THESIS

Drivers of post-fire responses and ecological resilience in restored Banksia woodlands

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This thesis is presented for the degree of
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School of Environmental and Conservation Sciences

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Thesis Declaration

I, Ebony Cowan, verify that in submitting this thesis;

the thesis is my own account of the research conducted by me, except where other sources are fully acknowledged in the appropriate format,

the extent to which the work of others has been used is documented by a percent allocation of work and signed by myself and my Principal Supervisor,

the thesis contains as its main content work which has not been previously submitted for a degree at any university,

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Date: 20th October 2023

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Statement of contribution to thesis

In accordance with the Murdoch University Graduate Degrees Regulations, it is acknowledged that this thesis represents the work of the Candidate with contributions from their supervisors and, where indicated, collaborators. The Candidate is the majority contributor to this thesis with no less than 75% of the total work attributed to their efforts.

Candidate　　　　　　　　　Principal Supervisor

Statement of thesis structure

This thesis has been designed to present the data collected during the degree of Doctor of Philosophy as a coherent piece of work incorporating a series of stand-alone manuscripts. Therefore, there is some degree of inevitable overlap in chapters, particularly of some introductory material, and the descriptions of the study area, study design, and survey methods. Each manuscript was written according to the authorship guidelines of the journal that the manuscript has been accepted for publication, submitted for review, or will be submitted to in the future. A statement of author attribution precedes each manuscript. All chapters are presented in a similar format with continuous referencing and table and figure numbering to maintain the continuity of the document.

Abstract

In a time of global biodiversity loss, ecological resilience — an ecosystem's ability to return to its prior state following a disturbance — is crucial for restoration success in disturbance-prone regions. Despite this, responses of restored plant communities to disturbances remain uncertain across most ecosystems.

My thesis explores the drivers of post-fire responses of restored Banksia woodlands in southwestern Australia and implications for their resilience. Measurements spanned from individual plants to the entire community. Using a chronosequence of sites aged between three and 27 years since restoration after mining, I investigated the effects of restoration age and environmental factors relating to climate at establishment and soil conditions on soil seedbank development, resprouting and plant community responses to fire. I used these findings to assess the resilience of these restored sites to fire.

Across all restoration ages, resprouting and seedling establishment occurred following fire, but the development of these attributes varied among plant functional groups and, in some cases, restoration age. Annual species dominated the seedbank of younger restoration ages, while perennials dominated older ages. Drivers of resprouting success varied among species, and restoration age, plant size and soil conditions (e.g., compaction) poorly explained resprouting success. In most restoration ages, obligate seeders diversity, rarefied richness and functional redundancy did not change following fire, but resprouters diversity declined in age 14 suggesting lower levels of resilience to fire in this age. Change in restored sites following fire often did not reflect that of reference (i.e., intact, unmined) Banksia woodlands, and restored and reference Banksia woodlands differed in perennial and annual species composition and dominance.

Overall, these data suggest mixed responses of resprouter species and altered perennial community composition in restored Banksia woodlands impede resilience to fire, so further consideration of perennial vegetation development in fire-prone restoration sites is warranted.

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Chapter One

General Introduction

The importance of resilience in restoration projects

In a time of global biodiversity loss and land-use change, improving the state of damaged, degraded, and destroyed ecosystems via ecological restoration is critical (Gann et al., 2019). Indeed, the importance of successful ecological restoration has been recognized worldwide and seen the development of ambitious initiatives such as ‘The Bonn Challenge’, which aims to restore 350 million hectares of degraded land globally by 2030, and the United Nations declaring 2021–2030 as the decade of ecological restoration (United Nations 2019). Endeavours such as these highlight the need for successful ecological restoration projects that promote desirable biodiversity outcomes and persist long into the future.

Wild-type disturbances (as opposed to modern anthropogenic disturbances) such as fires, floods and periodic droughts have shaped the evolution of ecosystems and species regeneration globally (Turner et al., 2010; Keeley et al., 2011; Lamont and He 2017). Therefore, understanding the responses of restored ecosystems to disturbances characteristic of their historical disturbance regime is important for restoration success (Shackelford et al., 2013; Miller et al., 2017; Chapter 2). Resilience to disturbances is considered a desirable and necessary attribute of successful restoration projects (SER 2004; Gann et al., 2019; Young et al., 2019; Manero et al., 2020; Buisson et al., 2021; Young et al., 2022). However, despite advances in ecological knowledge and technical capacity to improve restoration outcomes (Perring et al., 2015; Price et al., 2022), knowledge of the responses of restoration projects to disturbances is lacking. Such knowledge is essential for biodiversity conservation and restoration success where disturbances influence ecosystem functioning and stability.

Ecological resilience to disturbances is a key driver of long-term restoration success (Standish et al., 2014; Miller et al., 2017; Young et al., 2022). While inconsistencies in the definition and usage of ecological resilience exist (Gunderson 2000; Myers-Smith et al., 2012), ecological resilience was originally defined by 'Buzz' Holling (1973) as the ability of an ecosystem to maintain a similar state following a disturbance, that is, retain species and ecosystem structure and function after a disturbance (Walker et al., 2004). While some scientists use a broader definition (i.e., one that includes social elements; Folke 2006; Biggs et al., 2012) ecologists tend to defer to the core attributes of Holling's definition (Myers-Smith et al., 2012; Standish et al., 2014). The quantification of resilience is challenging, primarily due to difficulty in operationalising the concept and the dynamic nature of ecosystems (Standish et al., 2014). Nonetheless, resilience is a key concept for evaluating ecosystem changes following disturbances. In a restored site, restoration is necessary to improve recovery following the primary disturbance that degraded a site (e.g., land clearing, weed invasion, mining). Following restoration, a secondary disturbance may follow, such as fire or flood. To understand resilience, it is important to compare restored sites to a control site (restored sites that have had the same primary disturbance but no secondary disturbance) or reference sites (intact sites that have not experienced the primary disturbance but may or may not have had the same secondary disturbance). Utilizing these comparisons can indicate restoration success, as responses of restored sites are evaluated relative to those of reference sites (Wortley et al., 2013; Miller et al., 2017; Gann et al., 2019; Harries et al., 2023).

Fire is a common disturbance in ecosystems across the globe. Many plant species have evolved adaptations to fire that promote their persistence or regeneration within these ecosystems (Keeley et al., 2011; Pausas and Keeley 2014). Many plant species survive fire and resprout from buds within existing plant material such as roots or stems (Clarke et al., 2013). These are described as resprouters. For other species, all individuals are killed by fire and populations regenerate following fire as seedlings from canopy or soil-stored seedbanks, the latter typically smoke and/or heat-responsive. These are described as obligate seeders (Pausas and Keeley 2014). Some species, termed facultative resprouters, can do both (Keeley et al., 2011; Clarke et al., 2015). An ecosystems fire regime describes parameters used to explain fire activity and potential responses to fire, and is comprised of elements including fire intensity and/or severity, spatial attributes, interval and season (Pausas and Keeley 2009; Keeley and Pausas 2022). Modifications to the fire regime (e.g., inappropriate timing, season, or severity of fire) can degrade reference ecosystem states and their associated functions (e.g., Enright et al., 2014; Turner et al., 2019; McColl-Gausden et al., 2022). The same may be true of restored ecosystem states but this is largely unknown. Indeed, how key fire-response mechanisms develop in restored sites and contribute to resilience is largely underexplored.

Time is necessary for restored ecosystems to reach their desired state (Hobbs and Norton 1996; Grant 2006; Crouzeilles et al., 2016), which may suggest that resilience (an emergent property) and associated factors such as plant fire response mechanisms will also develop with time (Figure 1.1). However, this assumption overlooks the uncertainty surrounding ecosystem development and the non-linear, dynamic pathways of ecosystems, where multiple states are possible with implications for resilience (Figure 1.1; Scheffer et al., 2001; Clements and Ozgul 2018). Additionally, legacy effects (from previous land use or restoration processes) may influence trajectories and resilience in restored sites (Foster et al., 2003; Hilderbrand et al., 2005; Crouzeilles et al., 2016). These factors may include changes in soil composition (Herath and Lamont, 2009; Bizuti et al., 2022; Zhu et al., 2022), alterations in plant communities and development pathways (Erskine and Fletcher 2013; Mounsey et al., 2021), and limitations in dispersal (Buisson et al., 2006; Standish et al., 2007). Climate conditions during the establishment of restoration projects may influence plant development and the potential resilience of an ecosystem (Mounsey et al., 2021; Riviera et al., 2021; Power et al., 2023). Consequently, these factors can change restoration trajectories and influence resilience: from desirable to undesirable resilience depending on the stable state that develops (Standish et al., 2014). Understanding the effects of such drivers on the resilience of restoration projects is key to promoting biodiversity and restoration success.

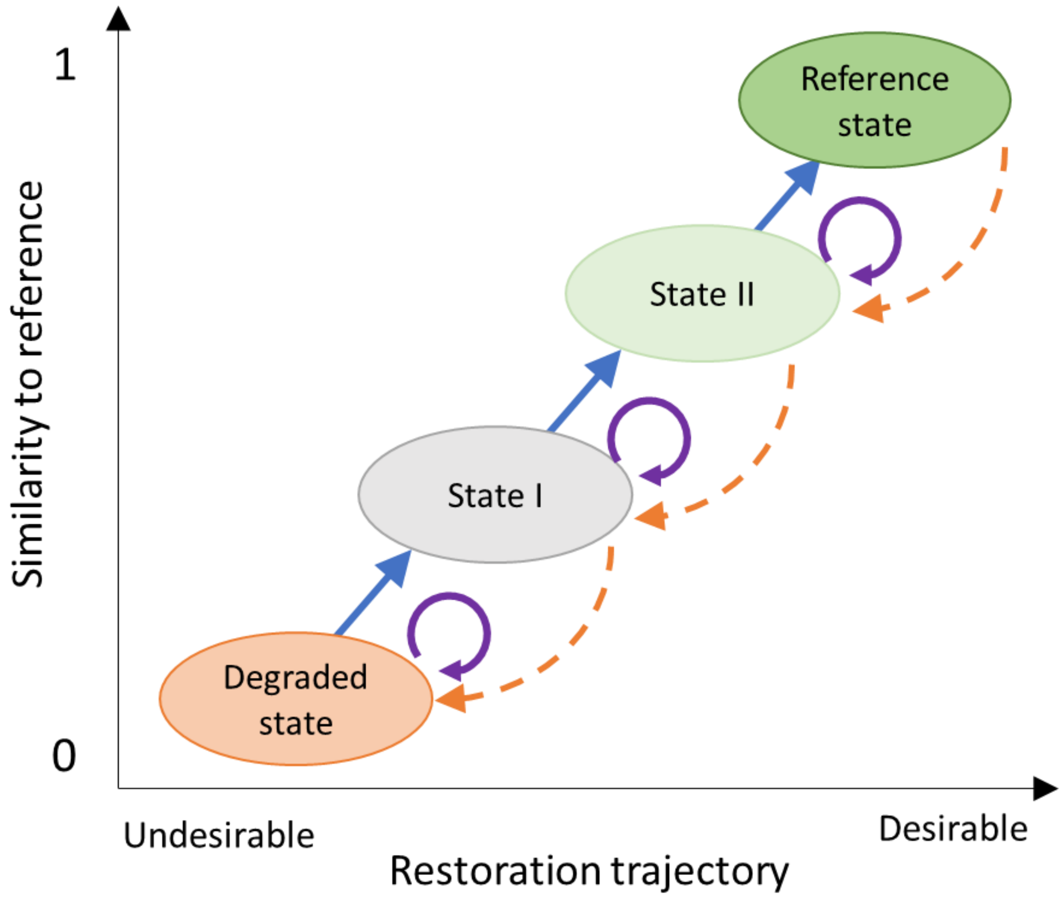


Figure 1.1: Conceptual diagram of how resilience to disturbances (e.g., fire) may develop in restoration projects. My research aims to assess which response (arrow type) occurs following disturbance in restored sites (States I and II), where restoration sites may increase in similarity to reference sites and move along a desirable restoration trajectory (blue arrows), or return to their pre-disturbance state, therefore demonstrating resilience (purple arrows). Or sites may undergo an undesirable transition (dashed orange arrows) towards a degraded state that is dissimilar to reference sites (not demonstrating resilience). I expect State I to be younger than State II as it develops earlier on the restoration trajectory and resilience may develop with time.

