Integrating functional connectivity and fire management for better conservation outcomes

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Land managers may conserve populations by using fire to sustain or enhance functional connectivity.

Abstract

Globally, the mean abundance of terrestrial animals has fallen by 50% since 1970, and populations face ongoing threats associated with habitat loss, fragmentation, climate change and disturbance. Climate change can influence the quality of remaining habitat directly, and indirectly by precipitating increases in the extent, frequency and severity of natural disturbances such as fire. Species are confronted with the combined threats of habitat clearance, changing climates and altered disturbance regimes, each of which may interact and have cascading impacts on animal populations. Typically, conservation agencies are limited in their capacity to mitigate rates of habitat clearance, fragmentation or climate change, yet fire management is increasingly used worldwide to reduce wildfire risk and achieve conservation outcomes. A popular approach to ecological fire management involves the creation of fire mosaics to promote animal diversity; however, this strategy has two fundamental limitations: (1) the effect of fire on animal movement within or among habitat patches is not considered; and (2) the implications of the current fire regime for long term population persistence are overlooked. Spatial and temporal patterns in fire history can influence animal movement, which is essential to the survival of individual animals, the maintenance of genetic diversity, and the persistence of populations, species and ecosystems. We argue that there is rich potential for fire managers to manipulate animal movement patterns, enhance functional connectivity, gene flow and genetic diversity, and increase the capacity of populations to persist under shifting environmental conditions. We describe a suite of recent methodological advances,

including spatio-temporal connectivity modeling, spatially-explicit individual-based simulation, and fire-regime modeling, and explain how these tools can be integrated to achieve better outcomes for biodiversity in human-modified, fire-prone landscapes.

Why factor animal movement into fire management?

Movement of individuals and their genes at multiple scales may allow populations to withstand disturbances, which affects the capacity of whole biomes to persist under changing climates (Banks et al. 2013; Moen et al. 2014; Doherty & Driscoll 2018; Nimmo et al. 2019). Genetic diversity is a fundamental aspect of biodiversity because it influences individual fitness, population viability and the capacity of species to adapt to environmental change (Hughes et al. 2008). Genetic diversity, including the presence of rare alleles (forms of a gene), underpins resilience because genes are at the foundation of biological function and response.

Levels of genetic diversity, and rates of individual and genetic interchange, are a function of dispersal capacities, movement choices, and landscape structure (Mandelik et al. 2003), which collectively influence functional connectivity: the degree to which the landscape facilitates or impedes movement (Taylor et al. 1993; Baguette et al. 2013). In fire-prone regions, functional connectivity may also be influenced by the spatial and temporal arrangement of the fire regime, which is defined by fire intensity, frequency and seasonality (Gill 1975; Bradstock et al. 2005).

Fire regimes can be described in terms of the visible mosaic, which is the patchwork of vegetation growth stages in a landscape at a point in time, and the invisible mosaic, which reflects fire frequency (Bradstock et al. 2005). The visible mosaic of vegetation growth stages results from the resetting (or partial resetting, if fire intensity is low) of the successional process in time and space (Kleyer et al. 2007). Growth stage (or time since fire) is a popular fire-regime variable because it is relatively easy to measure and manipulate (Di Stefano et al. 2013; Kelly et al. 2015; Mutz et al. 2017). Species may select different growth stages to meet their resource requirements (e.g. Pons et al. 2012; Swan et al. 2015), thus to persist in fire-prone landscapes, animals must be able to locate their preferred habitat as the arrangement of growth stages changes through time and space (Bowler & Benton 2005; Pereoglou et al. 2013).

While studies of relationships between animal occurrence or abundance and growth stage or time since fire are quite common, differences in rates of animal movement along successional gradients have rarely been investigated (Table 1). The handful of studies that report responses of animal movement to growth stage or time since fire indicate that movement rates can be influenced by differences in vegetation structure among growth stages, implying that a growth stage could represent a source of fragmentation in continuous habitat (Table 1; Templeton et al. 2011). For example, Neuwald & Templeton (2013) measured the influence of fire suppression on the eastern collared lizard (*Crotaphytus collaris collaris*), and found that ten years of fire suppression in the woodland resulted in a dispersal barrier, leading to local extinction. Subsequently, prescribed burning over a 12-year period facilitated colonization of unoccupied glades, increasing genetic diversity and resulting in a stable metapopulation (Neuwald & Templeton 2013). Understanding how growth stages or other fire-regime variables influence movement is a crucial knowledge gap because it has implications for the capacity of species to maintain functional connectivity and genetic diversity, and thereby reduce the risk of local extinction. Studies linking fire regimes with population viability are scarce; however, Potvin et al. (2017) used population modeling to show that frequent fire increased extinction risk in amphibian populations because fire reduced functional connectivity.

The influences of fire regimes on animal movement are likely to be affected by other aspects of landscape structure such as the spatial arrangement of habitat in a fragmented landscape, but the combined influences of fire and fragmentation on functional connectivity are have rarely been studied (but see Tulloch et al. 2016; Scroggie et al. 2019). Theoretical studies demonstrate that patch occupancy in fragmented landscapes is influenced by four parameters: colonization rate, extinction rate, disturbance frequency and the rate of succession (Amarasekare & Possingham 2001). The challenge facing managers of flammable ecosystems is to design fire regimes that allow all species in habitat patches to become established, reproduce and disperse (Amarasekare & Possingham 2001; del Castillo 2015; Tulloch et al. 2016). We suggest that managing fire to enhance functional connectivity could present an effective means of promoting population persistence for multiple species in the absence of detailed demographic data.

We follow Fahrig's (2007) definition of landscapes as spatially heterogeneous areas where the degree of heterogeneity is species-specific (Figure 1). In human-modified landscapes, the level of heterogeneity is influenced by human activity. In many cases, landscape structure (the composition and configuration of land-cover types) reflects human activities that result in fragmentation and habitat loss, and we define fragmented landscapes as those where 10-90% of natural habitat remains (McIntyre & Hobbs 1999). Our ideas apply to fragmented landscapes where fire is used as a management tool (Figure 1), as well as largely intact forest landscapes where fire management is applied. We limit our scope to the influence of landscape structure on animal functional connectivity in the context of longer-term successional changes occurring over years to centuries.

