), subtropical forests (Catterall *et al.*, 1997) and rainforests (Mendes-Oliveira *et al.*, 2012). In fire-sensitive rainforest, most plant species are disadvantaged, while a few pioneer plant species benefit from fire (Tabarelli, Peres & Melo, 2012). Frequent fire also disadvantages species that prefer long-unburnt habitat in what might be regarded as fire-adapted ecosystems such as grasslands (Herkert, 1994; Fenner & Bull, 2007; Curnutt *et al.*, 1998), woodlands and forests (Berry *et al.*, 2015; Herrando & Brotons, 2002; Catterall *et al.*, 1997). That species respond according to their successional preferences is consistent with long-standing expectations from disturbance theory (Pulsford, Lindenmayer & Driscoll, 2016) and explains why, generally, the same processes can be observed across ecosystems; the species in all ecosystems represent a spectrum of successional preferences.

Our review also shows that the typical effects of fire based on succession can be modified in interaction with fragmentation. Habitat fragmentation by land clearing can change the effects of fire, from a benign or beneficial effect, to a process that threatens the persistence of species. Cases from our review included when specialists in grassland, an ecosystem that is commonly burnt, are disadvantaged by fire (Fenner & Bull, 2007), and when fire fails to have the expected benefits because colonists cannot reach isolated remnants to access their favoured successional stage (Van Dyke *et al.*, 2004; Brown *et al.*, 2013; Alstad & Damschen, 2016). Small patch size can also magnify the short-term impacts of fire on species because populations are small, making them more vulnerable to extinction when patches are burnt, even though in large areas of habitat fire would rarely cause extinction (Brooker & Brooker, 1994; Benchimol & Peres, 2015*b*).

Further unexpected responses arose when fire improved or worsened the landscape or patch metrics, but the biotic response was in the opposite direction. These cases show that complex behaviours or interactions can arise to alter expected relationships. Examples included higher

predation or faster depletion of resources when fire improves connectivity (Ranius *et al.*, 2014), higher abundance in more isolated unburnt patches due to local attraction (Berry *et al.*, 2015), and edge attraction which increases species richness in patches that would generally be regarded as more degraded by having higher edge to area ratios (Herrando & Brotons, 2002).

Substantial variation in how fragmentation affected fire was introduced by differences in human use of fire. In a longitudinal study from Canada, Weir, Johnson & Miyanishi (2000) reported that fires during the land-clearing phase in the 1890s occurred more frequently than the background rate because fire was used to help clear land. However, by the mid-1940s when land clearing was complete, fire declined, which is typical of many agricultural landscapes that suffer from too little fire due to fire suppression (Leach & Givnish, 1996; Yates & Broadhurst, 2002). On the other hand, some grazing landscapes experience higher rates of fire, most notoriously in South American landscapes with remnant tropical rainforest (Le Page *et al.*, 2017; Cochrane, 2001). Managing the fire–fragmentation interaction is therefore intimately entwined with how people supress or exploit fire, and now much research attention is being given to social aspects of improving fire management (Eloy *et al.*, 2019; Mistry *et al.*, 2019; Moura *et al.*, 2019).

Very few studies have examined the effects of fire and fragmentation on a particular biotic response across multiple scales, including landscape, patch and edge scales. In the four papers we found that did so, the effects were in the same direction, suggesting that so far there is no evidence that scale interacts with fire and fragmentation to change the direction of effect, for example on abundance or species richness (Barbe *et al.*, 2017*a*; Baxley *et al.*, 2011; Davis *et al.*, 1997; Miller *et al.*, 2012). Fire, nevertheless, does have characteristic effects at different scales, by definition: causing or reducing fragmentation and loss, improving or worsening patch quality, and improving or worsening edge effects.

Our review demonstrates that research at each of these scales has provided insight into different mechanisms influencing the fire–fragmentation interaction. This includes the widely reported pattern that flammability typically increases at forest edges due to being drier and having more vegetation and dead plants. With expectations that climate change will bring increased drying and warming to many parts of the world, edge flammability will likely become a more important factor driving landscape fires (Le Page *et al.*, 2017; Cochrane, 2003; Malhi *et al.*, 2009).