Resilience in post-mining restored ecosystems

My thesis aims to determine the drivers of plant community responses to fire in post-mining restored Banksia woodlands. Banksia woodlands occur in one of the world's five Mediterranean Climate Ecosystems, which are characterised by hot-dry summers and cool-wet winters (Cowling et al., 1996). They previously dominated part of the Southwest Australian Floristic Region, a global biodiversity hotspot characterized by a high number of endemic and threatened species (Myers et al., 2000; Ritchie et al., 2021). However, substantial habitat loss saw Banksia woodlands of the Swan Coastal Plain being listed as a Threatened Ecological Community in 2016 by the Australian Federal Government (Department of Environment and Energy 2016). Banksia woodlands are a highly diverse ecosystem (>600 plant species) comprising a rich sclerophyllous understory and 2–3 dominant *Banksia* species in the overstorey (Stevens et al., 2016; Ritchie et al., 2021). Many plant species are adapted to respond to fire through seeding and resprouting mechanisms (~27 & 77% of species respectively; Fontaine and Standish 2019). Historical fire intervals are poorly documented, but estimates suggest typical intervals may be between 8–16 years or longer, based on fuel accumulation patterns (Burrows and McCaw 1990; Tangney et al., 2022) and to ensure the persistence of slow-maturing taxa (Hobbs and Atkins 1990; Wilson et al., 2014; Valentine et al., 2014; Ritchie et al., 2021).

Successfully restoring ecosystems following mining is challenging and expensive (Lamb et al., 2015; Sonter et al., 2018; Young et al., 2023). Clearing of Banksia woodlands for mining has increased in recent decades (Ritchie et al., 2021). This has prompted research to improve restoration outcomes in restored Banksia woodlands (Rokich 2016; Stevens et al., 2016; Ritchie et al., 2021). For example, advances in overcoming seed dormancy (Roche et al., 1998), appropriate topsoil handling (Rokich et al., 2001a), promoting seed establishment (Waryszak et al., 2021; Brown et al., 2023), and understanding the drivers of plant (Svejcar 2020; Mounsey et al., 2021) and soil microbial community development (Hart et al., 2019) have assisted in improving restoration outcomes. However, responses to fire, a key driver of plant community development in Banksia woodlands (Hobbs and Atkins 1990; Wilson et al., 2014; Ritchie et al., 2021), has not been assessed.

Following mining, the ability of restored sites to demonstrate resilience to disturbances common to that ecosystem (e.g., fire in many Australian ecosystems) is widely recognized as an important aspect of successful mine closure and relinquishment, where post-mining restored land is handed back to a specified land user (commonly governments, Traditional Owners or private landholders; Department of Foreign Affairs and Trade 2016; Young et al., 2019; Manero et al., 2020). Indeed, “self-sustaining” is an important attribute of post-mining vegetation communities (Department of Foreign Affairs and Trade 2016; Young et al., 2019; Kragt and Manero 2021; Harries et al., 2023), which is considered a facet of resilience (E. Cowan, unpublished data, 2023). Therefore, being unable to demonstrate resilience to disturbances may prevent or prolong mine closure and relinquishment as regulators have little certainty that the restored ecosystems will “bounce back” from a disturbance and return to desirable composition and functioning. Instead, sites may shift to an alternative (potentially undesirable) state likely requiring ongoing management (Figure 1.1).

Thesis overview

To understand how the effects of disturbances in restored plant communities have previously been quantified, I conducted a literature review of studies that have assessed responses to wild-type disturbances in restored plant communities globally (Chapter 2; Figure 1.2). This review (published in *Restoration Ecology*) provided the opportunity to consider the best approaches to assessing responses to disturbances and resilience in restored ecosystems, which I could then experimentally test in the field.

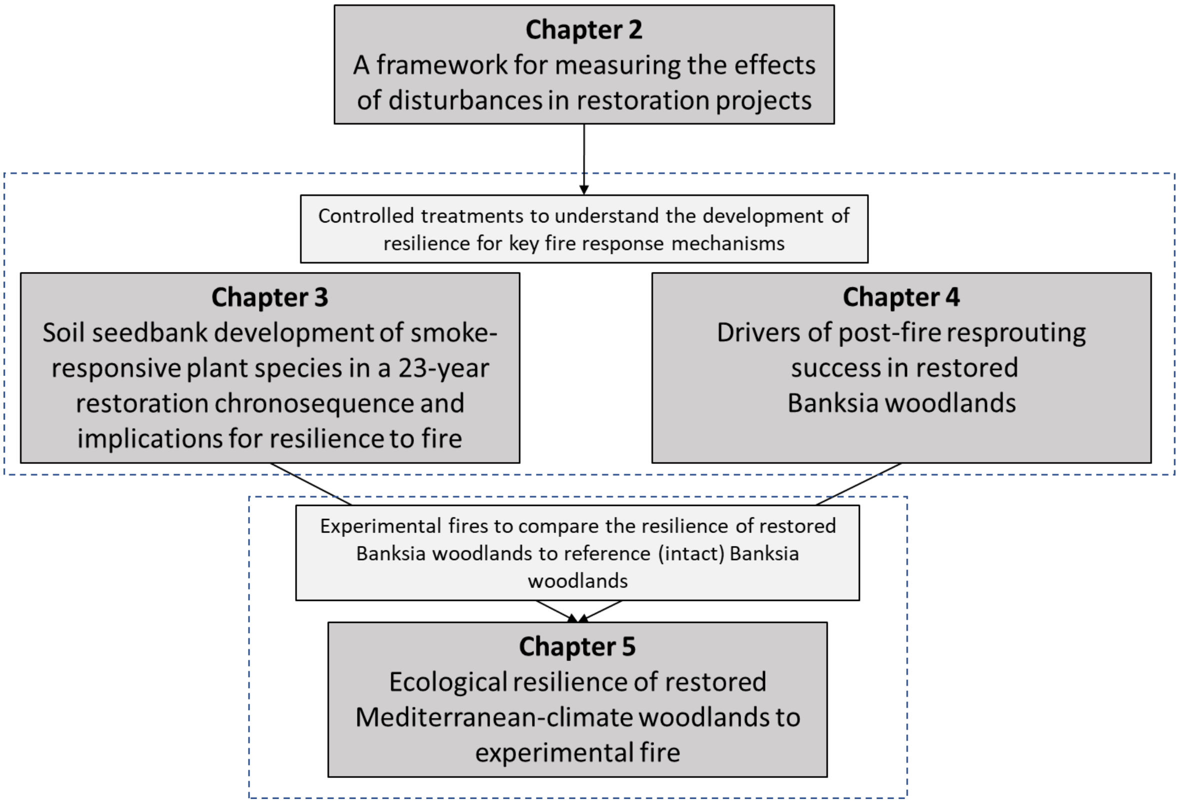


Figure 1.2: Conceptual diagram of thesis data chapters (dark grey rectangles) and key methods used to link chapters (light grey rectangles).

I tested resilience to fire at a sand mine operated by Hanson Heidelberg Construction Materials ('Hanson') approximately 25 km northeast of Perth, Western Australia. Hanson has restored Banksia woodlands following mining most years since 1991. I expected mechanisms used by plants to respond to fire would develop with restoration age, so I conducted field-based trials using a space-for-time approach. Therefore, I assessed responses to fire in a restoration chronosequence between three and 27 years since the beginning of restoration at Hanson (Figures 1.2, 1.3; Table 1.1).

Figure 1.3: Restored Banksia woodlands at different restoration ages, left to right: three, 11 and 26 years since establishment.

Table 1.1: Data chapters and associated technical aspects.

	Chapter 3: soil seedbank dynamics	Chapter 4: drivers of resprouting	Chapter 5: community responses to fire
Broad hypotheses	Soil seedbank size and richness to increase with restoration age	Resprouting and survival to peak in mid-sized and aged plants, with soils important for survival and vigour	Restoration age is important for regeneration, survival and resilience, with resilience increasing in older sites
Treatment	Smoke tent	Burning of resprouts	Experimental fire
Restoration ages (years)	3–26	4–27	14–27
Target plant trait types	Species with smoke-responsive seedbanks	Resprouters (perennial)	All
Number of species	Many	Nine	Many
Time of monitoring post-treatment	~6 months	~5 months and ~12 months	~5 months and ~17 months
Legacies analysed	Climate at establishment	Pre-fire plant size, soils	Fire impact, soils
Comparison type used to consider resilience	Unburnt restored control	NA	Pre-fire control sites, and reference Banksia woodlands

To understand resilience to fire in restored Banksia woodlands, I conducted three different experiments across the restoration chronosequence (Figures 1.2, 1.3; Table 1.1). Two experiments were used to determine the drivers of the two main fire-response mechanisms that can influence resilience in Banksia woodlands: 1) the development of smoke-responsive soil seedbanks (SSB) assessed via recruitment (Chapter 3; published in *Applied Vegetation Science*) and, 2) resprouting (Chapter 4; published in *Austral Ecology*; Table 1.1). These treatments were consistently applied and allowed for the prediction of likely responses to fire across the 3–27-year-old restoration chronosequence without experimental fire implementation (Figure 1.2). To develop a “real world” understanding of responses to fire (i.e., treatment reflected site conditions so was variable across sites), fine-scale experimental burns were implemented in restoration ages ≥14 years as fire was unlikely to spread due to high amounts of bare ground in younger ages (Chapter 5; in preparation for submission to *Ecological Monographs*; Table 1.1). This chapter allowed me to quantify responses to fire for all species in restored Banksia woodlands and track their regeneration and survival for ~1.5 years after fire (Figure 1.2; Table 1.1). I also compared pre and post-fire restored sites to reference (i.e., intact unmined) Banksia woodlands to consider resilience to fire.

While I expected restoration age to be a key driver of responses to fire, the establishment, development, and resilience of restored plant communities may be influenced by site legacies (Herath and Lamont 2009; Herath et al., 2009; Rokich 2016; Mounsey et al., 2021; Riviera et al., 2021). Therefore, I determined the effect of climate at plant establishment (Chapter 3) and soil conditions after fire (Chapters 4, 5; Table 1.1) on plant responses. Responses may also differ for plant functional groups (e.g., differing seedbank sizes and development times for resprouters vs obligate seeders; Pate et al., 1990; Lamont and Wiens 2003), so I considered the effect of plant traits in all chapters. To consider if responses to fire were desirable, I compared treatment responses to a restored control (i.e., undisturbed restoration; Chapters 3, 5), or reference Banksia woodlands (Chapter 5; Table 1.1). In Chapter 4, I accessed the drivers of resprouting success against factors including pre-fire plant size and soils (Table 1.1). These analyses allowed me to consider the potential resilience of these restored sites to fire.

All chapters (except for general discussion) have been written in manuscript form and have either been published (Chapters 2, 3 and 4) or are in preparation for submission (Chapter 5) to international peer-reviewed journals and have been formatted accordingly. Supporting information for each chapter is available in the appendices. The chapters were written to be standalone, so this thesis does not contain a chapter describing the study area and methods. Therefore, there is some degree of inevitable overlap in chapters, particularly of some introductory material, and the descriptions of the study area, study design, and survey methods. Figures, tables and supplementary material are labelled as ‘Figure x.y’ or ‘Table x.y’, where x refers to the Chapter and y refers to the Figure/Table number. S refers to the supplementary material. Plant taxonomy used follows Florabase (Western Australian Herbarium 1998–).

Due to COVID-19 influencing treatment implementation, restoration ages reported differ among chapters reported (Chapter 3 = 3–26 years (treated in 2020) vs Chapters 4 and 5 = 4–27 years (treated in 2021), but sites are the same. Ages 16 and 18 in Chapter 5 were not assessed in Chapters 3 and 4 due to suggestions of the presence of *Phytophthora cinnamomi* (a pathogen causing dieback of native species) which was later confirmed not to be present.

Chapter Two

The following chapter has been drafted in accordance with *Restoration Ecology*.

The current manuscript is published.

Cowan, E. L., Standish, R. J., Miller, B. P., Enright, N. J. and Fontaine, J. B. (2021) 'A framework for measuring the effects of disturbance in restoration projects', *Restoration Ecology*, 29(4), pp. e13379. https://doi.org/10.1111/rec.13379

The following authors contributed to this manuscript as outlined below.

Authorship order	Contribution (%)	Concept development	Data collection	Data analyses	Drafting of manuscript
Ebony Cowan	80	X	X	X	X
Joe Fontaine	6	X			X
Rachel Standish	6	X			X
Ben Miller	5	X			X
Neal Enright	3	X			X

By signing this document, the Candidate and Principal Supervisor acknowledge that the above information is accurate and has been agreed to by all other authors.