In this essay, our main objectives are to (1) identify empirical approaches and simulation tools that could be used to estimate the influence of fire regimes on functional connectivity, and (2) outline how land managers could use fire to alter functional connectivity for conservation gains. We begin by discussing the importance of placing fire regimes in the context of human-modified landscapes, where the fire regime is embedded in a matrix of land uses, and functional connectivity may be influenced by multiple elements of landscape structure.

Fire management in human-modified landscapes

Human-modified landscapes pose a challenge to fire managers because the fire regime is embedded in a patchwork of land uses and tenures. The extent of intact forest landscapes (defined by a minimum area of 500 km^2) has been reduced by 919,000 km^2 worldwide since 2000, and 77% of the global forest area is currently considered fragmented (Potapov et al. 2017). Through the lens of island biogeography, fragmented landscapes are viewed as dichotomies of habitat patch "islands" surrounded by a static and inhospitable "ocean" or matrix of other land-cover types (MacArthur & Wilson 1967; Levins 1970). A paradigm shift recognizes the habitat islands and matrix as points along a continuum of habitat alteration (McIntyre & Hobbs 1999). The matrix may influence population persistence through its effects on movement and dispersal; for example, replacement of pasture with pine (*Pinus radiata*) plantations promoted habitat patch colonization by forest bird species (Lindenmayer et al. 2008). Furthermore, processes such as fire, and temporal flux in the matrix, are regarded as integral to landscape structure in human-modified landscapes (Driscoll et al. 2013; del Castillo 2015). Fifty percent of terrestrial ecosystems are fire prone (Shlisky et al. 2007) and most are influenced by human activity (Potapov et al. 2017), yet species responses to spatial discontinuities in their habitat are rarely considered in fire management (Gillson et al. 2019).

Currently, species preferences for different growth stages often form the basis of ecological fire management. For example, the proportions of growth stages that maximize a species diversity index can be defined by applying numerical optimization to data describing the abundance of species in different growth stages (Di Stefano et al. 2013; Kelly et al. 2015). This method has gained traction because of its strong theoretical basis and practical benefits – input data are obtained via standard ecological survey methods, and outputs provide an operational target for practitioners that reflects the needs of multiple species (McCarthy et al. 2014). Crucially, however, this and other common approaches to ecological fire management do not account for the influence of fire on animal movement within or among growth stages and habitat patches in human-modified landscapes. Understanding how fire influences both habitat suitability and connectivity will help managers maintain a range of growth stages that suit the requirements of multiple species, as well as a network of habitat patches that permits the movement of individuals and genes.

Linking functional connectivity and fire management

Successful biodiversity conservation in flammable, human-modified landscapes requires a shift in the focus of research and management from patterns in species' occurrence or abundance to the underlying ecological and evolutionary processes (Driscoll et al. 2010; Nimmo et al. 2019). Factoring animal movement into fire management requires mapping functional connectivity for individual species or species groups. Connectivity maps require two main inputs: (1) a resistance (or cost) surface that reflects resistance to movement of different elements of landscape structure and (2) a connectivity algorithm such as cost distance (Dijkstra 1959), implemented in the R package gdistance (van Etten 2017; R Core Team 2019), or circuit theory (McRae et al. 2008), applied in the software Circuitscape (Figure 2). Resistance surfaces can be derived from genetic data or any data source that reflects habitat suitability among land-cover types such as growth stages, paddocks or plantation forestry (Figure 1). The simplest assumption is that resistance is the linear negative inverse of habitat suitability; however, alternative transformations may be more appropriate if dispersing individuals tolerate habitat that they would not normally occupy, or competitors impede movement through high-quality habitat (Pavlacky et al. 2009; Zeller et al. 2018). The influence of fire-regime variables on resistance may be subtle relative to more static components of landscape structure, and we recommend using genetic data in connectivity mapping where possible; reductions in functional connectivity associated with fire have been identified in genetic data without a detectable reduction in animal abundance (Potvin et al. 2017). Although genetic data or GPS (Global Positioning System) telemetry data will generally yield better estimates of functional connectivity, opportunistic presence-only data or presence-absence data may contribute to reasonable estimates of resistance (Zeller et al. 2018).

The performance of connectivity algorithms and metrics is a function of data type, and there is no single best approach to quantifying functional connectivity (Kindlmann & Burel 2008; Zeller et al. 2018). Cost distance algorithms minimize the cumulative cost between two points on a resistance surface, but assume animals base movement decisions on perfect knowledge of the landscape (Adriaensen et al. 2003); in contrast, current flow models based on circuit theory assume no knowledge of the landscape beyond one step ahead (McRae et al. 2008). Available metrics include current density, which represents net movement probabilities of random walkers through an individual grid cell, and effective resistance, which provides a pairwise distance-based metric of isolation among sites or populations (McRae et al. 2008). Habitats are often delineated as discrete patches, and connectivity measures reflect emigration and immigration between patches; however, measurement of within-patch connectivity is crucial in disturbance-prone systems (Spanowicz & Jaeger 2019). High performance computing now permits application of connectivity algorithms to large datasets at fine resolutions (Leonard et al. 2016), and concurrent innovations in data visualization tools help to present dynamic connectivity maps effectively (Dickson et al. 2018).

In conjunction with established connectivity mapping tools such as gdistance and Circuitscape, increasingly sophisticated statistical techniques can distinguish the influences of interacting landscape-structure variables on functional connectivity (e.g. Phillipsen et al. 2015). For example, mixed-effects models account for nonindependence in spatial data, and can be applied to relationships between functional connectivity and landscape features in the R statistical environment using the package ResistanceGA (Clarke et al. 2002; Peterman 2018). New statistical tools that accommodate the complexity of real-world landscapes will enhance the precision of connectivity models.