(1) Knowledge gaps

Among 274 cases of fire and fragmentation interacting, we found only 12 cases reporting full interactions that included the four essential strata, which were fragmented and unfragmented landscapes that both span contrasting fire histories (Fig. 3), highlighting a substantial knowledge gap. There are some papers where the data seemed to be available, but the authors did not test for an interaction, either because it was not their key focus (Yates & Ladd, 2005), or possibly because statistical power was limiting, making it hard to fit interaction models (McLean *et al.*, 2018; Van Dyke *et al.*, 2007). Some progress may therefore be possible if researchers explicitly test for interactions whenever their data allow.

The small number of cases showing the four strata of the full fire–fragmentation interaction (Fig. 3) is partially because fire and fragmentation are not independent in studies in which fire influences fragmentation or fragmentation influences fire. In cases where fire creates habitat and reduces fragmentation, or when fire destroys habitat and increases fragmentation, there are no conditions for evaluating the effect of fire alone. Similarly, when fragmentation influences fire, these processes are always correlated, with more fragmentation leading to more or less fire. However, if fire can be decoupled from fragmentation then independent effects of fire and fragmentation could be examined more often. Decoupling is readily

achieved using simulations (Tierney, 2018; Regan *et al.*, 2010). However, in reality, decoupling could be achieved by using fire suppression at more flammable edges or natural variation in fire occurrence (e.g. Benchimol & Peres, 2015*b*), by introducing fire to fire-suppressed landscapes, or by changing burning practices of local land users to reduce burning.

Unfortunately, many ecosystems are entirely fragmented so opportunities to define the interaction fully have already been lost. Nevertheless, important inferences for conservation management can be made by using subsets of the four strata, particularly fragmented strata if there are also contrasting fire histories (e.g. the timing, type and severity of fires) (Fig. 3). These highlight the effects of fire in a fragmented landscape and, regardless of independent effects of fragmentation and fire, the conservation benefits of increased (Fig. 3C) or decreased fire (Fig. 3B, D and E) can still be recognised (e.g. Marschalek *et al.*, 2016; Wirth *et al.*, 1999).

When fragmentation affected fire, two-thirds of papers (28 papers) reported the change in fire only, not its consequences for biodiversity. Of those papers, 21 used remotely sensed data or other mapping, suggesting this bias may have arisen because desk-top studies are more feasible than costly fieldwork. Understanding how fire is affected by fragmentation is the essential first step. However, taking the next step to understand the consequences for species will enhance our knowledge of fire–fragmentation interactions. Given the rapidly changing, and in many cases novel conditions now emerging in many ecosystems driven by fire (Nolan *et al.*, 2020), the value of empirical information on biotic responses for making cost-effective management decisions (Bolam *et al.*, 2019) may justify more research attention.

While feedback mechanisms were partially identified, full feedback loops between fire and fragmentation resulting in habitat conversion (Fig. 2A) have been characterised only in the destruction of the Amazon (da Silva *et al.*, 2018; Cumming *et al.*, 2012). Feedback loops are

possible in ecosystems where fire can degrade habitat and where either more fire is introduced by people or there are strong edge effects increasing fire risk. This potential for feedbacks has also been identified in Canada (Gralewicz *et al.*, 2012), and so feedbacks may be a more widespread threat to ecosystems than currently recognised. Research to define these mechanisms and support management to break the feedback is a priority.

Almost half of the cases examined fire occurrence, with valuable implications drawn across taxa, scales and geographic regions. But given that recent fires in Australia achieved 'unprecedented' status based on their massive extent (Nolan *et al.*, 2020), better understanding of the effects of fire extent is imperative. For species that must disperse to colonise patches with suitable habitat, the limited consideration of the extent of fires relative to the species' dispersal capability and pattern of fragmentation is a major knowledge gap. A second important gap is our knowledge of fragmentation interactions with fire severity. Fire severity had conspicuously few cases in our review (Table 1) (Benchimol & Peres, 2015*b*; Brown *et al.*, 2018; Hossack *et al.*, 2013), but severity is expected to increase in many places with climate change (Flannigan *et al.*, 2013). Measuring severity can be challenging, particularly separating ground fires from unburnt areas beneath intact tree canopies (Gibson *et al.*, 2020). However, new remote-sensing analyses are improving our capacity to map severity across large areas (Gibson *et al.*, 2020; Quintano, Fernández-Manso & Roberts, 2020).