E L Cowan

Candidate Principal Supervisor

A framework for measuring the effects of disturbance in restoration projects

Abstract

Ecological resilience is widely acknowledged as a vital attribute of successful ecosystem restoration, with the potential for restoration practice to contribute to this goal. Hence, defining common metrics of resilience to naturally occurring disturbances is essential for restoration planning, efforts, and monitoring. Here, we reviewed how plant community ecologists have measured the resilience of restoration projects to disturbances and propose a framework to guide measurement of restoration projects to disturbance. We found 22 studies that investigated the impact of disturbances on restoration projects, from three continents and for three disturbance types. Over half of the studies were from Australia, with the dataset biased towards fire responses of restored, or partially restored, forest ecosystems. Native plant species richness, cover and density were common response variables. Studies varied in restoration context, design, response variables and statistical approaches, limiting generalisations. Nonetheless, we have identified several response variables that offer potential as lagging indicators (e.g., species richness) and leading indicators (e.g., recruitment) of resilience in diverse vegetation types exposed to a variety of disturbance regimes. We suggest a third set of variables, proxy measures of resilience (e.g., functional redundancy), to complement lagging and leading indicators. We conclude with a framework to guide decisions about when to use each of the three types of measures to assess resilience of restoration projects to disturbance, providing some clarity to decision making despite the uncertainty of changing disturbance regimes. Lastly, we invite

researchers to understand the impact of disturbance on the resilience of restoration projects, rather than assume resilience.

Implications for practice:

- Our review suggests further investigation encompassing a broader range of native ecosystems and disturbance types on disturbance responses of restoration projects is required, particularly for ecosystems that are considered ‘fully restored’ as opposed to ecosystems along the restoration trajectory. Press disturbances were underrepresented compared with pulse disturbances.
- Several commonly measured variables can be used by practitioners to assess resilience of restoration projects to disturbance.
- Our framework offers the opportunity to evaluate the conventional wisdom that resilience emerges with time as restoration proceeds.

Introduction

Land-use changes associated with urban expansion, agriculture, mining, and industry have impacted ecosystems globally (Lambin et al., 2001; Newbold et al., 2015). Such impacts may contribute to regional and global environmental change (Hoegh-Guldberg et al., 2018), reduce soil health and productivity (Koch et al., 2013), and alter the functioning of ecosystems and the delivery of ecosystem services (Mooney et al., 2009). Ecological restoration (i.e., human intervention to improve ecosystem recovery; Benayas et al., 2009) is needed to enhance the functional status of these degraded, damaged, and destroyed ecosystems and to retain biodiversity (Jordan et al., 1988; SER 2004). Indeed, the importance of conserving and maintaining biodiversity and ecosystems in the face of increasingly rapid global change is widely recognized, and ecological restoration has been identified as a global priority by the United Nations (United Nations 2019).

Ecological resilience, which refers to the ability of an ecosystem to persist in a structurally and functionally similar way following a disturbance (Holling 1973), is commonly identified as a desirable, if not critical, attribute of restored ecosystems (SER 2004; Miller et al., 2017). Here, we use the term ‘natural disturbance’ to refer to disturbances with historical precedence, that is, with influence on adaptation and evolution of species living with the disturbance regime (sensu Newman 2019 - such as fire, major drought, wind, flood). Thus, ideally, ecological restoration should aim to ensure that ecosystems are resilient to local, historically precedented disturbance types and their associated regimes of frequency, intensity, extent, and season (Lake 2013; Shackelford et al., 2013). Such resilience would assist in promoting long-term biodiversity and species persistence, and in reducing the need for future management interventions (Oliver et al., 2015). Additionally, resilient ecosystems can promote the maintenance of ecosystem services, enhancing human well-being through the provisioning of needs such as food and water, productive soils and places for recreation (de Groot et al., 2002; Biggs et al., 2012). Consensus exists on the importance and application of resilience as a concept in restoration, but there is less consensus on its measurement (Standish et al., 2014). This is partly due to the vagueness of the term (Myers-Smith et al., 2012; Dornelles et al., 2020) and the difficulty in identifying leading indicators of change to an alternative stable state for different ecosystems (Peterson et al., 1998; Carpenter and Brock 2006).

Typically, restoration projects are considered as ‘successfully restored ecosystems’ (i.e., recovered) when they are similar to a target reference ecosystem (Figure 2.1; SER 2004; Miller et al., 2017) in most key attributes. Specific attributes of restored ecosystems may include characteristic assemblages of species, key functional groups and ecosystem functions, and importantly, resilience to disturbance typical of that ecosystem (SER 2004). Attributes tend to develop over time following restoration interventions (i.e., recovery), and are usually evaluated relative to a historic reference ecosystem and specifically, ecosystem composition, structure and function (Moore et al., 1999; McNellie et al., 2020). However, this assumption is untested for resilience – the evidence that resilience develops over time after restoration intervention is unexplored.

Conceptually, the responses of restored, or partially restored ecosystems, to disturbances are likely to be broadly similar to the responses of reference ecosystems, but some differences may exist. As in a reference ecosystem, after disturbance, a restored ecosystem may develop towards a desirable, pre-disturbance state if it is resilient (e.g., Vander Yacht et al., 2017), or to an undesirable state if it is not (e.g., Herath et al., 2009; Figure 2.1). Responses of restoration projects to disturbances are likely to depend on the maturity of the restoration project, with early-stage projects on the trajectory to restoration potentially less resilient than later-stage projects (e.g., Ross et al., 2004; Figure 2.1). Similarly, restoration projects tend to be species-poor subsets of the historical reference ecosystems (e.g., Sluis 2002; McClain et al., 2011), which may reduce resilience to disturbances because of lower functional diversity or absence of keystone or dominant species. Lastly, ecological legacy effects including changes to soil structure (Yates et al., 2000), dispersal limitation due to patch size (Standish et al., 2007) and plant community assembly (Flinn and Vellend 2005; Cramer et al., 2008) likely occur, which may influence ecosystem functioning, stability and responses to disturbances (Foster et al., 2003). While the ecological literature on responses of reference ecosystems to disturbance inform metrics for restoration projects (e.g., Cushman and McGarigal 2019), the differences between restored, partially restored, and reference ecosystems may require different approaches.

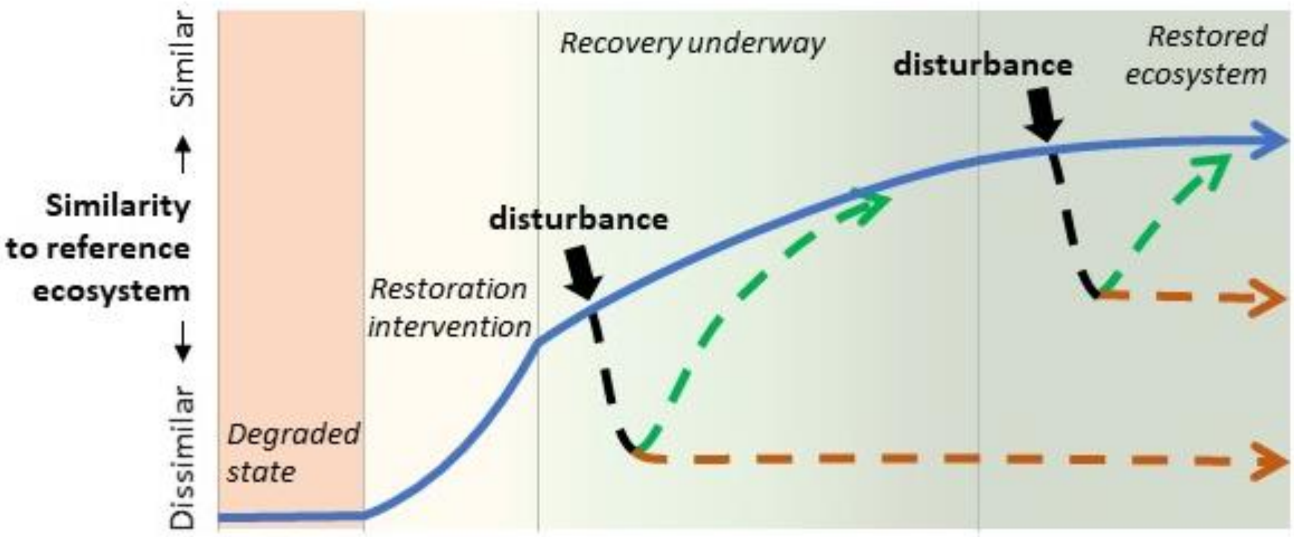


Figure 2.1: Hypothetical restoration trajectories following disturbance of a restoration project, including a desirable trajectory without a disturbance (solid blue arrow), resilience to the disturbance (dashed green arrows showing return to desirable trajectory) and no resilience to the disturbance (dashed amber arrows leading to an alternative, and undesirable, state). Black lines indicate the initial, immediate response to disturbance.

Here, we review the available literature on ways researchers have measured responses to disturbances in restoration projects globally. We synthesise our findings by ecosystem, disturbance, and land-use history type. Disturbances include fire, drought, and storms, including cyclones and tornados. We conclude with guidelines for measuring the resilience of restoration projects to disturbance informed by our findings.

Methods

To locate past work investigating responses of restoration projects to disturbance, ‘Scopus’ and ‘Google Scholar’ were searched using the terms: ‘restor*’ and ‘disturbance’ and the disturbance types of fire, drought, cyclone, tornado and flood. Criteria for papers to be included in the review were: a) studies of restoration projects undergoing ecological restoration or restored, b) such projects had been impacted by disturbance, and c) studies had compared a restoration project to either a control or historic reference ecosystem (Figure 2.1). We focused on literature investigating the responses of plants and excluded other organisms given these are likely to require a different set of attributes to assess their resilience. All searches were conducted between May and July 2019 with no restriction on study year.

We limited our scope to studies examining disturbance following ecological restoration. We excluded studies that had used disturbance as a restoration tool in degraded ecosystems (e.g., prescribed burning in logged and fire-excluded forests; Fulé et al., 2012). While potentially informative, such degraded ecosystems are likely stuck in a resilient state (i.e., ‘undesirable resilience’; Standish et al., 2014) requiring alternative approaches to restoration and management. All studies reported responses of restoration projects to a single disturbance event though five authors mentioned the occurrence of prior disturbance events (i.e., the reported disturbance was not the first disturbance in the restoration process). We acknowledge that past disturbances may have influenced vegetation responses to the disturbance event under study.

While demonstrating resilience to anthropogenic disturbances is important to long-term ecosystem persistence, a key attribute of successful restoration is an ecosystem’s capacity to weather disturbances consistent with historical expectations for the reference ecosystem (i.e., a particular disturbance regime; SER 2004; Newman 2019). Therefore, we focused on disturbances, rather than contemporary anthropogenic events, as the former are internal to a restored system, and likely represent part of the historic range of natural variability intrinsic to the desired or historic reference state (SER 2004; Newman 2019). If ecosystems are disturbance-prone in their reference state (e.g., fire-prone or flood-prone), resilience to this disturbance regime should be an objective of restoration (Shackelford et al., 2013). Additionally, such disturbances may enable critical processes to occur such as recruitment in post-fire environments (Lamont et al., 1991; Bond and Keeley 2005). Therefore, as these disturbances may be expected in ecosystems, resilience to them is critical to promoting a persisting, self-sustaining and functioning ecosystem. In contrast, human-mediated disturbances are often purposeful to bring about a specific outcome, such as grazing or mowing to improve species richness or reduce competitive species cover (Henning et al., 2017). These kinds of disturbances are deliberate and may be managed or excluded if undesirable and are not considered here.

Data structure

Based on the selected search terms, we identified 1352 papers published between 1936 and 2019, 22 of which met our search criteria. A further 14 studies were found that met criteria a) and b), but not c), i.e., did not compare to a reference or control ecosystem, and were excluded. To understand the measuring effort for studies of responses of restoration projects to disturbances, relevant evidence was collated into a table of 22 rows (one for each study) and 13 columns (information type; Table 2.1), including ecosystem and disturbance type, site age and attributes measured. These measures assisted in developing a comprehensive understanding of disturbance in restoration projects, particularly what has been measured, where and under what contexts (e.g., site age, land-use history).

Table 2.1: Information gathered from each study to understand how researchers have investigated disturbances in restoration projects.

Information type	Details
Evidence source	Author and paper title
Ecosystem	Reference ecosystem type
Location	State (if applicable) and country
Land-use history	Land-use history prior to restoration intervention (i.e., mining, agriculture, mixed or unknown)
Disturbance type	Fire, drought, cyclone or tornado (the latter two combined to form ‘storm’)
Temporal or spatial control	Compared to itself before disturbance (temporal control) or undisturbed historic reference ecosystem (spatial control, hereafter ‘reference’)
Study design	Pre-post, space-for-time, post only, combination
Site age when disturbed	Age of restored site (in years) when disturbed
Number of times measured after disturbance	How often site was measured following disturbance
Years after disturbance when measured	When measuring occurred following disturbance
Disturbance details	Measurements of the disturbance itself (if applicable) such as fire intensity or wind speed. Does not include measures of severity.
Attributes measured	Attributes assessed to understand responses disturbances in the restoration projects, separated by lagging (indicate a state change has occurred) and leading indicators (can predict future restoration success)
Statistical analysis conducted	Grouped into: summary, testing of variance between means, ordination and regression.