Connectivity metrics and maps form a strong basis for conservation action by identifying land-cover types or corridors which are particularly important to population persistence; however, most applications in terrestrial ecosystems assume a static landscape (but see Martensen et al. 2017; Bishop-Taylor et al. 2018), which is particularly problematic in fire-prone systems where landscape structure is a function of the fire regime. Incorporation of temporal change into connectivity models is a fruitful area for development. For example, Martensen et al. (2017) developed a network-based model of landscape dynamics using bird and mammal data collected in fragmented landscapes in the Atlantic Forest of Brazil, and parameterized the model using dispersal distances. When spatio-temporal links (occurring where habitat patches form temporary stepping stones) were included, functional connectivity was on average 30% higher than connectivity associated with purely spatial models. The extent to which these results may translate to fire-prone landscapes is unclear, and there is an urgent need to quantify the response of connectivity to fire-regime variables through time.

Simulation allows inference in the face of real-world constraints

Efforts to empirically quantify animal responses to interactions between landscape structure and fire regimes are hampered by the need for landscapes containing covarying gradients in habitat amount, configuration and matrix permeability. Additionally, fire-regime variables must vary systematically along landscape-structure gradients. Powerful individual-based simulation methods offer capacity to overcome limitations encountered by empirical researchers (e.g. HexSim; Schumaker & Brookes 2018) (Figure 2). Flexible simulation-based approaches allow exploration of multiple interacting factors over large spatial and temporal scales and eliminate the need for study landscapes that feature covarying gradients in multiple factors (Davies et al. 2016; Banks et al. 2017). Further, when combined with empirical research, simulation provides an effective means of separating the influences of habitat-mediated dispersal and population density on genetic diversity (Smith et al. 2016). We emphasize that empirical research is crucial for parameterizing simulation models and validating their outputs. Together, empirical and simulation approaches are poised to provide new insights into the influence of current fire management practices on functional connectivity and population viability.

Using fire simulation to guide conservation action

Coupling a spatially and temporally explicit fire-regime simulator (e.g. FIRESCAPE (Cary & Banks 2000) or FROST (Penman et al. 2015a)) with empirical research and/or individual-based simulation will highlight the consequences of current management actions for future functional connectivity (Banks et al. 2017). Fire-regime simulation has practical applications at the scales of both individual fire events and fire regimes (Figure 2). At the scale of individual fire events, fire simulation may assist decision-making by allowing managers to quantify and compare the influence of fire events on connectivity. For example, a planned fire in one location may have a greater positive influence on functional connectivity than another fire of similar size if the spatial configuration or surrounding landscape structure differs. “Pinch points” act as bottlenecks to movement if a lack of alternative paths exists nearby (McRae et al. 2008; Figure 1); planned fire or fire suppression at pinch points may have a disproportionate impact on connectivity for some species. If connectivity models include fire regime variables such as severity or seasonality, it will be possible for managers to compare the influences of these factors on functional connectivity at small scales and adjust management operations accordingly.

At larger spatial scales, fire simulators may provide insight into the consequences of alternative fire regimes for functional connectivity and population persistence over decades to centuries. Innovative fire-regime simulation tools such as FROST (Fire Regime and Operation Simulation Tool) allow comparison of risks posed to houses, water, carbon and ecological assets at successive timesteps (Penman et al. 2015a). In this context, risk is defined as the product of the probability of fire and the expected fire damage (Hardy 2005). FROST builds on the fire behavior simulator Phoenix RapidFire (Tolhurst et al. 2008) and is parameterized using fuel loads, topography and weather to quantify risk given alternative fire-management scenarios and stochastic wildfire. It uses Bayesian Networks to capture uncertainty associated with risk estimates and generates realistic simulations by incorporating dynamic interactions between previous fires to determine subsequent fire intensity. Fire-regime simulation tools will allow measurement of functional connectivity responses to planned-fire scenarios where the percent of total habitat burnt per year is varied; for example, in south east Australia, plausible planned fire treatments range from 1.5-5% of total habitat burnt per year (Connell et al. 2019).

Climate change has potential to alter fire regimes worldwide (Abatzoglou et al. 2018), and simulation tools can help to identify the consequences of changing climates for future fire, species distributions and connectivity. Climate influences fire through two key processes: first, low precipitation reduces fuel moisture and increases the likelihood of ignitions; and second, high precipitation increases vegetation biomass, which increases the likelihood of both ignition and fire spread (Westerling et al. 2002). Interactions among climate, fire and vegetation dynamics are difficult to disentangle, and most research to date has investigated the effects of weather on fire events (Abatzoglou & Williams 2016). High temperatures, low humidity and high wind speed define severe fire weather, which is expected to occur more frequently in many regions, although the magnitudes of predicted changes are strongly context-dependent (Pausas 2004; Keeley & Syphard 2016).

Fire-regime simulation tools offer a means of understanding the interdependencies among climate, vegetation biomass and fire, as well as testing the sensitivity of animal responses (Penman et al. 2015a). To date, the influences of alternative fire regimes and climate-change scenarios on species distributions have been considered separately (Sirami et al. 2017), or the combined influences of fire and climate have been represented aspatially such that the likelihood of a fire occurring in one cell is not influenced by fire in neighboring cells (Penman et al. 2015b). Fire-regime simulation tools that include planned burning and stochastic wildfire under alternative climate scenarios will highlight the role fire managers may play in sustaining connectivity and mitigating extinction risk (Figure 2).

Research challenges

We identify four important challenges for future research. First, the interplay between species' generation times and rates of temporal flux in landscape structure are likely to have complex ecological ramifications. Individual-based simulation offers a platform for examining how functional connectivity is influenced by species' traits, such as generation time and average dispersal distance, and may lend further realism by accommodating competitive interactions and predation (Schumaker & Brookes 2018).

Second, we advocate a multi-species approach to fire management in human-modified landscapes, while recognizing that prioritization of species or species groups is often essential. Initially, integration of functional connectivity and fire management should focus on species with distinct growth-stage preferences, as well as less mobile species, such as flightless beetles or small mammals. In theory, less mobile species are less resilient to environmental change if they are unable to recolonize following local extinction (Hanski & Thomas 1994). However, this assumption does not necessarily hold if mortality rates are elevated in mobile species through greater exposure to human-dominated land-cover types (Fahrig 2007). Information on the structure of the landscape where the species evolved may prove useful where empirical data on movement and mortality are lacking (Ceia-Hasse et al. 2018). We emphasize that our proposed framework applies to any taxonomic group whose movement capacity may be influenced by landscape structure and fire; for example, plants may feature among priority species in some systems (Pérez-Méndez et al. 2018).