There was almost no research on the independent effects of habitat fragmentation *per se* and habitat loss *per se* in interaction with fire. Fragmentation and loss are typically correlated, making it hard to separate their effects (Fletcher *et al.*, 2018). Habitat loss must by definition, be detrimental, but fragmentation *per se* has both positive and negative outcomes, and there is debate over how often those outcomes should be expected (Fahrig, 2017; Fletcher *et al.*, 2018). Habitat configuration nevertheless has an important influence on species and

communities, *via* mechanisms linked to dispersal (Fahrig, 2017). Because conservation management may be able to manipulate habitat configuration to improve conservation outcomes, understanding the effects of fragmentation *per se* in interaction with fire could prove informative. Although a substantial undertaking, future research could stratify sampling in landscapes by the interaction of remaining habitat and degree of fragmentation *per se* (Radford & Bennett, 2007), with an additional stratification of aspects of the fire regime.

Looking to the future, the most rapid progress in this field may come from natural experiments by studying ecosystems that span a range of fragmentation levels and have contrasting fire histories. Natural experiments take advantage of the natural variation in parameters of interest, and will play an important part in understanding interactions among threatening processes because other approaches can be infeasible (Turner *et al.*, 2020). Natural experiments can be used to explore realistic fire sizes and severities, overlaying actual fragmented habitat, with potential to use space-for-time substitutions to examine processes that can span thousands of years (Wang *et al.*, 2003). Data from this kind of study could be used to inform simulation models that further explore interactions. Manipulative experiments have a role, such as for understanding short-term effects of planned burning and disentangling fine-scale mechanisms (Fordyce *et al.*, 2016), but they are usually limited to low fire severities at small spatial and temporal scales (Driscoll *et al.*, 2010). Natural experiments offer opportunities to expand our knowledge of fire–fragmentation interactions rapidly, provided that other environmental variables do not confound results profoundly (Driscoll *et al.*, 2010).

The extraordinary series of fires that extended down the east coast of Australia in 2019–2020 burnt 12 million ha and were the product of extreme drought associated with human-caused climate change (Nolan *et al.*, 2020). Climate change is likely to alter fire regimes in most

parts of the globe, with many increases and some decreases in fire occurrence (Flannigan *et al.*, 2013; Pechony & Shindell, 2010; Syphard *et al.*, 2019). At the same time, demands from a growing human population motivate land clearing (IPBES, 2019), and in some parts of the world, such as the Amazon basin, deforestation fires ignited by people generate exceptionally large burnt areas during dry periods (Withey *et al.*, 2018). Consequently, we can expect increasing interactions between altered fire regimes and habitat fragmentation and loss. We hope the framework that we have developed in this review will help to guide clear thinking about the nature of these interactions and how best to approach framing and designing research into fire–fragmentation interactions.

XI. CONCLUSIONS

(1) Fire–fragmentation interactions can be classified as either: (*i*) fire influences fragmentation, where fire in relatively intact landscapes either destroys and fragments habitat, or creates and connects habitat; (*ii*) fragmentation influences fire, where, after habitat is reduced in area and fragmented, fire progression is obstructed, or fire in the landscape is subsequently altered by suppression or ignition of fires by people or by increased edge flammability, and; (*iii*) fire and fragmentation do not influence each other but interact to affect a biotic response, whereby habitats are fragmented by causes other than fire, but fire still occurs in the landscape, and together they affect responses like species richness, abundance and extinction risk in a way that can differ from their independent effects.

(2) Where fire and fragmentation influence each other, feedback loops are possible that can lead to ecosystem conversion; a key threatening process in the Amazon, but with potential to impact other biomes.

(3) Fire interacts with fragmentation through scale-specific mechanisms, such as by creating edges and driving edge effects, by altering patch quality and by altering landscape-scale connectivity.

(4) Examination of interactions requires four essential strata: unburnt–unfragmented, unburnt–fragmented, burnt–unfragmented and burnt–fragmented. We found only 12 cases that examined all four strata, highlighting a key knowledge gap. Nevertheless, these simulation and empirical studies show that fire and fragmentation can interact synergistically, multiplicatively, antagonistically or additively.

(5) The direction of effect of fire–fragmentation interactions upon biota is often determined by the preferred successional stage of a species; adding fire to landscapes benefits early-successional species, whereas reducing fire benefits late-successional species.

(6) When fire interacts with fragmentation, the direction of effect of fire on a biotic response could be substantially modified from the effect expected by a species' successional preferences. Adding fire to fragmented landscapes can be detrimental for species that would normally co-exist with fire.

(7) Human land use and behaviour has an important influence on how fragmentation affects fire, by humans igniting or suppressing fires.