For ease of synthesis, ecosystems were assigned to one of the six following types: floodplains, grasslands, shrublands, temperate forests, tropical forests, and woodlands. Cyclones and tornados are combined under storm disturbances. Actual restoration interventions (e.g., soil profile reconstruction, planting) were excluded due to lack of available detail, however, we acknowledge these will influence restoration success and monitoring. Attributes that were included in analysis were those that compared responses after a disturbance in restoration projects. Attributes were assigned to one of two categories: lagging indicators (i.e., attributes that develop over long periods of time that may indicate a state change has already occurred) or leading indicators, which can be measured at early stages of restoration and can provide an indication of future restoration success (Manero et al., 2020). Although difficult to identify, leading indicators are variables within ecosystems that may change before large, long-lasting regime shifts occur, often resulting in substantial re-organisation of ecosystems (Carpenter and Brock 2006; Carpenter et al., 2007). They can signal a pending shift to an alternative undesirable state and associated loss of resilience (Scheffer et al., 2001 Carpenter et al., 2007; Scheffer et al., 2009).

Statistical evidence for attributes was grouped into the following four categories: summary (e.g., means, range, standard error and confidence intervals), tests of variance between means (e.g., results from *t*-test and ANOVA, included *p*-values, F statistics and ratios), regression (from simple linear to mixed effect models of continuous or categorical predictors) and ordination (which included classification due to both being based on similarity measures). Evidence was tallied through enumeration and summarised by percentages of studies using each approach. We created a framework showing potential response attributes and their time of measurement along the restoration trajectory to facilitate measurement of resilience.

Results

General study information

We identified 22 studies investigating the effect of disturbances on restoration projects globally, spanning three continents, six ecosystems, and three disturbance types (Figures 2.2a,b). Studies were conducted between 1986 and 2015. Globally, 73% of studies measured responses to fire, with 18% of studies investigating responses following a storm disturbance (either cyclone or tornado) and 9% following drought. All disturbances were pulse disturbances (i.e., brief, with a spike in intensity and then decline; Bender et al., 1984). Over half of the studies were conducted in Australia (59% of studies) where fire was the most studied (50% of studies).

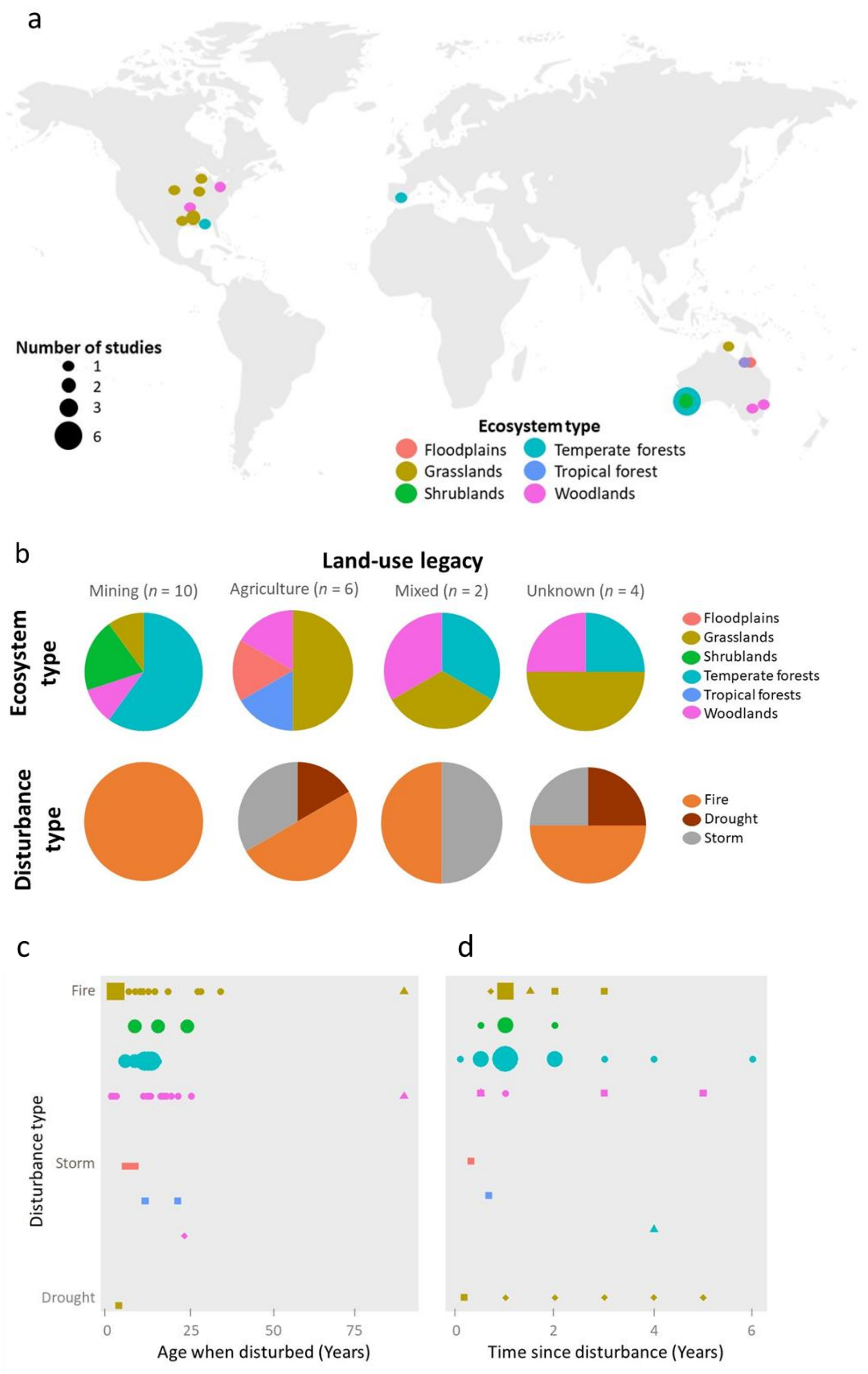

a
Number of studies
1
2
3
6
Ecosystem type
Floodplains
Grasslands
Shrublands
Temperate forests
Tropical forest
Woodlands
b
Land-use legacy
Mining (*n* = 10)
Agriculture (*n* = 6)
Mixed (*n* = 2)
Unknown (*n* = 4)
Ecosystem type
Disturbance type
Floodplains
Grasslands
Shrublands
Temperate forests
Tropical forests
Woodlands
Fire
Drought
Storm
c
d
Disturbance type
Fire
Storm
Drought
0
25
50
75
Age when disturbed (Years)
0
2
4
6
Time since disturbance (Years)

Figure 2.2: a) World map showing locations of studies which have investigated the effects of disturbances on restoration projects with dot size representing number of studies, and colour representing ecosystem type. b) Different land-use histories and the proportion of ecosystems and disturbance types studied for each. c) Age of restored site when disturbed and d) time since disturbance when attributes were measured separated by disturbance type, ecosystem (colours same as Figure 2.2a) and land-use history (shapes) type. The bigger the dot, the higher frequency of being studied, with dot sizes ranging from one (smallest dot) to five (largest dot). Shapes reflect land-use history: square = agriculture, circle = mining, triangle = mixed, diamond = NA. Most studies stated site ages when disturbed, while for two studies, ages were inferred based on other information in the paper. Four studies were excluded as the age of sites could not be determined. Time since disturbance when measured could not be determined for two studies (which were excluded), and could be estimated for a further two studies. Five studies had undergone prior disturbance, and their age was determined as time since last disturbance, with time since disturbance when measured included for the disturbance that was the focus of the paper. One study measured more than one ecosystem type, and both ecosystem types were recorded.

Temperate forests were measured more than other ecosystems (36% of studies) with jarrah (*Eucalyptus marginata*) forests in southwestern Australia restored after bauxite mining representing all but two studies of temperate forests. One study investigated the effect of fire in both a restored woodland and grassland ecosystem (Vander Yacht et al., 2017). Restoration projects were aged 0.5 to 90 years since the initiation of restoration at the time of disturbance (Figure 2.2c). Studies often included a chronosequence of restoration ages, with most site ages falling between 8 and 14 years. Only one study had a site age greater than 50 years when disturbed (Figure 2.2c). In relation to previous land-use history, most studies were of restoration projects after mining or agriculture (45 and 27% of studies respectively; Figure 2.2b). Land-use history prior to restoration was unknown for 18% of studies, while 9% of studies were for sites with a history of logging and agriculture.

In restoration projects, 75% of studies investigated responses after prescribed fire, while only one study investigated responses following a wildfire (6% of studies). Fire origin was unknown for 19% of studies investigating fire. One of two studies measuring drought had conducted experimentally imposed drought treatments. Characteristics of the disturbance were described in 73% of studies, with fire intensity and wind speeds often detailed.

Sampling design

Comparison to undisturbed controls, either nearby historic reference sites (45% of studies) or pre-disturbance restored sites (36% of studies) were used, with 18% of studies using both. Fifty percent of studies measured attributes multiple times, sampling up to five times after disturbance. Responses were tracked from two months to six years following disturbance (Figure 2.2d). Studies that measured attributes once were commonly measured within one year of disturbance. Measurement before and after a disturbance (i.e., pre-post study type) was the most common design (81% of studies) for studies comparing to a historic reference site, or pre-disturbance restored site. A space-for-time chronosequence approach and measuring only after a disturbance were also used (63 and 9% of studies respectively). Over half of all studies (55%) used a combined pre-post and space-for-time study design.

Attributes measured

A total of 31 different attributes have been used to measure responses of restoration projects to disturbance, with 34% of these being limited to only a single study (Table 2.2). The number of attributes measured per study ranged from one to twelve, with an average of five. Lagging indicators that develop over long periods of time and can determine vegetation state were commonly measured (84% of all attributes) with the remainder being leading indicators of state change which can predict future restoration success (Table 2.2). Additionally, 16% of attributes may be classified as either a lagging or leading indicator based on disturbance and measurement context. Lagging indicators were measured in all but one study, while leading indicators were measured in 41% of studies.

Lagging indicators of state change were commonly measured, specifically native plant cover and richness (55% of studies, respectively), followed by native plant density (45%), structure and native diversity (32 and 27%, respectively; Table 2.2). Native plant cover and richness were measured across all disturbance types and ecosystems except shrublands, floodplains and tropical forests (Table 2.2). Plant cover was assessed for all species present (i.e., including non-native species) in the survey area in 25% of studies. Most studies assessing cover measured it by life form (58% of studies) including grasses, forbs, and woody species (41, 33 and 16% of studies investigating cover, respectively). Structure of plant communities was measured differently across studies, with plant size (commonly measured as plant height or diameter), species composition and proportion of live and dead plants often used for its assessment. Native plant richness, cover and density were measured more frequently than the equivalent attribute for non-native species (54, 54 & 45% vs 9, 9 & 18% of studies respectively), with no measure of non-native species for restoration projects affected by drought.

Table 2.2: Attributes, from most to least common, measured in studies of disturbances in restoration projects. Studies are pooled together based on the disturbance type, with colours reflecting ecosystem type. Attributes are separated into lagging indicators (describe the state of the ecosystem) and potential leading indicators (can predict restoration success). Attributes with an * refer to those that may be categorised as either lagging or leading indicators based on disturbance measured and inference. Study numbers match those provided in Table S2.1 and are ordered based on pooling of disturbance and then ecosystem type. Recruitment may also be included in studies investigating seedling survival due to mass recruitment often observed following fire (Bond and Keeley 2005). Survival was assessed within one year of disturbance, while persistence was assessed at least one year after disturbance. Coarse woody debris is classed as objects >75 mm in diameter with fine fuel loads <75 mm, with one study not providing size but has been classed as coarse woody debris. All results are reported for a specified plot area, with counts of individuals (e.g., stems) expressed as density or abundance; we bundle both under density here.