Third, fire management planning is currently undertaken in many regions (e.g. Penman et al. 2011; Fernandes et al. 2013; Kobziar et al. 2015), providing scope for managers to use fire to enhance functional connectivity. However, we acknowledge major changes in fire regimes expected due to global warming (Abatzoglou et al. 2018) may render conservation interventions impractical in some contexts. For example, increasingly frequent wildfires may shift the focus from long-term planning to emergency response, reducing the capacity of land management agencies to use fire to achieve conservation objectives.

Finally, we operate in a socio-ecological system where the risk of land management actions to ecological assets must be traded off against their effects on other values. In this context, mitigating the risk of fire management to connectivity will be an ongoing challenge. Currently, the prevailing purpose of fire management globally is mitigation of wildfire risk to human life and assets, and the protection of natural resources, including biodiversity, is usually secondary (Penman et al. 2011; Fernandes et al. 2013). While protection of people and property will always take precedence, public understanding of the ecological role of fire is increasing, and there is growing political will to invest in ecologically-sensitive fire management (DellaSala & Hanson 2015; DELWP 2015). Fire-regime simulation tools will help managers design fire regimes that minimize risk to both human and ecological assets (Penman et al. 2015a). Amid public concern about the dangers presented by large wildfires, policy makers should pursue strategies that protect people and property while avoiding actions that may detrimentally impact biodiversity (DellaSala & Hanson 2015). Where wildfire risk to humans is low, greater focus may be placed on promotion of functional connectivity.

Conclusions

We argue that a shift in the focus of fire management from patterns in species occurrence and abundance to underlying processes is timely given rapidly accelerating rates of climate change (Bevis et al. 2019). A focus on sustaining functional connectivity should enhance population persistence without a need for detailed demographic data, though we recommend building connectivity models from genetic data where possible because patterns in genetic diversity can reveal reduced dispersal rates long before declines in animal abundance are evident (Potvin et al. 2017). Integration of empirical research, individual-based simulation and fire-regime simulation will help identify land management strategies that ultimately yield better conservation outcomes under changing climates.

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Literature cited

Abatzoglou JT, Williams AP. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences **113**:11770–11775. Available from http://www.pnas.org/lookup/doi/10.1073/pnas.1607171113.

Abatzoglou JT, Williams AP, Boschetti L, Zubkova M, Kolden CA. 2018. Global patterns of interannual climate–fire relationships. Global Change Biology **24**:5164–5175.

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E. 2003. The application of "least-cost" modelling as a functional landscape model. Landscape and Urban Planning **64**:233–247.

Amarasekare P, Possingham H. 2001. Patch dynamics and metapopulation theory: The case of successional species. Journal of Theoretical Biology **209**:333–344.

Baguette M, Blanchet S, Legrand D, Stevens VM, Turlure C. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews **88**:310–326.

Banks SC, Cary GJ, Smith AL, Davies ID, Driscoll DA, Gill AM, Lindenmayer DB, Peakall R. 2013. How does ecological disturbance influence genetic diversity? Trends in Ecology & Evolution **28**:670–679.

Banks SC, Davies ID, Cary GJ. 2017. When can refuges mediate the genetic effects of fire regimes? A simulation study of the effects of topography and weather on neutral and adaptive genetic diversity in fire-prone landscapes. Molecular Ecology **26**:4935–4954.

Banks SC, Lorin T, Shaw RE, McBurney L, Blair D, Blyton MDJ, Smith AL, Pierson JC, Lindenmayer DB. 2015. Fine-scale refuges can buffer demographic and genetic processes against short-term climatic variation and disturbance: A 22-year case study of an arboreal marsupial. Molecular Ecology **24**:3831–3845.

Bevis M et al. 2019. Accelerating changes in ice mass within Greenland, and the ice sheet's sensitivity to atmospheric forcing. Proceedings of the National Academy of Sciences **116**:1934–1939.

Bishop-Taylor R, Tulbure MG, Broich M. 2018. Evaluating static and dynamic landscape connectivity modelling using a 25-year remote sensing time series. Landscape Ecology **33**:625–640. Springer Netherlands. Available from https://doi.org/10.1007/s10980-018-0624-1.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews **80**:205–225.

Bradstock RA, Bedward M, Gill AM, Cohn JS. 2005. Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. Wildlife Research **32**:409–423.

Cary GJ, Banks JCG. 2000. Fire regime sensitivity to global climate change: An Australian perspective.

Pages 233–246 in J. L. Innes, M. Beniston, and M. M. Verstraete, editors. Biomass Burning and Its Inter-Relationships with the Climate System. Springer, Dordrecht.

Ceia-Hasse A, Navarro LM, Borda-de-Água L, Pereira HM. 2018. Population persistence in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of dispersal. Ecological Modelling **375**:45–53.

Clarke RT, Rothery P, Raybould AF. 2002. Confidence limits for regression relationships between distance matrices: Estimating gene flow with distance. Journal of Agricultural, Biological, and Environmental Statistics **7**:361–372.

Connell J, Watson SJ, Taylor RS, Avitabile SC, Schedvin N, Schneider K, Clarke MF. 2019. Future fire scenarios: Predicting the effect of fire management strategies on the trajectory of high-quality habitat for threatened species. Biological Conservation **232**:131–141. Elsevier. Available from https://linkinghub.elsevier.com/retrieve/pii/S0006320718308206.

Davies ID, Cary GJ, Landguth EL, Lindenmayer DB, Banks SC. 2016. Implications of recurrent disturbance for genetic diversity. Ecology and Evolution **6**:1181–1196.

del Castillo RF. 2015. A conceptual framework to describe the ecology of fragmented landscapes and implications for conservation and management. Ecological Applications **25**:1447–1455.