(8) Climate change will increasingly alter fire regimes throughout the world, and a growing human population ensures that habitat loss and fragmentation will be a permanent feature of our landscapes. Developing improved understanding of how fire interacts with fragmentation is needed for conserving biodiversity faced with these challenges.

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XIV. SUPPORTING INFORMATION

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

Appendix S1. Methods for selecting papers used in the review.

Table S1. Rules used to exclude papers and the number of papers excluded at each step.

Appendix S2. Data collected from each case within the three categories of fire–fragmentation interaction and other data collected for all papers.

Appendix S3. Categories within each of the areas of data collection.

Appendix S4. Converting fragmentation trait and direction of response to simplified categories.

Appendix S5. Converting fire trait and direction of response to simplified categories.

Appendix S6. Converting biotic responses and their direction of effect for fire influences fragmentation to simplified categories.

Appendix S7. Converting biotic responses and their direction of effect for fragmentation influences fire to simplified categories.

Appendix S8. Converting biotic responses and their direction of effect for fragmentation and fire do not influence each other to simplified categories.

Figure Legends

Fig. 1. There are three main ways that fire and fragmentation interact: (1) fire can influence fragmentation (left) by causing fragmentation traits at a landscape, patch or edge scale to improve (e.g. reduced fragmentation), worsen (e.g. reduced patch size), or change (e.g. non-linear responses or changes to an edge effect that are not directional); (2) fragmentation can influence fire (centre), such as when edge drying causes more frequent fire, fire suppression or anthropogenic ignitions with increased access to forests; and (3) neither may influence the other, but together have an interactive effect on a biotic response (right), such as when habitat fragmentation and loss increase due to land clearing (e.g. isolating populations), and subsequent fire or lack of fire causes local extinctions. These three types of interaction can cause community, population- or individual-level traits to improve, worsen or change. The circular arrow indicates that feedbacks can occur where fragmentation and fire influence each other. There is the potential for a transition between 'fire influences fragmentation' and 'fire and fragmentation do not influence each other' as fire size approaches patch size (Fig. 2). Illustrative background images from *Google Earth* (Landscat/Copernicus/CNES/Airbus/Maxar Technologies) including fragmented mallee woodland in Australia where fire destroys habitat for old-growth-specialist birds, but creates habitat for open-country species (Berry *et al.*, 2015) (left), prairie remnants fragmented by agriculture and urbanisation where people suppress fires (Leach & Givnish, 1996) (centre top left), expansion of wetlands and infrastructure fragments flammable Scotts Pine in Siberia (Wirth *et al.*, 1999) (centre top right); herringbone-patterned land clearing in Brazil where edges become more flammable and graziers deliberately set fire to the landscape (Cumming *et al.*, 2012) (centre bottom), perched swamps in Blue Mountains Australia where fire

regimes are not substantially changed by fragmentation, and the primary cause of fragmentation is clearing for urbanisation, not fire (Gorissen *et al.*, 2015) (right).

Fig. 2. (A) Feedback loops. Fire can influence fragmentation by, for example, destroying habitat, and increased fragmentation can increase fire risk, such as by creating more flammable edges or increased anthropogenic ignitions, with potential for this feedback to transform ecosystems. (B) Transitions between categories. Where patch size is large enough to contain multiple fires, fire may cause (or reduce) fragmentation within the patch, representing 'fire influences fragmentation' cases. If such intact landscapes are subsequently converted to agriculture or urbanised, remnant patch sizes may be too small to include a fire mosaic. Consequently, the effects of fire are on patch quality rather than the main cause of landscape fragmentation. Thus, cases of 'fire influences fragmentation', when patch size is large relative to fire size, can transition to 'fire and fragmentation do not influence each other', where fire is no longer the main cause of fragmentation. To persist in highly fragmented landscapes subjected to fire, species must either disperse through the novel matrix between patches of suitable habitat (blue arrow in bottom panel) or survive *in situ*, alongside other pressures from the altered matrix (Driscoll *et al.*, 2013).