DISTURBANCE TYPE	DROUGHT		FIRE																STORM				TOTAL
study number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
lagging indicators																							
native plant cover	🟨			🟨	🟨	🟨				🟦	🟦	🟦				🟪		🟪		🔷	🟦	🟪	12
native richness	🟨				🟨	🟨		🟩		🟦		🟦	🟦			🟪	🟪	🟪			🟦	🟪	12
native density		🟨	🟨			🟨				🟦	🟦	🟦	🟦					🟪			🟦	🟪	10
structure								🟩	🟦			🟦	🟦		🟦	🟪				🔷			7
*coarse woody debris			🟨						🟦			🟦		🟦	🟦					🔷			6
native diversity						🟨				🟦		🟦				🟪		🟪			🟦		6
bare ground	🟨			🟨		🟨									🟦					🔷			5
*fine fuel loads									🟦			🟦			🟦								4
*plant damage			🟨													🟪			🟥		🟦		4
non-native density										🟦		🟦					🟪	🟪					4
*litter fall			🟨												🟦								2
native evenness										🟦											🟦		2
non-native cover																🟪						🟪	2
non-native richness																	🟪					🟪	2
soil properties													🟦			🟪							2
basal area																						🟪	1
below ground bud density		🟨																					1
canopy closure																		🟪					1
dominance																					🟦		1
importance																					🟦		1
incidence					🟨																		1
percent frequency of occurrence						🟨																	1
relative density																					🟦		1
relative dominance																					🟦		1
species similarity											🟦												1
*soil seedbank composition														🟦									1
leading indicators																							
survival of seedlings								🟩									🟪	🟪		🔷			5
persistence of established plants			🟨					🟩													🟦		3
survival of established plants							🟩									🟪							2
persistence of seedlings								🟩													🟦		2
tree growth			🟨									🟦											2

Ecosystem type

🟥 floodplain	🟩 shrublands	🔷 tropical forest
🟨 grasslands	🟦 temperate forest	🟪 woodlands

While there was variation among study designs, pre-post and space-for-time chronosequence designs were used for the top eight most frequently measured attributes (Figure 2.3). All except one of the top eight most frequently measured attributes (seedling survival) were lagging indicators, with coarse woody debris being either a lagging or leading indicator depending on the disturbance context. Coarse woody debris was measured using both a pre-post and space-for-time design in all studies in which it was measured. Native plant cover was the only attribute that was measured using all three study designs.

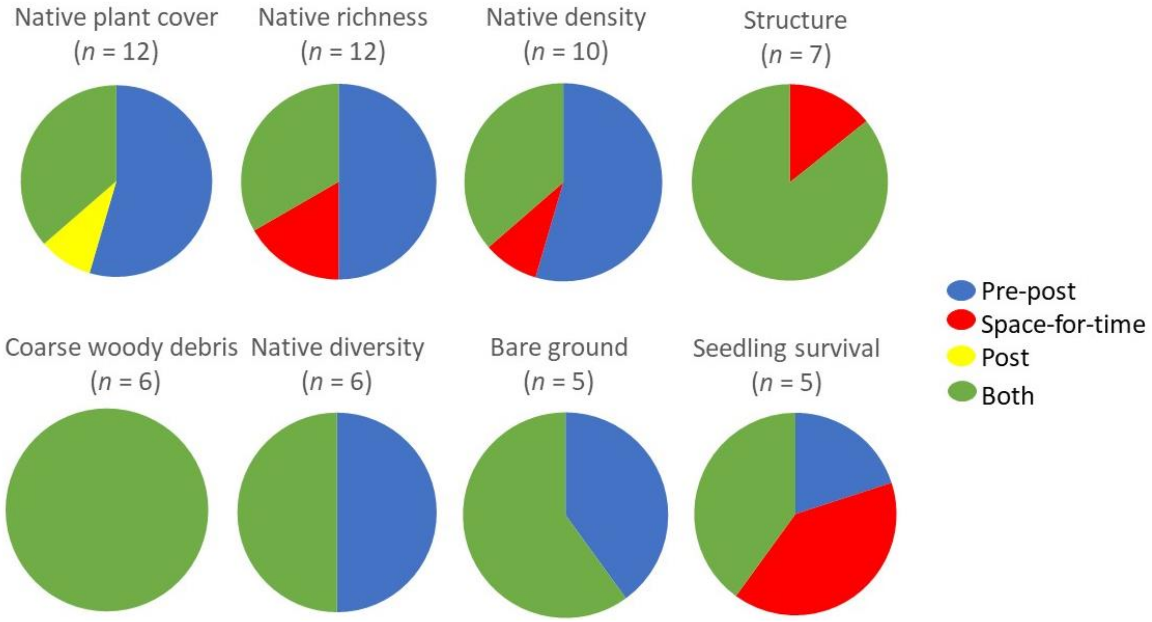
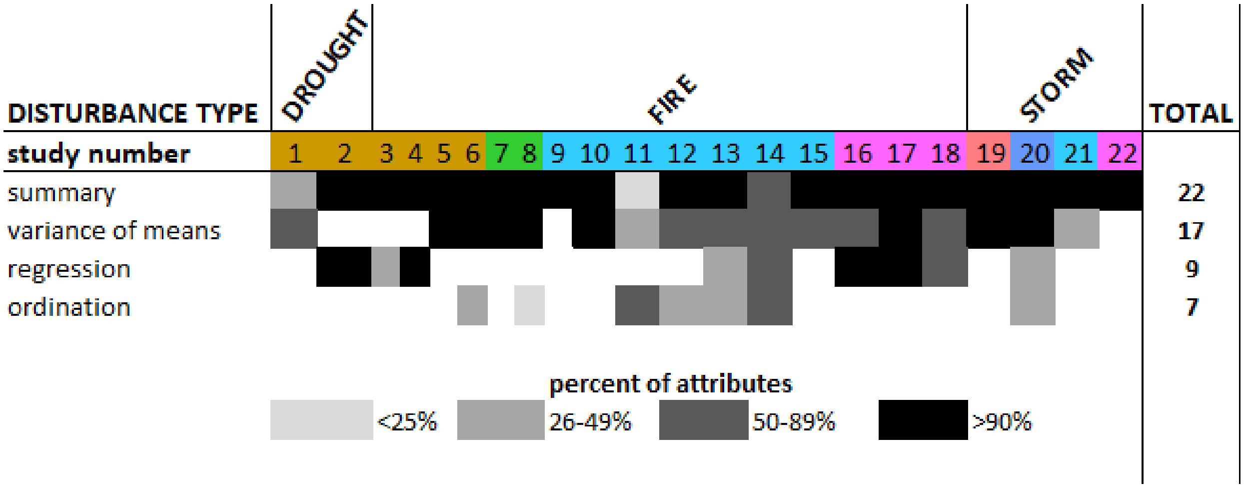


Figure 2.3: Proportions of studies using the different study design types for the eight most frequently measured attributes according to Table 2.2. Labels are attribute and number of studies, with attributes ordered by most to least frequently measured. Studies that used both a pre-post and space-for-time chronosequence are included in the ‘Both’ group.

Statistical evidence

There was variation across studies in the types of statistical evidence used to compare responses of restoration projects to disturbance (Table 2.3). All studies provided at least some summary statistics. Means were commonly presented across studies and attributes, in conjunction with standard errors and ranges. All but five studies presented statistics which assess the significance of difference between means for measured attributes, with *p*-values, *F* statistics and ratios commonly reported. Within this evidence type, *t*-tests and ANOVA were common. Both summary statistics and those assessing differences between means were used across all ecosystems and disturbance types (Table 2.3). Regression analysis, including linear regression, general linear modelling or mixed model ANOVA, was used in 41% of studies, and included all disturbance types. Two studies used all four statistical analysis types. Community ordination using non-metric multidimensional scaling and detrended canonical correspondence analysis was used in 32% of studies, focussing on plant community composition using cover, density and structure. One of these studies used classification based on plant cover and density. Fire was the disturbance examined in all but one of the studies which used an ordination method.

Table 2.3: Types of statistical analyses used to measure the effect of disturbances on restoration projects. Study number and colours reflect those in Table 2.2. Colour ramp (grey scale) shows the percentage of attributes analysed using statistical analysis types.



DISTURBANCE TYPE	**DROUGHT**		**FIRE**																**STORM**				**TOTAL**
study number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
summary	▒	█	█	█	█	█	█	█	█	█	░	█	█	▓	█	█	█	█	█	█	█	█	**22**
variance of means	▓				█	█	█	█		█	▒	▓	▓	▓	▓	▓	█	▓	█	█	▒		**17**
regression		█	▒	█									▒	▓		█	█	▓		▒			**9**
ordination						▒		░			▓	▒	▒	▓						▒			**7**

percent of attributes

░ <25% ▒ 26-49% ▓ 50-89% █ >90%

Summary statistics were used in all studies, with over 90% of attributes in 86% of studies reported in this way (Table 2.3). Statistical assessment of differences between means was also widely used, with 47% of studies using these statistics for greater than 90% of measured attributes. Over half of all studies (55%) utilizing regression conducted regression analysis on over 90% of attributes measured. Ordination (and classification) was used for between 50 and 89% of attributes for 86% of studies using this analysis type, with some attributes likely unsuitable for use in these forms of analysis.

Both pre-post and chronosequence study designs had a similar proportion of attributes measured according to the different statistical types, with summary statistics used in over half of all attributes measured (55% for pre-post studies, and 52% for chronosequence studies; Figure 2.4a). Post only studies utilised summary and regression-based statistics.

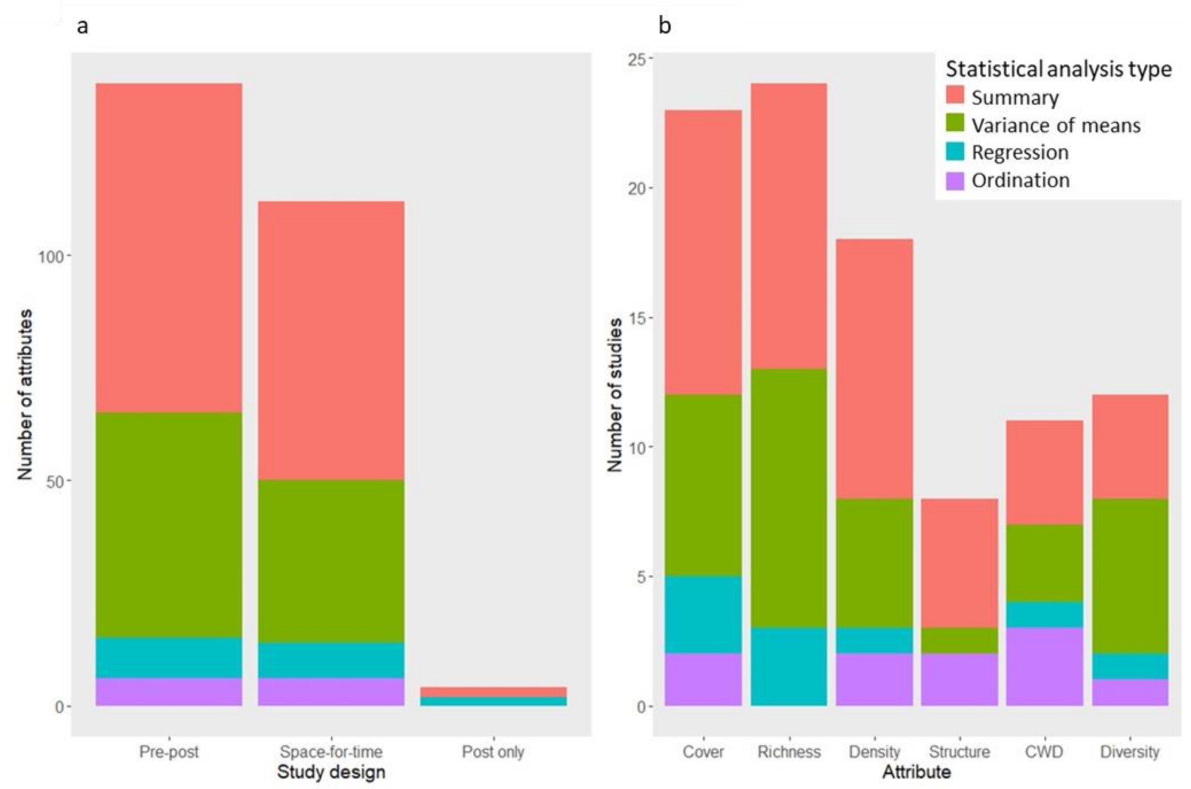
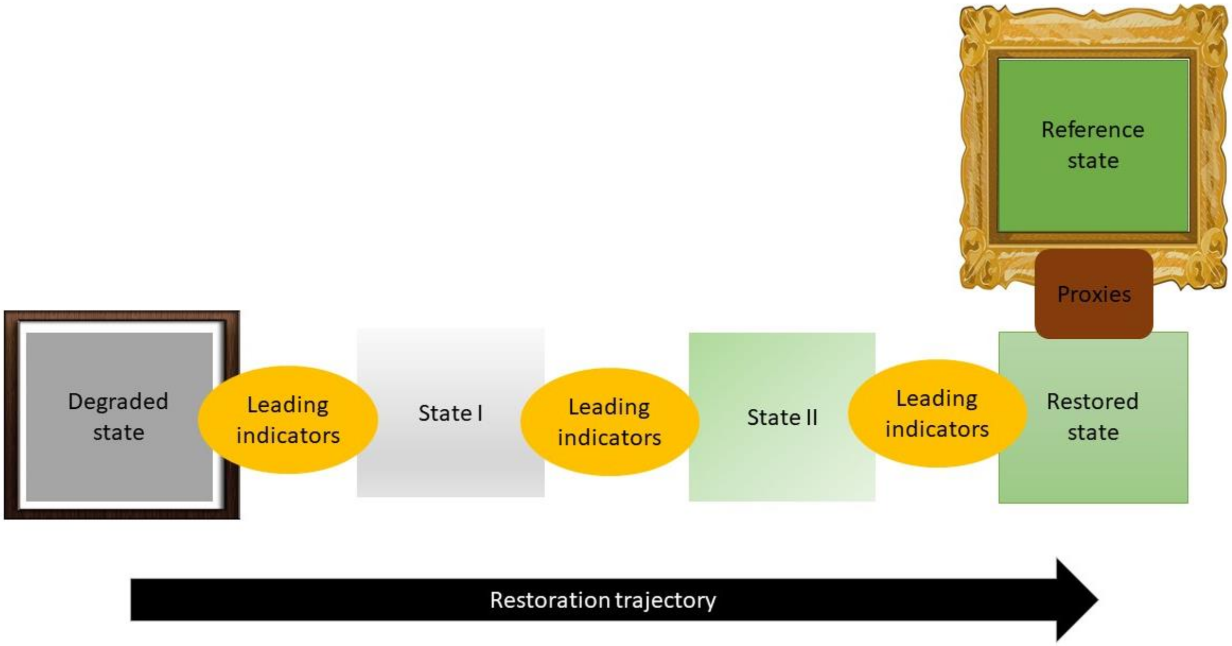