DellaSala DA, Hanson CT. 2015. The Ecological Importance of Mixed Severity Fires Nature’s Phoenix. Elsevier.

DELWP. 2015. DELWP Policy Position – Measuring ecosystem resilience in strategic bushfire management planning:1–5. Victorian Department of Environment, Land, Water and Planning. Melbourne, Australia.

Di Stefano J, McCarthy MA, York A, Duff TJ, Slingo J, Christie FJ. 2013. Defining vegetation age class distributions for multispecies conservation in fire-prone landscapes. Biological Conservation **166**:111–117. Elsevier Ltd. Available from http://linkinghub.elsevier.com/retrieve/pii/S0006320713002048.

Dickson BG et al. 2018. Circuit-theory applications to connectivity science and conservation. Conservation Biology **0**:1–11. Available from http://doi.wiley.com/10.1111/cobi.13230.

Dickson BG, Roemer GW, McRae BH, Rundall JM. 2013. Models of regional habitat quality and connectivity for pumas (*Puma concolor*) in the Southwestern United States. PLoS ONE **8**:1–12.

Dijkstra EW. 1959. A Note on Two Problems in Connexion with Graphs. Numerische Mathematik **1**:269–271.

Doherty TS, Driscoll DA. 2018. Coupling movement and landscape ecology for animal conservation in production landscapes. Proceedings of the Royal Society B: Biological Sciences **285**:20172272. Available from http://rspb.royalsocietypublishing.org/lookup/doi/10.1098/rspb.2017.2272.

Driscoll DA et al. 2010. Fire management for biodiversity conservation: Key research questions and our capacity to answer them. Biological Conservation **143**:1928–1939.

Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology & Evolution **28**:605–613. Elsevier Ltd. Available from http://dx.doi.org/10.1016/j.tree.2013.06.010.

Fahrig L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology **21**:1003–1015.

Fernandes PM et al. 2013. Prescribed burning in southern Europe: Developing fire management in a dynamic landscape. Frontiers in Ecology and the Environment **11**:e4--e14.

Ferreira D, Pinho C, Brito JC, Santos X. 2019. Increase of genetic diversity indicates ecological opportunities in recurrent-fire landscapes for wall lizards. Scientific Reports **9**:1–11.

Fordyce A, Hradsky BA, Ritchie EG, Di Stefano J. 2015. Fire affects microhabitat selection, movement patterns, and body condition of an Australian rodent (*Rattus fuscipes*). Journal of Mammalogy **97**:102–111. Available from http://jmammal.oxfordjournals.org/lookup/doi/10.1093/jmammal/gyv159.

Gill A. 1975. Fire and the Australian Flora: A Review. Australian Forestry **38**:4–25.

Gillson L, Whitlock C, Humphrey G. 2019. Resilience and fire management in the Anthropocene. Ecology and Society **24**:14.

Hanski I, Thomas C. 1994. Metapopulation dynamics and conservation: a spatially explicity model applied to butterflies. Biological Conservation **68**:167–180.

Hardy CC. 2005. Wildland fire hazard and risk: Problems, definitions, and context. Forest Ecology and Management **211**:73–82.

Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M. 2008. Ecological consequences of genetic diversity. Ecology Letters **11**:609–623.

Keeley J, Syphard A. 2016. Climate Change and Future Fire Regimes: Examples from California. Geosciences **6**:37. Available from http://www.mdpi.com/2076-3263/6/3/37.

Kelly LT, Bennett AF, Clarke MF, McCarthy MA. 2015. Optimal fire histories for biodiversity conservation. Conservation Biology **29**:473–481.

Kindlmann P, Burel F. 2008. Connectivity measures: A review. Landscape Ecology **23**:879–890.

Kleyer M, Biedermann R, Henle K, Obermaier E, Poethke HJ, Poschlod P, Schroder B, Settele J, Vetterlein D. 2007. Mosaic cycles in agricultural landscapes of Northwest Europe. Basic and Applied Ecology **8**:295–309.

Kobziar LN, Godwin D, Taylor L, Watts AC. 2015. Perspectives on trends, effectiveness, and impediments to prescribed burning in the southern U.S. Forests **6**:561–580.

Kozakiewicz CP, Carver S, Austin JJ, Shephard JM, Burridge CP. 2017. Intrinsic factors drive spatial genetic variation in a highly vagile species, the wedge-tailed eagle *Aquila audax*, in Tasmania. Journal of Avian Biology **48**:1025–1034.

Leonard PB, Duffy EB, Baldwin RF, McRae BH, Shah VB, Mohapatra TK. 2016. Gflow: Software for Modelling Circuit Theory-Based Connectivity At Any Scale. Methods in Ecology and Evolution:n/a--n/a. Available from http://dx.doi.org/10.1111/2041-210X.12689.

Levins R. 1970. Extinction. Providence, RI, USA.

Lindenmayer DB, Cunningham RB, MacGregor C, Crane M, Michael D, Fischer J, Montague-Drake R, Felton A, Manning A. 2008. Temporal changes in vertebrates during landscape transformation: A large-scale “natural experiment.” Ecological Monographs **78**:567–590.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Mandelik Y, Jones M, Dayan T. 2003. Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk. Evolutionary Ecology Research **5**:501–515.

Martensen AC, Saura S, Fortin MJ. 2017. Spatio-temporal connectivity: assessing the amount of reachable habitat in dynamic landscapes. Methods in Ecology and Evolution **8**:1253–1264.

McCarthy MA, Moore AL, Krauss J, Morgan JW, Clements CF. 2014. Linking Indices for Biodiversity Monitoring to Extinction Risk Theory. Conservation Biology **28**:1575–1583.

McIntyre S, Hobbs R. 1999. A framework for conceptualizing human effects on landscapes and its relevance fo management and research models. Conservation Biology **13**:1282–1292.

McRae BH, Dickson BG, Keitt TH, Shah VB. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology **89**:2712–2724.

Moen J et al. 2014. Eye on the Taiga: Removing Global Policy Impediments to Safeguard the Boreal Forest. Conservation Letters **7**:408–418.