Fig. 3. (A) Defining different types of interactions where the independent and joint effects of fire and fragmentation have been evaluated (after Cote *et al.*, 2016), for a hypothetical species that is disadvantaged by both fire and fragmentation. Unburnt Unfrag: effect in areas that represent a long unburnt unfragmented area (blue bar). Burn Unfrag: areas burnt but not fragmented (difference from baseline as orange bar). Unburnt Frag: areas not burnt but subject to fragmentation (difference from baseline as grey bar). Burn × Fragmentation has five alternative responses: Additive – overall effect is equal to the sum of the effects of burn

and fragmentation; Multiplicative – effect is smaller than the summed effects but larger than the largest individual effect; Dominance – an effect equal to the largest independent effect of fragmentation or fire; +Synergy – the effect is larger than the sum of independent effects; – Synergy – the effect is smaller than the smallest individual effect. Values for the interaction that are less than additive have also been called antagonisms (Cote *et al.*, 2016). (B) Long-toed salamander (*Ambystoma macrodactylum*) population size in wetlands, USA (Hossack *et al.*, 2013). (C) Plant community richness in prairie remnants in the USA (Alstad & Damschen, 2016). (D) Average abundance of water skinks (*Eulamprus leuraensis*) in bogs embedded in forest from Australia (Gorissen *et al.*, 2015). (E) Simulated *Pinus* occupancy in the Mediterranean (Pausas, 2006). In B, D and E, effects driving values below the 'baseline' are indicated by unfilled rectangles and left-pointing arrows (for example, in B, fire had a negative effect in unfragmented landscapes, reducing log(population size) from 6 to ~3.5). In the theoretical example (A), interaction effects such as +synergy are illustrated as consisting of increases in both the effects of fire and fragmentation. However, in the empirical and simulation examples (B–E), interactions (Burn × Fragmentation) cannot be attributed to individual changes in effects of fire and fragmentation. Interactions are therefore indicated by the parallel left-pointing arrows.

Table 1. Number of cases examining each fire trait across the three types of interactions. Correlation among fires describes when fires are spatially and/or temporally correlated.

Fire trait	Fire influences fragmentation	Fragmentation influences fire	Neither influences the other	Total
Occurrence	113	12	8	133
Frequency	14	29	14	57
Extent	11	10	12	33
Time since fire	22	1	7	30
Intensity	0	13	0	13
Severity	1	2	2	5
Correlation among fires	0	2	0	2
Patchiness	1	0	0	1
Total	162	69	43	274

Table 2. Number of cases that examined each fragmentation trait across the three types of interaction.

Fragmentation trait	Fire influences fragmentation	Fragmentation influences fire	Neither influences the other	Total
Fragmentation	56	34	18	108
Patch condition	29	0	0	29
Edge	29	0	0	29
Edge condition	9	17	2	28
Landscape connectivity	15	2	8	25
Patch size	10	7	8	25
Patch connectivity	1	3	5	9
Patch edge length	2	6	0	8
Inferred fragmentation & loss	5	0	0	5
Fragmentation *per se*	1	0	2	3
Matrix condition	3	0	0	3
Habitat amount *per se*	2	0	0	2
Total	162	69	43	274

Table 3. Number of cases reporting changes to biotic responses caused by increasing fire which influences fragmentation traits. Fragmentation traits are classified in relation to landscape, patch or edge scale (see Appendices S3–S6, for details of classification scheme).

		Change in fragmentation traits by increasing fire				
Scale	**Biotic response**	**Improve**	**Worsen**	**Changed**	**Unchanged**	**Non-linear**
Landscape	Improves	22	5	1	0	0
Landscape	Worsens	1	26	0	1	0
Landscape	Changed	0	4	1	0	0
Landscape	Unchanged	1	4	1	1	0
Landscape	Non-linear	2	1	0	0	0
Landscape	None	2	8	0	0	1
Patch	Improves	14	3	3	0	0
Patch	Worsens	0	13	1	0	1
Patch	Unchanged	0	0	3	0	0
Patch	None	1	2	0	1	0
Edge	Edge improves	0	0	0	10	0
Edge	Edge worsens	0	1	3	15	0
Edge	Edge unchanged	0	0	0	1	0
Edge	Unchanged	0	0	0	5	0
Edge	Changed	0	0	0	1	0
Edge	None	0	0	2	0	0

Table 4. Number of cases in which increased fire improved or worsened fragmentation and the biotic response, depending on ecosystem, region, taxon, experimental design, or organisation level of the biotic response. *P* = *P* value of Fisher's exact test using all data; Mean *P* = average *P* value of 100 tests after randomly sampling only one case from each paper; SD = standard deviation of the mean. BACI = before–after-control–impact design.