Figure 2.4: a) Number of attributes for each of the study design types that have been analysed using different statistical methods. For studies that used more than one design type, attributes measured were represented in each design type. b) Number of studies conducting different types of statistical measurement for the six most frequently measured state attributes according to Table 2.2. The number of studies measuring each attribute is greater in this figure than Table 2.2 due to multiple statistical types commonly being used to measure a single attribute. The legend in Figure 2.4b applies to Figure 2.4a. CWD = coarse woody debris.

For the six most frequently measured lagging indicators, summary statistics were analysed most for all but one attribute (diversity; Figure 2.4b). Similar to study design types, variance of means-based statistics were also frequently used to explore all five attributes. Cover, diversity, and coarse woody debris data was analysed using all four types of statistical analysis. Leading indicators of state change were mostly measured using summary and variance of means analyses.

We highlight observed trends in the measurement of restoration projects following a disturbance, and present a framework suggesting key considerations when investigating the responses of disturbances. We also suggest attributes and their time of measurement to further assist in assessing resilience to disturbances in restoration projects (Figures 2.5a,b).

a


Reference state
Proxies
Degraded state
Leading indicators
State I
Leading indicators
State II
Leading indicators
Restored state
Restoration trajectory

b

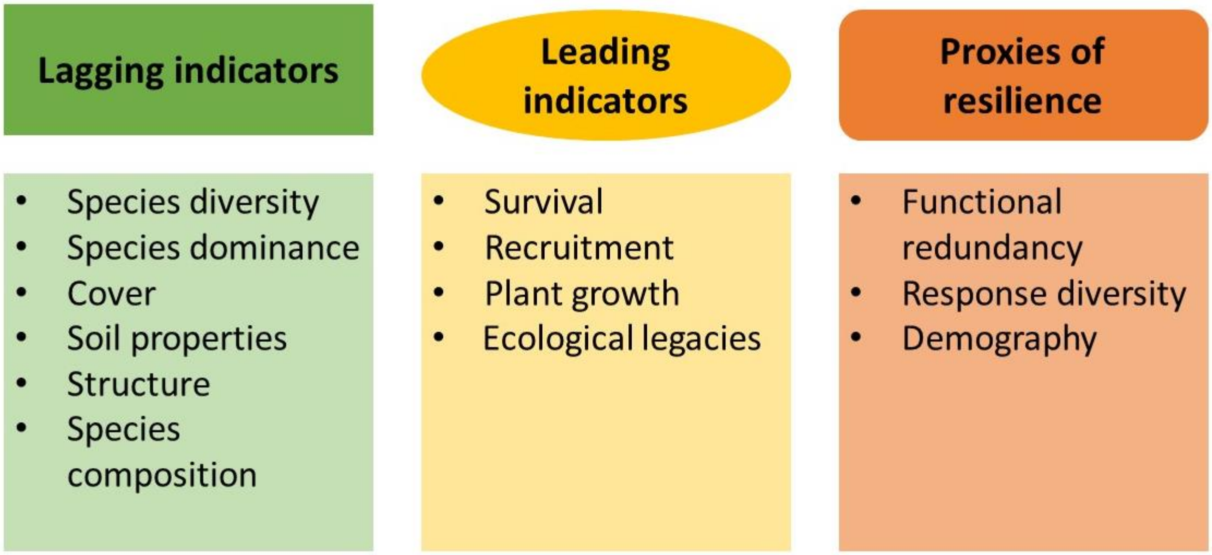

Lagging indicators
Leading indicators
Proxies of resilience
Species diversity
Species dominance
Cover
Soil properties
Structure
Species composition
Survival
Recruitment
Plant growth
Ecological legacies
Functional redundancy
Response diversity
Demography

Figure 2.5: a) Simplified diagram of how lagging indicators (attributes showing the system state at a single point in time; e.g., State I, State II, Restored state), leading indicators (which often relate to rates of change requiring multiple measurements) and proxy measures (which may infer resilience) can help us to monitor, assess and restore ecosystem states that are resilient to disturbances. We assume land managers can identify key states and suggest: i) measuring leading indicators of state change to determine progress on the restoration trajectory and; ii) developing proxy measures of resilience using known responses of the reference state to disturbance. Proxy measures can be used to assess the development of resilience in the restored state. Use of lagging and leading indicators is common in restoration whereas proxy measures are less common. We suggest the extra effort to measure both sets of attributes is warranted given the likely cost savings of restoring states that are resilient to disturbances. Resilience can be helpful (Figure 2.5a; gilded frame) and unhelpful (black frame) in the restoration context (Standish et al., 2014). States are indicated by squares, single-time point measures by rounded rectangles and processes by ovals. b) Bundles of attributes we suggest should be measured to understand responses of restoration projects to disturbance, and assess ecological resilience. Bundles are separated into lagging indicators (which show state), leading indicators (rates of change), and proxy measures of resilience. Structure of a monitoring plan for these bundles is provided in Figure 2.5a.

Discussion

Our review highlights the paucity of published studies of the measurement of lagging and leading indicators for restoration projects following disturbances with historical precedence, therefore making it difficult to assess the resilience of restoration projects to disturbances. Despite the significance of resilience in descriptions of successfully restored sites (SER 2004; Miller et al., 2017), it is perhaps surprising that we identified just 22 studies, from three continents that measured three disturbance types globally. Among measured attributes plant cover, richness, density and structure were most consistently reported for most disturbance and ecosystem types, but there was little consistency among other attributes. Statistical analysis of responses varied among studies, with summary and means-based statistics the most common. We summarise our findings below and provide rationale for our suggested framework and additional attributes that may offer proxy measures of resilience.

Trends in the measurement of disturbances in restoration projects

We found an inconsistent effort across disturbance types, ecosystems and site ages measured. Over a quarter of all studies were for the eucalypt forests of Western Australia restored after mining and disturbed by fire. Therefore, understanding the resilience of restored forests to fire under the restoration methods measured at the time may have the least uncertainty, albeit restricted to one forest type.

Recovery times vary by ecosystem and disturbance type and range from around 1 to 120 years (Jones and Schmitz 2009). We found most studies measured restoration projects once, one year following disturbance. This schedule is unlikely to have allowed full recovery time for most ecosystems, meaning that resilience – based on ability to return to its pre-disturbance state – is also likely difficult to assess. The exception may be grasslands, which typically show quick recovery from disturbance (Loydi et al., 2020), because resident species tend to have short generation times (Shackelford et al., 2016). We found grasslands were measured a maximum of five years following disturbance, but commonly between one and two years. However, forest ecosystems typically take longer to recover after a disturbance due to the longer mean time to maturity of the resident species (Attiwill 1994; Chazdon 2003). We found temperate forests were measured at a maximum of six years after disturbance, but most commonly between one and two years after disturbance. While measurement 1–2 years after disturbance is appropriate for quantification of impact and early response, longer-term studies are required for forest ecosystems and others dominated by slow-growing woody plants.

Generally, measurements were taken prior to ‘full’ ecosystem recovery, thus leaving scientists, managers and regulators to infer whether communities are on a successional trajectory to return to their former state (i.e., suggesting resilience), or if the trajectory suggests a shift towards a different state. Loss of ecological resilience may lead an ecosystem to switch to an alternative state (Scheffer et al., 2001). Leading indicators such as plant growth and survival, and their use when assessing ecosystem responses may allow for a clearer understanding of the likely ecosystem recovery trajectory or when a regime shift may occur (Carpenter and Brock 2006). When approaching a regime shift or threshold, leading indicators have been shown to have increased variance (Carpenter and Brock 2006; Carpenter et al., 2007) or to respond more slowly to disturbances (i.e., critical slowing down; van Nes and Scheffer 2007; Dakos et al., 2008). Repeated measuring of leading indicators across a restoration trajectory may assist in determining these changes and predicting when a critical state change may occur.

Flexibility of study design allows for different inferences to be made about resilience to disturbance. The use of a control, either reference or pre-disturbance restored state, is critical to assessing recovery (i.e., resilience). We found that a pre-post study design was most frequently used when compared to a historic reference or pre-disturbed reference site, particularly in studies after mining, likely due to the requirement to continuously measure restoration efforts in countries such as Australia (Young et al., 2019). This approach permitted quantification of changes after a disturbance, and if tracked for long enough, comparison to its pre-disturbance state. The use of a space-for-time chronosequence approach allows for an ecological trajectory to be assessed without remeasuring the same site over multiple years and may be suited to studies that have a short time frame for completion or for study ecosystems with lengthy recovery times (e.g., forest). Using a chronosequence or repeated measures approach is likely to assist in establishing leading indicators of recovery of the desired vegetation state.

We found that the most frequently measured ecological attributes were lagging indicators, including native species richness, cover, density, and structure. These attributes are frequently measured to evaluate restoration success (Ruiz-Jaen and Aide, 2005) likely due to their ease of measurement in the field. They provide measures of vegetation state, and if measured more than once, can provide indications of ecological resilience through evidence that restoration projects are on a trajectory towards the desirable state. Leading indicators were measured less frequently. For example, repeated measure of attributes associated with seedling recruitment and establishment such as soil seedbank composition could be leading indicators for many ecosystem types. Therefore, measurement of ecological attributes relating to both lagging and leading indicators should be measured in a repeatable manner in restoration projects interested in restoring resilience to disturbance.

Robust statistical evidence is crucial for measuring change that may have occurred between variables, and particularly, the level of confidence that observed change has not occurred by chance and must include a measure of variation. We found that studies used up to four different levels of statistical analysis: (1) All papers used summary statistics to report findings, with means most reported. Some papers did not report variation and the lack of error estimates or standard deviation made it difficult to link change to the influence of disturbance. (2) Analysis of variability between means comparing site types (e.g., control or reference vs disturbed; Carter et al., 2012) was commonly tested using *t*-test or ANOVA. Such statistical analyses assist in determining the extent of change between means and the amount of evidence to support it. (3) Regression-based analyses are useful in determining how variables may relate to each other, therefore assisting in predicting their outcomes under different scenarios. Regression also offers the ability to predict and identify ecological thresholds and regime shifts (Toms and Lesperance 2003; Andersen et al., 2009), thereby being useful in understanding factors influencing resilience and predicting how a community may respond to disturbance. (4) Ordinations were commonly used to assess species composition, and changes in density and cover among sites and treatments, providing useful information to assess if these attributes and ecosystems along the restoration trajectory are shifting towards a reference or pre-disturbance state (e.g., Grant 2003). If these measures are shifting towards their pre-disturbance state, this can allow for an assessment of resilience based on the ability of the restoration project to recover (Shackelford et al., 2016), and consequently influencing restoration success. It is thus perhaps surprising that ordinations were not used more frequently as resilience is a characteristic of ecological communities (Holling 1973; Peterson et al., 1998), and community dissimilarities approaches have been used to assess ecosystem recovery (Shackelford et al., 2016) or identify factors that reflect variability in ecosystem states (e.g., McFarlane et al., 2000). Careful consideration of statistical analyses is required to allow for a stronger inference when understanding resilience following a disturbance in restoration projects. Because of the variation in methodology and limited number of studies, it is not possible to present a synthesis of responses to disturbances.