Mutz J, Underwood N, Inouye BD. 2017. Time since disturbance affects colonization dynamics in a metapopulation. Journal of Animal Ecology **86**:1065–1073.

Neuwald JL, Templeton AR. 2013. Genetic restoration in the eastern collared lizard under prescribed woodland burning. Molecular Ecology **22**:3666–3679.

Nimmo DG et al. 2019. Animal movements in fire-prone landscapes. Biological Reviews **94**:981–998.

Pausas JG. 2004. Changes in fire and climate in the Eastern Iberian Peninsula (Mediterranean Basin). Climatic Change **63**:337–350.

Pavlacky DC, Goldizen AW, Prentis PJ, Nicholls JA, Lowe AJ. 2009. A landscape genetics approach for quantifying the relative influence of historic and contemporary habitat heterogeneity on the genetic connectivity of a rainforest bird. Molecular Ecology **18**:2945–2960. Available from http://doi.wiley.com/10.1111/j.1365-294X.2009.04226.x.

Penman T, Ababei D, Chong DMO, Duff T, Tolhurst KG. 2015a. A fire regime risk management tool. Pages 270–276 in J. J. Sharples, editor. 21st International Congress on Modelling and Simulation. Gold Coast, Australia.

Penman TD et al. 2011. Prescribed burning: how can it work to conserve the things we value? International Journal of Wildland Fire **20**:721–733.

Penman TD, Keith DA, Elith J, Mahony MJ, Tingley R, Baumgartner JB, Regan TJ. 2015b. Interactive effects of climate change and fire on metapopulation viability of a forest-dependent frog in south-eastern Australia. Biological Conservation **190**:142–153. Elsevier Ltd. Available from http://dx.doi.org/10.1016/j.biocon.2015.05.020.

Pereoglou F, Lindenmayer DB, MacGregor C, Ford F, Wood J, Banks SC. 2013. Landscape genetics of an early successional specialist in a disturbance-prone environment. Molecular Ecology **22**:1267–1281.

Pérez-Méndez N, Jordano P, Valido A. 2018. Persisting in defaunated landscapes: Reduced plant population connectivity after seed dispersal collapse. Journal of Ecology **106**:936–947.

Peterman WE. 2018. ResistanceGA: An R package for the optimization of resistance surfaces using genetic algorithms. Methods in Ecology and Evolution **9**:1638–1647.

Phillipsen IC, Kirk EH, Bogan MT, Mims MC, Olden JD, Lytle D a. 2015. Dispersal ability and habitat requirements determine landscape-level genetic patterns in desert aquatic insects. Molecular Ecology **24**:54–69. Available from http://www.ncbi.nlm.nih.gov/pubmed/25402260.

Pons P, Clavero M, Bas JM, Prodon R. 2012. Time-window of occurrence and vegetation cover preferences of Dartford and Sardinian Warblers after fire. Journal of Ornithology **153**:921–930.

Potapov P et al. 2017. The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Science Advances **3**:e1600821.

Potvin DA, Parris KM, Smith Date KL, Keely CC, Bray RD, Hale J, Hunjan S, Austin JJ, Melville J. 2017. Genetic erosion and escalating extinction risk in frogs with increasing wildfire frequency. Journal of Applied Ecology **54**:945–954.

R Core Team. 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rickbeil GJM, Hermosilla T, Coops NC, White JC, Wulder MA. 2017. Barren-ground caribou (*Rangifer tarandus groenlandicus*) behaviour after recent fire events; integrating caribou telemetry data with Landsat fire detection techniques. Global Change Biology **23**:1036–1047.

Schrey AW, Fox AM, Mushinsky HR, McCoy ED. 2011. Fire increases variance in genetic characteristics of Florida Sand Skink (*Plestiodon reynoldsi*) local populations. Molecular Ecology

20:56–66.

Schumaker NH, Brookes A. 2018. HexSim: a modeling environment for ecology and conservation. Landscape Ecology **33**:197–211. Springer Netherlands. Available from https://doi.org/10.1007/s10980-017-0605-9.

Scroggie MP, Peterson GNL, Rohr DH, Nicholson E, Heard GW. 2019. Disturbance has benefits as well as costs for fragmented populations of a cryptic grassland reptile. Landscape Ecology **34**:1949–1965. Springer Netherlands. Available from https://doi.org/10.1007/s10980-019-00865-0.

Shlisky A et al. 2007. Fire, ecosystems and people: Threats and strategies for global biodiversity conservation. The Nature Conservancy, Arlington, VA.

Sirami C, Caplat P, Popy S, Clamens A, Arlettaz R, Jiguet F, Brotons L, Martin JL. 2017. Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. Global Ecology and Biogeography **26**:385–394.

Smith AL, Landguth EL, Bull CM, Banks SC, Gardner MG, Driscoll DA. 2016. Dispersal responses override density effects on genetic diversity during post-disturbance succession. Proceedings of the Royal Society B **283**:20152934. Available from http://rspb.royalsocietypublishing.org/content/283/1827/20152934?etoc.

Spanowicz AG, Jaeger JAG. 2019. Measuring landscape connectivity: On the importance of within-patch connectivity. Landscape Ecology **34**:2261–2278. Springer Netherlands. Available from https://doi.org/10.1007/s10980-019-00881-0.

Styger JK, Kirkpatrick JB, Marsden-Smedley JON, Leonard SWJ. 2011. Fire incidence, but not fire size, affects macropod densities. Austral Ecology **36**:679–686.

Swan M, Christie F, Sitters H, York A, Di Stefano J. 2015. Predicting faunal fire responses in heterogeneous landscapes: The role of habitat structure. Ecological Applications **25**:2293–2305.

Taylor PD, Fahrig L, Henein K, Merriam G. 1993. Connectivity is a vital element of landscape structure. Oikos **68**:571–573.

Templeton AR, Brazeal H, Neuwald JL. 2011. The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. Ecology **92**:1736–1747.

Tolhurst K, Shields B, Chong D. 2008. Phoenix: Development and Application of a Bushfire Risk Management Tool. The Australian Journal of Emergency Management **23**:47–54.