Variable	**Category**	**Improve**	**Worsen**
Ecosystem	Forest	10	19
P = 0.028	Grassland/prairie	3	5
Mean *P* (SD) = 0.253 (0.11)	Shrub/heathland	4	9
Range = 0.124–0.426	Woodland/savannah	15	5
	Other/multiple	4	2
Region	North America	24	20
P = 0.113	South America	0	3
Mean *P* (SD) = 0.234 (0.073)	Oceania	8	15
Range = 0.107–0.354	Rest of world	4	2
Taxa	Amphibian	1	2
P = 0.435	Bird	11	12
Mean *P* (SD) = 0.675 (0.089)	Ecosystem	0	2
Range = 0.542–0.815	Insect	4	2
	Mammal	6	10
	Plant	3	6
	Reptile	11	6
Experimental design	Before–after	4	3
P = 0.426	BACI	4	7
Mean *P* (SD) = 0.294 (0.075)	Control–impact	4	9
Range = 0.141–0.414	Longitudinal	3	5
	Space for time	20	15
Organisation level	Individual	9	10
P = 0.188	Population	26	24
Mean *P* (SD) = 0.151 (0.134)	Community	1	6
Range = 0.008–0.551			

Table 5. Number of cases reporting how different aspects of the fire regime influenced fragmentation traits at the landscape, patch and edge scale (see Appendices S3–S6 for details of classification scheme). Fire responses represent increasing fire.

Scale	Fire trait and direction	Improve	Worsen	Unchanged	Changed	Non-linear
Landscape	Extent increase	4	6	0	0	0
Landscape	Frequency increase	1	7	0	0	1
Landscape	Occurrence	17	32	2	1	0
Landscape	Patchiness decrease	0	0	0	1	0
Landscape	Severity increase	0	0	0	1	0
Landscape	Time since fire decrease	6	3	0	0	0
Patch	Extent increase	0	1	0	0	0
Patch	Frequency increase	3	1	1	0	0
Patch	Occurrence	4	13	0	7	0
Patch	Time since fire decrease	8	3	0	0	1
Edge	Occurrence	0	0	32	5	0
Edge	Time since fire decrease	0	1	0	0	0

Table 6. Number of papers reporting worsening fragmentation traits which influence the amount of fire and, in a small number of cases, subsequently influence a biotic response (None: no biotic response reported). Fragmentation traits are classified as landscape, patch or edge scale (see Appendices S3–S5 and S7 for details of classification scheme).

Scale	Biotic response	Less fire	More fire	Non-linear
Landscape	Improves	3	1	0
Landscape	Worsens	5	0	0
Landscape	Non-linear	2	0	0
Landscape	None	6	17	2
Patch	Worsens	2	0	0
Patch	None	4	8	1
Edge	Edge improves	2	0	0
Edge	Edge worsens	0	2	0
Edge	None	0	12	0

Table 7. Number of cases where worsening landscape-scale fragmentation led to less or more fire, depending on ecosystem, region, and experimental design. *P* = *P* value of Fisher's exact test using all data; Mean *P* = average *P* value of 100 tests after randomly sampling only one case from papers that presented more than one case; SD = standard deviation.

Variable	**Category**	**Less fire**	**More fire**
Ecosystem	Forest	9	37
$P < 0.001$	Woodland/savanna	5	2
Mean *P* (SD) = 0.013 (0.017)	Shrub/heathland	7	1
Range = 0.000–0.058	Grassland/prairie	2	0
	Other/multiple	1	2
Region	North America	9	4
$P < 0.001$	South America	0	31
Mean *P* (SD) = 0.000 (0.000)	Oceania	6	1
Range = NA	Rest of world	9	6
Experimental design	BACI	0	1
$P = 0.030$	Control-Impact	1	7
Mean *P* (SD) = 0.080 (0.066)	Edge influences fire	3	16
Range = 0.011–0.209	Longitudinal	4	5
	Space-for-time	15	13

Table 8. Number of cases where changes in particular fragmentation traits led to less fire, more fire, or non-linear changes in fire.

Scale	Fragmentation change	Less fire	More fire	Non-linear
Landscape	Fragmentation increase	13	14	2
Landscape	Fragmentation occurred	2	3	0
Landscape	Landscape connectivity decreases	1	1	0
Patch	Patch connectivity decreases	2	1	0
Patch	Patch edge length increases	0	5	1
Patch	Patch size decreases	4	3	0
Edge	Edge condition changes	2	15	0

Table 9. The number of cases where fire and fragmentation traits do not influence each other but act together to influence the biotic response, classified by (A) scale; (B) fire trait and direction; and (C) fragmentation trait and direction. (A) The number of cases reporting how increasing fire and deteriorating landscape, patch and edge metrics combine to influence a biotic response. (B) Number of cases reporting the effect on a biotic response of worsening fragmentation traits and particular changes in the fire regime. (C) Number of cases reporting the effect on a biotic response of increased fire alongside particular changes in the fragmentation trait (see Appendices S3–S5 and S8 for details of classification scheme).