A framework to measure resilience in restoration projects

Our review has highlighted factors to be considered in the design of studies aiming to measure the resilience of restoration projects to disturbance. The review shows that researchers have tended to measure both lagging indicators of state change (i.e., state variables) and leading indicators of state change with researchers more commonly measuring lagging indicators. While researchers have measured many attributes following a disturbance in restoration projects, some attributes can be lagging or leading indicators based on ecosystem and disturbance type (i.e., resilience of what to what; Carpenter et al., 2001). For example, following fire, soil seedbank composition may be identified as a lagging indicator as it showing what came before the disturbance (i.e., development from live plants), but a leading indicator due to the ability to predict responses to disturbance through plant establishment. Therefore, we suggest careful consideration of attributes measured and their possible inference when assessing disturbed restoration projects. Additionally, while only measured in one study in our review, ecological or biological legacies can help predict ecosystem responses to disturbance and consequently, resilience (Johnstone et al., 2016). Such legacies refer to past impacts or conditions that carry effects on current processes or properties (Monger et al., 2015) and are attributes relating to biota and biological material. In the restoration context they might include native soil seedbanks (positive legacy) or soils conditioned by exotic plants (negative legacy).

While not used in papers included in this review, we suggest additional proxy measures which may indicate restoration success and resilience (Standish et al., 2014). Such proxies may help because they integrate disparate trait and community data to predict community responses (Cadotte et al., 2011). Such proxy measures include functional redundancy and response diversity (Standish et al., 2014). Functional redundancy describes the number of species contributing similarly to an ecosystem function (Walker 1992) and response diversity investigates how species contributing to the same ecosystem function respond differently to disturbance (Elmquist et al., 2003; Mori et al., 2013). Both may provide an indication of resilience.

Alternative proxy measures may relate to species demography (i.e., life history measures that drive plant population dynamics; Harper and White 1974), as determining a species population's regenerative capacity likely influences its ability to persist following a disturbance. Demographic measures may include species life history attributes, proportion of population flowering, seed production, or senescence in mature populations. Such information may offer predictions about when and where a target plant population might regenerate following disturbance (Enright et al., 2014; Enright et al., 2015). Demographic proxies could be particularly important for managing rare plant meta-populations and species.

There are key phases in vegetation development where measures of attribute bundles and proxies can assist in understanding the post-disturbance trajectory of restoration projects. To further enhance understanding of the effects of disturbances, some essential study design features include:

- a pre-post study design, if possible, with a spatial control to evaluate response to disturbance;
- measurement before the disturbance (determine its pre-disturbance state), immediately after the disturbance (determine state change) and longer term (reflective of likely successional times to assess recovery) with repeated measures at different ages of recovery to capture the successional trajectory;
- comparison to an undisturbed control or a desirable historic reference ecosystem to provide context which may be promoted through the use of a planned disturbance;
- include measurement of leading indicator of state change (e.g., recruitment, survival <1 year following disturbance and persistence >1 year following disturbance) at multiple time points along the restoration trajectory to assess rate of change;
- simple statistics that differentiate change associated with recovery from random change. These can be quantitative (i.e., variance-based) and either single or multi-variate (i.e.,

ordination). In the latter, measures of community similarity show community measures of recovery;

- research on resilience proxies such as functional redundancy to assess their ability to predict resilience of restoration projects.

Conclusion

Restoration efforts are essential for reversing global degradation and achieving biodiversity conservation. Increasingly, restoration projects will be subjected to changed disturbance regimes, adding to the list of the many impacts expected to affect future restoration efforts, and represent poorly understood challenges in ecological restoration. Therefore, restoring ecological states that are resilient to disturbances is essential for biodiversity conservation and maintenance of ecosystem services. To meet these imperatives, guidelines on effective measurement of ecological resilience will assist in restoration project management and more broadly ensure the efficacy of global restoration efforts. Currently, few studies have investigated the effects of disturbance on restoration projects and there is bias towards partially restored ecosystems and a few disturbance types. Our framework for measuring resilience aims to address this bias. Our hope is that its adoption will enhance restoration efforts towards biodiversity conservation during a time of unprecedented global environmental change.

Chapter Three

The following chapter has been drafted in accordance with *Applied Vegetation Science.*

The current manuscript is published.

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The following authors contributed to this manuscript as outlined below.

Authorship order	Contribution (%)	Concept development	Data collection	Data analyses	Drafting of manuscript
Ebony Cowan	80	X	X	X	X
Joe Fontaine	7	X	X		X
Ben Miller	5	X	X		X
Rachel Standish	5	X			X
Neal Enright	3	X			X

By signing this document, the Candidate and Principal Supervisor acknowledge that the above information is accurate and has been agreed to by all other authors.

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Soil seed bank development of smoke-responsive plant species in a 23-year restoration chronosequence and implications for resilience to fire

Abstract

Questions: Responses of ecological restoration projects to disturbances are rarely explored, yet their capacity to withstand and recover from disturbance (resilience) is a critical measure of restoration success. In many plant communities, the soil seedbank (SSB) provides an important source of propagules for species persistence and community resilience to disturbance. Understanding how SSBs develop with time can inform restoration of resilient ecosystems. Here, in fire-prone Banksia woodland restoration following sand mining, we ask: i. How does the smoke-responsive (dormancy broken by smoke) SSB develop through time, ii. What plant-trait and climate factors influence its development? and, iii. What do the data suggest for the resilience of these restored woodlands to fire?

Location: Ellenbrook, Swan Coastal Plain, Western Australia (lat. -31.76, lon. 115.95)

Methods: We used smoke, a key germination cue associated with fire disturbance, to trigger germination of the SSB in Banksia woodland restoration. Using a chronosequence of nine ages between three and 26 years since initiation of restoration, we tested how the SSB develops using counts and richness of germinating native and invasive annuals, and native perennial obligate seeding and resprouting species. To understand the contribution of aboveground restored vegetation to SSB development, we compared Sørensen's similarity of the smoke germinable SSB ('smoked SSB') and untreated germinable SSB ('control SSB') to aboveground vegetation.

Results: Smoked SSB germinant density decreased with restoration age for both native and invasive annuals but was stable for native perennials. Similarity between smoked SSB and aboveground vegetation was higher for perennial obligate seeders than for resprouters and peaked for perennials at 23 years.

Conclusions: Post-fire regeneration potential of the SSB was evident across the chronosequence, with restoration age influencing the density of native annuals and overall composition of the SSB. The findings for perennial species suggest an increase in resilience to fire with restoration age.

Introduction

In a time of global biodiversity loss, restoring sites which demonstrate ecological resilience (i.e., ability to return to a similar state following a disturbance; Holling 1973) is crucial to successful restoration (Standish et al., 2014; Miller et al., 2017). Demonstrating resilience to both historical and changed disturbance regimes is key to long-term persistence of restoration (Shackelford et al., 2013). However, empirical studies of responses of restored vegetation to disturbances are lacking (Chapter 2). Fire is a common disturbance globally (Bowman et al., 2009), and many plant species have evolved adaptations promoting regeneration following fire including smoke-responsive, persistent soil seedbanks (SSB; Pausas and Keeley 2014). They provide a crucial source of seeds for restoration (Waryszak et al., 2021) and can indicate the availability of seeds for post-fire recruitment (Smith et al., 2000). Understanding SSB development with time can assist in predicting likely responses to disturbances.

In fire-prone ecosystems, plant species are typically adapted to either persist through fire, or to recruit after it, and recruitment without fire may be limited (Pausas and Keeley 2014). Species that survive fire resprout from vegetative buds rather than depending solely on seeds (i.e., resprouters; Clarke et al., 2013), while those killed by fire (i.e., obligate seeders; Pausas and Keeley 2014) recruit from accumulated seedbanks in the canopy or soil. Within intact fire-prone ecosystems, accumulation of seeds in the soil relies upon multi-year seed longevity and dormancy where heat and/or smoke are usually required to cue seed germination (Bell et al., 1993; Roche et al., 1998). In restoration, the SSB is formed either *in-situ* (from seed accumulation from restored aboveground vegetation) or is transferred in topsoil from storage or directly from elsewhere, and is crucial for plant establishment (Waryszak et al., 2021). How the SSB develops over time and its contribution to the resilience of restoration projects to future disturbances, such as fire, is largely unknown.

Resilience to fire is crucial to the long-term persistence of restored vegetation in fire-prone ecosystems. In intact fire-prone ecosystems, resilience generally develops with time since fire (e.g., Enright et al., 2014) and is reliant on both resprouting and seedling recruitment. In contrast, resilience of restored fire-prone ecosystems established from transferred topsoil initially will be reliant on seeds alone until resprouting species have had time to develop rootstock with buds and stored energy. Perennial obligate seeders are likely well represented in the SSB but may also be sensitive to fire intervals: a short fire interval can cause recruitment failure due to insufficient time to develop adequate seedbanks, while seeds may lose viability with time after long fire intervals (Pausas and Keeley 2014; Chick et al., 2015). Also, some annuals tend to have long-lived seedbanks and favour disturbed environments (Ma et al., 2013) compared with perennials, so may not be sensitive to fire intervals. Therefore, the perennials’ SSB may take longer to develop than the annuals’ SSB due to longer timeframes required for seed production. Because persistence may vary between functional types as restoration develops, it is important to assess their potential SSB resilience separately.

In addition to fire response, species origin (native or invasive) may influence species densities or persistence in the seedbank. For example, invasive species may be present in the SSB at higher densities and for longer due to broad ecological niches and recent disturbances (Leder et al., 2017). Additionally, origin is commonly used to evaluate restoration success as exotic species typically are undesirable and contrary to goals (Chapter 2). Lastly, factors that contribute to varying establishment success in restoration such as climate may have legacy effects on seed production in established vegetation (Yang et al., 2021). For example, unusually hot and/or dry conditions in the first few years of restoration may result in reduced plant establishment and subsequent seedbank development. This may influence the size and composition of SSBs and warrants inclusion in the analysis of SSB development.

To assess the effect of restoration age, plant species responses to fire and climate at establishment on smoke-responsive SSB development, we applied an *in-situ* smoke treatment to stimulate germination across a 23-year restoration chronosequence. We compared germinants in smoke-treated and untreated control plots to assess SSB development. To account for differences in plant persistence and seed production, we used species fire-response types (perennial obligate seeders, perennial resprouters and annuals) and species origin (invasive or native) to understand how different species type responses to smoke influence restored plant community development with time. Specifically, we expected perennial species SSB density and richness to increase with restoration age due to the time required for species to deposit seeds into the SSB, while annual species would peak in younger ages due to their short life cycle and decreased growing space as perennial vegetation develops. Due to the potential for future warming and drying to influence plant establishment and SSB development, we used regression analyses to consider the effect of unfavourable climate at establishment on SSB development in restoration. Lastly, we used indicator species analysis to explore changes in relative abundance and community composition in the SSB over time, and used community analysis to determine SSB similarity to the aboveground vegetation. We use these findings to infer potential resilience to fire.

Methods

Study region

Banksia woodlands are a highly speciose (>600 plant species; Stevens et al., 2016) fire-prone ecosystem found across the south-west of Western Australia (Ritchie et al., 2021). They are a threatened ecosystem where ~2-3 *Banksia* tree species are co-dominant with a highly diverse understory (Ritchie et al., 2021). Most native plant species are adapted to fire through different life history traits and regeneration strategies including resprouting, serotiny (canopy-stored seedbanks) and SSBs (Ritchie et al., 2021). Soil seed storage occurs in >70% of species (Rokich et al., 2001b), with most seedbanks persistent for >1 year up to 40 years (Onans and Parsons 1980). Most SSB species rely on cues from fire, including heat or smoke, to stimulate germination (Bell et al., 1993; Turner et al., 2022; Table S3.1). Fire regimes in Banksia woodlands are not well documented, but estimates based on local plant species demography suggest a fire interval of 8–16 years to ensure the persistence of slow-maturing woody taxa (Hobbs and Atkins 1990; Valentine et al., 2014; Wilson et al., 2014; Ritchie et al., 2021).

Study site

This study was conducted at the Hanson Heidelberg Construction Materials sand mine, approximately 25 km northeast of Perth, Western Australia (lat. -31.76, lon. 115.95). The mine is in the Bassendean dune system (Bastian 1996) characterized by nutrient-poor, acidic siliceous coarse sands with poor water-holding capacity (Salama et al., 2005). The study site experiences a Mediterranean-type climate with hot dry summers and cool wet winters. Between 1980 and 2020, mean annual precipitation at the nearest climate station (~10 km NE to the study site) was 634 mm, with the majority of rainfall in winter. Maximum and minimum summer (January) temperatures average 33.5 and 17°C respectively, while winter (July) temperatures average 18 and 8.3°C respectively (Bureau of Meteorology 2021). Mean temperatures over the past century have risen by ~1°C while days >40°C have more than doubled and heatwave events increased by 1.5× (Breshears et. al., 2021).