Tulloch AIT, Pichancourt JB, Gosper CR, Sanders A, Chadès I. 2016. Fire management strategies to maintain species population processes in a fragmented landscape of fire-interval extremes. Ecological Applications **26**:2175–2189.

van Etten J. 2017. R Package gdistance: Distances and Routes on Geographical Grids. Journal of

Statistical Software **76**. Available from http://www.jstatsoft.org/v76/i13/.

Westerling AL, Gershunov A, Cayan DR, Barnett TP. 2002. Long lead statistical forecasts of area burned in western U.S. wildfires by ecosystem province. International Journal of Wildland Fire **11**:257–266.

Zeller KA, Jennings MK, Vickers TW, Ernest HB, Cushman SA, Boyce WM. 2018. Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Diversity and Distributions **24**:868–879.

Table 1. Examples of empirical studies relating animal movement to the fire regime. Asterisks (*) denote studies that are directly relevant to our proposed framework because they focus on animal responses to longer-term successional changes occurring over years to centuries. Other studies examine changes in animal movement occurring immediately after fire, which normally results in sudden change in vegetation structure and animal mortality.

Reference	**Species and location**	**Response variable(s)**	**Fire-regime variable(s)**	**Results and conclusions**
Banks et al. (2015)	Mountain brushtail possum (*Trichosurus cunninghami*); Central Highlands of Victoria, southeast Australia.	Movement derived from mark-recapture data.	Burnt/unburnt over three durations (<1 year after fire, <2 years, <4 years).	Net movement was directional, from unburnt refuges to the burnt zone. Conserving unburnt refuges can mediate short-term effects of fire on demographic processes.
Ferreira et al. (2019)*	Wall lizard (*Podarcis guadarramae*); northern Portugal.	Genetic diversity	Burnt (2–8 fires between 1975 and 2013) or unburnt.	Greater genetic diversity in burnt than unburnt areas at the population level; weak genetic structure indicating no fire effect at the regional level. Recurrent fire gives ecological opportunities to lizards that benefit from open habitat.

Fordyce et al. (2015)	Bush rat (*Rattus fuscipes*); Otway Ranges, Victoria, southeast Australia.	Turning angles and step lengths derived from spool-and-line tracking devices.	Burnt/unburnt (before-after, control-impact design).	Movement pathways became more convoluted post-fire because animals used unburnt patches within the fire perimeter and turned sharply when encountering patch edges. Impacts of prescribed fire depend on the resulting mosaic of burnt and unburnt patches and how they correspond to species' resource requirements.
Neuwald & Templeton (2013)*****	Eastern collared lizard (*Crotaphytus collaris collaris*); Ozarks, Missouri, central USA.	Genetic diversity	Time since commencement of management action (10 years of fire suppression, followed by 12 years of prescribed fire)	Eastern collared lizards avoid dispersal through long-unburnt woodland; prescribed fire promotes connectivity.
Pavlacky et al. (2009)	Logrunner (*Orthonyx temminckii*); southeast Queensland, east Australia.	Genetic diversity	Historic landscape structure, in which wildfire was the dominant disturbance agent, versus contemporary landscape structure, involving deforestation and fire suppression.	Heterogeneous fire mosaics that maintained enclaves of rainforest may have facilitated dispersal across extensive areas of open forest and woodland. Contemporary deforestation was the most important barrier to dispersal.
Pereoglou et al. (2013)*****	Eastern chestnut mouse (*Pseudomys gracilicaudatus*); Booderee National Park, southeast Australia.	Genetic diversity	Burnt/unburnt	Recently burnt vegetation had greater conductance for gene flow than unburnt habitat. Variation in habitat quality between occupied patches did not affect gene flow.
Potvin et al. (2017)	Southern brown tree frog (*Litoria ewingii*), Victorian tree frog (*Litoria*	Genetic diversity	Before/after wildfire	Levels of inbreeding increased after wildfire, and effective population size declined. Fire managers should consider the timing

	paraewingi); Kinglake region of Victoria, southeast Australia.			of prescribed burns and maintenance of habitat connectivity.
Rickbeil et al. (2017)	Barren-ground caribou (*Rangifer tarandus groenlandicus*); North West Territories and Nunavut, Canada.	Movement velocity and turning angle derived from telemetry data	Time since fire, fire severity	Caribou used burnt areas as movement habitat rather than foraging habitat throughout the 26-year post-fire timeframe examined. Low severity fire resulted in a more rapid increase in foraging behaviour.
Schrey et al. (2011)*	Florida sand skink (*Plestiodon reynoldsi*); Florida Scrub, USA.	Genetic diversity	Three time-since-fire categories: long unburnt, intermediately burnt, recently burnt	Long unburnt sites had greater genetic diversity than intermediately or recently burnt sites. Infrequent fire may benefit skinks, and too-frequent fire may reduce genetic diversity.
Smith et al. (2016)*	Star knob-tailed gecko (*Nephrurus stellatus*); Eyre Peninsula, South Australia.	Genetic diversity	Time since fire, fire frequency	Vegetation succession (greater time since fire) increased resistance to gene flow and decreased dispersal and genetic diversity beyond the influence of changes in population density alone.