	Effect on biotic response				
	Improves	**Worsens**	**Unchanged**	**Non-linear**	**Edge worsens**
(A) Scale					
Landscape	5	14	5	3	1
Patch	1	7	5	0	0
Edge	0	0	1	0	1
(B) Fire trait and direction					
Extent increase	1	11	0	0	0
Frequency increase	4	4	3	3	0
Occurrence	1	3	3	0	1
Severity increase	0	2	0	0	0
Time since fire decrease	0	1	5	0	1
(C) Fragmentation trait and direction					
Edge condition changes	0	0	1	0	1
Fragmentation increase	1	8	4	2	1
Fragmentation *per se* increases	1	1	0	0	0
Fragmentation occurred	2	0	0	0	0
Landscape connectivity decreases	1	5	1	1	0
Patch connectivity decreases	1	3	1	0	0
Patch size decreases	0	4	4	0	0

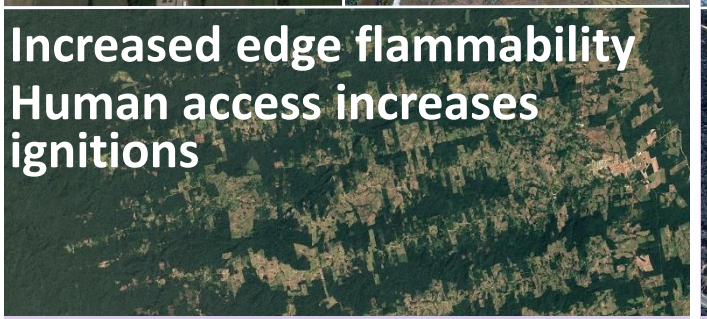
Fire influences fragmentation

Fire causes landscape, patch or edge traits to improve, worsen or change

Feed-backs

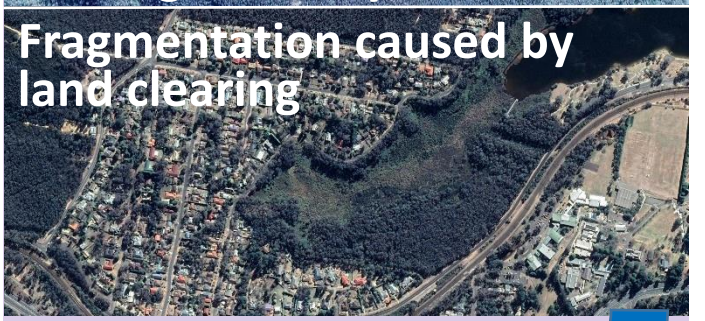
Fragmentation influences fire

Changing landscape, patch or edge traits cause more, less or changed fire



Fragmentation and fire do not influence each other but interact to affect biotic response

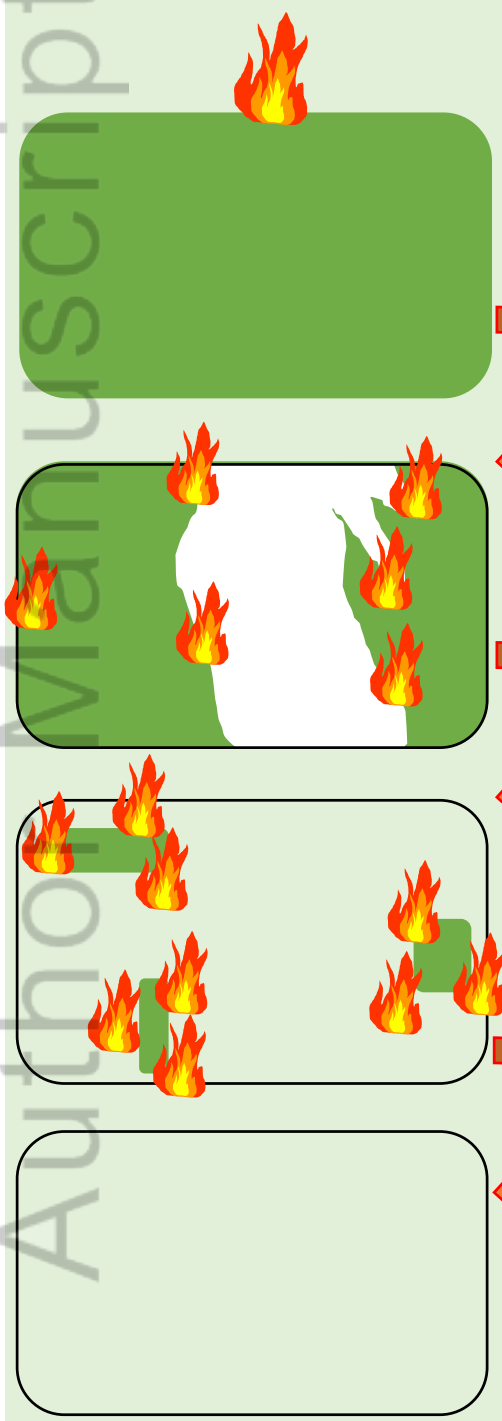
Fire + changed landscape, patch or edge traits



BIOTIC RESPONSE to fire–fragmentation interaction

Community, population or individual responses improve, worsen or change

(A) Feedback loops



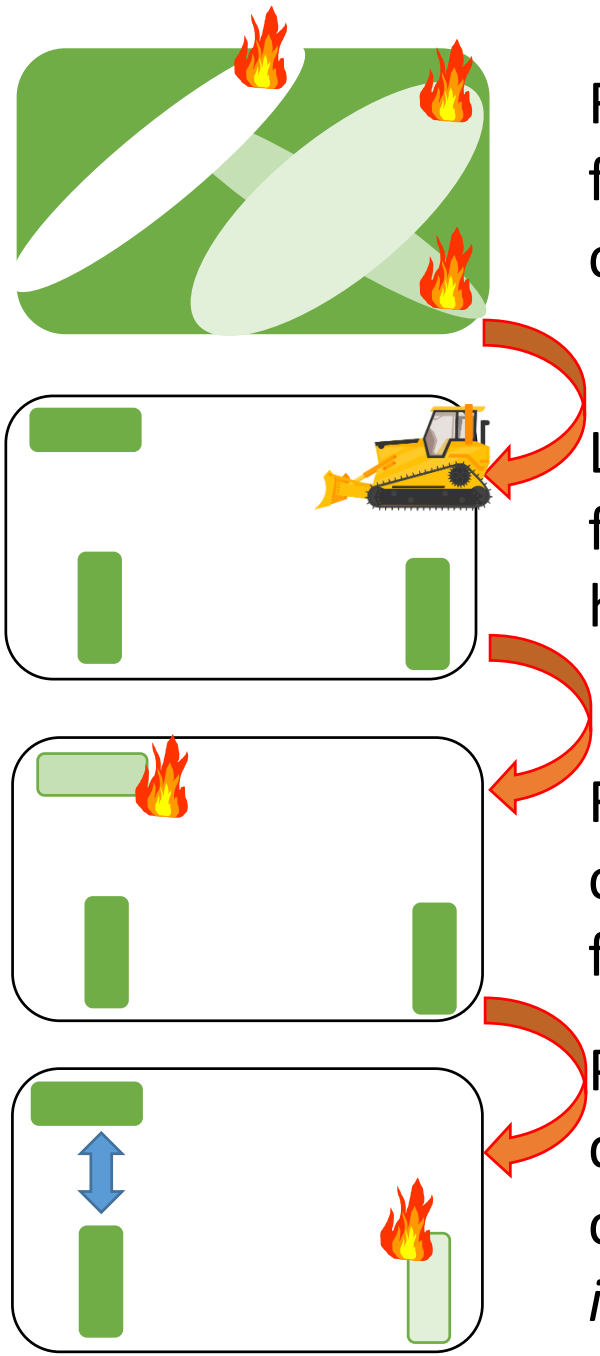
Fire fragments ecosystem

Promoting more fire

With more ecosystem loss

Potential for ecosystem transformation

(B) Transition from ‘fire influences fragmentation’ to ‘fire and fragmentation do not influence each other’



Fire causes fragmentation in continuous habitat

Land clearing fragments habitat

Fire changes patch condition but not fragmentation

Persistence depends on colonisation and *in-situ* survival in novel landscape