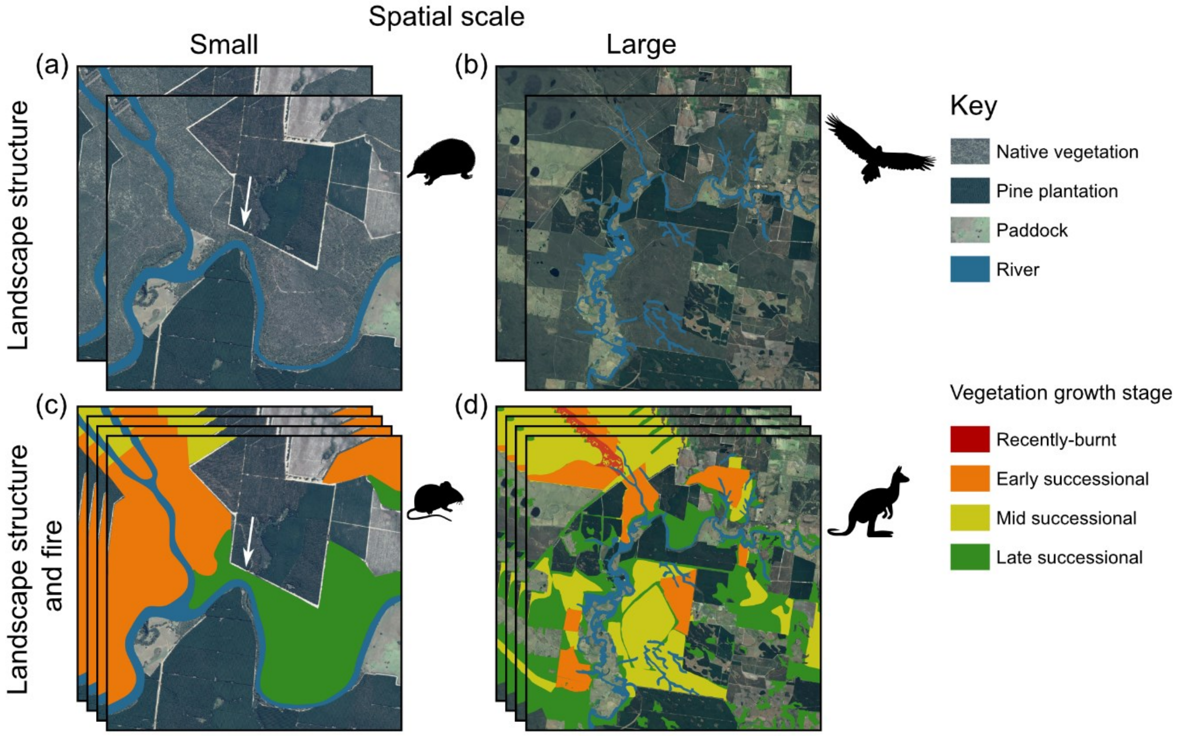

Figure 1. Landscape structure and fire in the Glenelg Region of southeast Australia. Landscape structure reflects the composition and configuration of land-cover types (a, b), and normally changes at a slower rate than the visible mosaic of vegetation growth stages associated with the fire regime (c, d). Species perceive landscape structure and fire at different spatial and temporal scales: for example: (a) Short-beaked Echidna (*Tachyglossus aculeatus*) responds to landscape structure at smaller spatial scales (Swan et al. 2015) and (b) Wedge-tailed Eagle (*Aquila audax*) responds at larger spatial scales (Kozakiewicz et al. 2017); (c) Eastern Chestnut Mouse (*Pseudomys gracilicaudatus*) responds to both landscape structure and fire at smaller spatial scales (Pereoglou et al. 2013), and (d) Eastern Grey Kangaroo (*Macropus giganteus*) responds at larger spatial scales (Styger et al. 2011). The narrow strip of native vegetation indicated by the white arrow represents a potential "pinch point", which may act as a bottleneck to movement if a lack of alternative pathways exists nearby (Dickson et al. 2013).

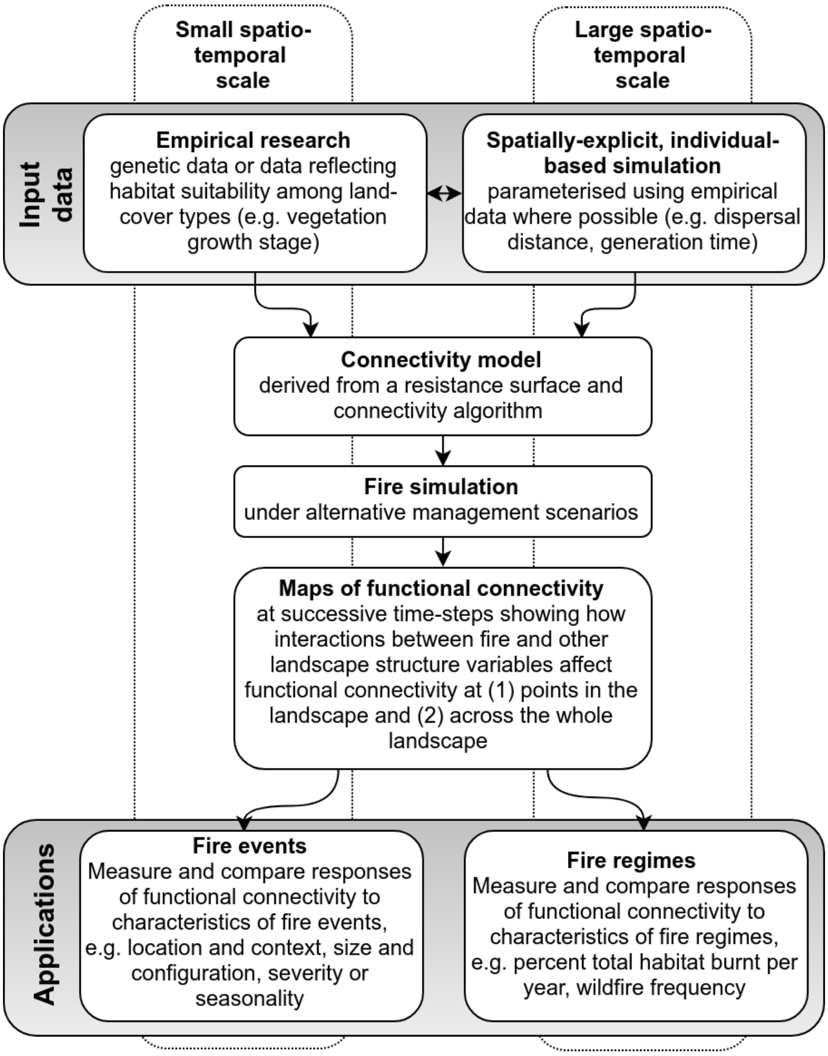

Figure 2. Linking empirical research, individual-based simulation and fire-regime simulation to promote functional connectivity in human-modified landscapes.

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