Restoration practice

Clearing of Banksia woodlands, sand mining and subsequent restoration have been undertaken in most years since 1991. Typical practices include vegetation clearing, removal and storage of the first 10 cm of topsoil for generally <3 months to maximize seed survival (Rokich et al., 2001b; Z. Keller, pers. comm., April 2021), and mining the first 5–50 m of the soil profile (Stevens et al., 2016). The mined pit is filled with overburden (sand below the topsoil with a high amount of organic matter) or sand (<5% organic matter with higher clay amounts; B Fruin and D. Hardy, pers. comm., November 2021) 2–4 meters deep, with a 10 cm topsoil layer (Stevens et al., 2016; Table 3.1). After topsoil application, sites are usually ripped to reduce soil compaction. Most sites were ripped to 10 cm depth (6 sites), but practices varied, with two sites not ripped and one site ripped to 50 cm depth (Table 3.1). Supplementary seeding and planting of difficult-to-establish species, especially resprouting and serotinous species, usually occurs within the first four years after topsoil application. Soil disturbance from topsoil transfer and ripping stimulates germination of smoke-responsive species in the first year of restoration (Fowler et al., 2015), possibly due to the release of the same compound found in smoke (Dixon et al., 2009).

Generally, seedling mortality in Banksia woodland restoration can be high during the first two years of restoration due to summer drought (Rokich 2016; Mounsey et al., 2021).

Table 3.1: Restoration ages, practices and climate data for the first two years after topsoil transfer. Ripping depth: shallow = 10–15 cm, deep = 50 cm. Climate data were sourced from the Bureau of Meteorology (2021), rainfall and temperature data were sourced from weather station 9053, heatwave data from weather station 9021.

Restoration age (years)	Year established	Ripping depth	Soil profile composition	Rainfall (mm)	Average max. January temperature (°C)	Total number of heatwaves
3	2017	Shallow	Sand	1221.6	32.9	0
5	2015	Shallow	Sand	1365.0	33.7	3
8	2012	Shallow	Sand	1130.4	34.3	3
11	2009	None	Sand	913.7	35.4	5
13	2007	Shallow	Sand	1245.5	35.0	1
16	2004	Shallow	Sand	1215.8	31.9	0
21	1999	Shallow	Sand	1341.8	31.6	1
23	1997	Deep	Overburden	1193.2	33.1	3
26	1994	None	Overburden	1310.0	33.7	3

Study design

We assessed SSB and aboveground vegetation composition in nine sites aged 3–26 years since topsoil transfer. Sites ranged from 0.26–5.75 ha (mean = 2.71±0.48 SE ha), with ages 3–16 years in a ~34 ha area. Sites aged ≥21 years occupied an area of ~6 ha and were located ~4 km south of the other site. All plots were located >10 m from any site boundary. At each site we established three 1×4 m smoke treatment plots and three untreated control plots of the same size to assess germination. Aboveground vegetation composition was measured in five 4×4 m plots in each site.

Smoke treatment

To stimulate the germination of seeds in the SSB, we applied smoke *in-situ* using plastic tents (Figure S3.1). Before smoking, all leaf litter was removed, and live and dead plants in each plot were cut at ground level and removed to maximize the spread of smoke. Plastic sheeting was placed over each plot in a temporary ~20 cm tall tent, sealed at ground level to retain smoke. Smoke from combusting the collected plant material and leaf litter was pumped into the tents for 10 minutes and left to linger for one hour. Smoke treatments were applied in late April (autumn) 2020 (City of Swan Permit no: 16606) prior to the onset of winter rains. Smoke temperature was cool and should not have stimulated germination of heat-responsive species. Each smoke tent was within 10 m of another due to the length of the pipes delivering smoke from the barrel of combusting material.

Data collection

Six months later, in October 2020 (spring), we assessed composition of the SSB via germination response in smoke-treated and control plots across the restoration chronosequence. All germinants (i.e., individuals that germinated in the winter or spring of 2020, including annuals) were counted and identified to species level, or if not possible, to genus level. Genus level counts were included in analyses. Between smoke treatment and germination response data collection, there was 417 mm of rain (~66% of the long-term average) and average winter (July) maximum and minimum temperatures were 2.8 and 0.9°C warmer than the long-term average (Bureau of Meteorology, 2021).

Aboveground vegetation was quantified in spring 2019 (October and November). The number of individuals of all perennial species (including mature plants and seedlings) was counted within 4×4 m plots, and annuals within two 0.7×0.7 m subplots in opposite corners of each plot.

Due to differences in plant strategies, we used species fire-response type and origin (native, invasive) sourced from databases or observations (Table S3.2) in a single ‘trait group’ variable. Trait groups were defined as: native perennial obligate seeder, native perennial resprouter, native annual and invasive annual (Table S3.3). High seedling mortality in Banksia woodland restoration during the first two years of restoration is common (Rokich 2016; Mounsey et al., 2021). Therefore, we tested the effects of average rainfall, daily maximum January temperature, and number of heatwaves for the two-years following restoration establishment on SSB development (Table 3.1).

Data analysis

We quantified the SSB in relation to restoration age, plant fire-response and life history traits and climate predictors, and compared compositional similarity of the SSB to the aboveground vegetation. Therefore, we conducted regression on germinant counts and species richness of germinants as well as community analyses of germinants and aboveground vegetation. Analysis was conducted in R Studio (version 4.0.4; R Core Team 2020) with figures made in *ggplot2* (Wickham 2016), *cowplot* (Wilke 2020) and *ggnewscale* (Campitelli 2022).

Characterizing restored Banksia woodland development

Due to differences in plant evolution and potential impacts on SSB development, we used the previously defined trait groups as the dominant trait for analysis. We removed invasive perennials from modelling due to low frequency of observations, and perennial species that store their seeds in the canopy which do not form part of the smoke-responsive SSB and comprised a small proportion of the species densities (Table S3.4). To assess changes with restoration age, we calculated means and 95% confidence intervals (CI) for plant density and richness in the three treatment types (control SSB, smoked SSB and aboveground vegetation) across the restoration chronosequence as this is a common measure of restoration success (Ruiz-Jaen and Aide 2005). Lack of overlap in CI error bars was interpreted as evidence of a statistical difference at $p<0.05$ (Ramsey and Schafer 2002).

To visualize community similarity between smoked SSB, control SSB and aboveground restored vegetation (treatment types), we conducted a 3D nonmetric-multidimensional scaling ordination (NMDS) of all treatment types and restoration ages. We calculated Bray-Curtis similarity with a Wisconsin double standardization of densities (i.e., species are standardized by maxima, and then sites are standardized by site totals; Bray and Curtis 1957; Oksanen et al., 2020). We removed species which occurred just once across the chronosequence (n = 19) and added a biplot of significant species ($p<0.05$) and centroids of restoration age for all treatments. Using the R package *vegan* (Oksanen et al., 2020), we used the “anosim” function to test for differences within similarities of communities between different treatment types and restoration ages.

Modelling of species counts and richness following smoking

We used linear mixed-effect models in the R package *glmmTMB* (Brooks et al., 2017) to model the influence of species fire-response and life history traits and climate predictors on species counts per plot (i.e., 1×4 m) following smoke treatments (see Figure S3.2 for relationships between restoration age and climate data). Species counts were modelled separately for native and invasive annuals, and native perennials.

To evaluate climate effects, we modelled climate variables as separate linear predictors (Table 3.1; Figure S3.3). Heatwaves are defined as at least three consecutive days where maximum daily temperatures were >90th percentile of the reference period (1992–2021) and were calculated using Climpact v3.1.3 (see www.climpact-sci.org). Continuous covariates (Table 3.1) were standardized by subtracting the mean of each value and dividing by the standard deviation (Zuur et al., 2009; Schielzeth 2010). Correlation coefficients of climate data and restoration age were calculated in the R package *corrplot* (Wei and Simko 2021) to exclude confounding variables in models if necessary (Figure S3.4).

To determine effects of restoration age and climate on smoked SSB species counts, we used a negative binomial distribution to account for overdispersion in count data following smoking (McCullagh and Nelder 1989; Zuur et al., 2009). All species traits and predictors were fixed effects, with separate random effects of smoke tent replicate nested in restoration age and species specified to account for the sampling design that includes plots nested within each age (Zuur et al., 2009). We added interaction terms to investigate changes in species fire response and life history traits with restoration age. We assessed collinearity of covariates, normality and heterogeneity of model residuals, and model performance using the R package *performance* (Lüdecke et al., 2021). Levels of non-normality and heterogeneity of residuals were observed when modelling species counts, potentially due to 35 observations >2 SD from the mean from a mixture of restoration ages and trait groups, but these were retained in the analysis due to the large number of observations. Best models include all predictors because removing predictors from initial models did not result in a change to Akaike Information Criteria (AIC; Akaike 1973) of ΔAIC<2, a widely used rule of thumb to distinguish informative from uninformative models (all models within 2 AIC; Burnham and Anderson 2004).

We modelled species richness following smoking using a Poisson distribution as no overdispersion was observed (Zuur et al., 2009). Due to small sample sizes (i.e., one count per trait group per plot, compared to counts per species per plot), we tested only the effects of age (for native and invasive annuals) and age and trait group (obligate seeder and resprouter) for native perennials on richness.

Characterizing similarity of aboveground vegetation and SSB germinants

We analyzed Sørensen's similarity (i.e., presence/absence equivalent of Bray-Curtis and inverse of *vegan* output) comparing composition of smoked and control SSB to aboveground vegetation for perennials in the R package *vegan* (Oksanen et al., 2020). Comparing smoked and control SSB for perennial species allowed us to isolate the smoke response and inform implications for resilience to fire. Additionally, we modelled native perennial similarity against restoration age, comparison type (i.e., smoked or control SSB similarity to aboveground vegetation), and the interaction between the two using a gaussian distribution (Zuur et al., 2009). We used these data to make inferences about resilience based on the ability to regenerate following fire along the chronosequence. Comparing similarity between control and smoked annuals demonstrated the effect of smoke and was therefore not assessed due to a lack of implications for their resilience.

Indicator species analysis

To understand species associations with restoration age, we used an Indicator Species Analysis of smoked plots using the R package *Indicspecies* (De Cáceres and Legendre 2009). Species with high indicator values suggest both high frequency and abundance within a given restoration age (De Cáceres and Legendre 2009). We report species with $p<0.05$.

Results

Restored Banksia woodlands community composition

Across the 23-year Banksia woodland restoration chronosequence (3–26 years in age), we found 107 species in the SSB, with 85 of these (79%) also found in the aboveground vegetation. An additional 26 species were found only in the aboveground vegetation. Of these 133 species (SSB plus aboveground), 85% were native and 90% possessed a SSB. These included 61 resprouters (45 in SSB, 53 in aboveground vegetation), 35 obligate seeders (26, 30) and 37 annuals (36, 28; Table S3.3). The most common families were Myrtaceae (14 species: 9 in SSB, 13 in aboveground vegetation), Asteraceae (13 species: 13, 10) and Fabaceae (12 species: 8, 10; Table S3.1).

Smoke was associated with increased density and richness of germinants relative to control plots in all restoration ages (range of 30–150% greater; Figure S3.5). Over a quarter (26%) of all resprouting and obligate seeding species were found in aboveground vegetation, but not in the SSB. Of the species recorded in the SSB, 30 were recorded in smoked plots only, while eight were recorded only in control plots. Treatment types varied in similarity (ANOSIM R=0.264, $p<0.001$) with NMDS revealing different aboveground vegetation composition from the SSB, albeit with considerable overlap (stress = 0.179; Figure 3.1). Aboveground vegetation was characterized by the presence of heat-responsive perennial species, including *Acacia pulchella, Daviesia triflora* and *Jacksonia floribunda* (all Fabaceae) while the SSB included high densities of a range of both native and invasive annuals. The smoked SSB plots were a nested subset of the control SSB plots (Figure 3.1), their tight clustering was driven especially by high densities of the obligate seeder perennial *Leucopogon conostephioides* and native smoke-responsive annual *Austrostipa compressa*. Restoration ages differed in species composition (ANOSIM R=

0.377, *p*=<*0*.001), with NMDS revealing that restoration ages 3–8 were dissimilar to ages 13–26 years, with age 11 an outlier (Figure 3.1). The third axis revealed more differentiation between the smoked and control SSB compared to Figure 3.1.

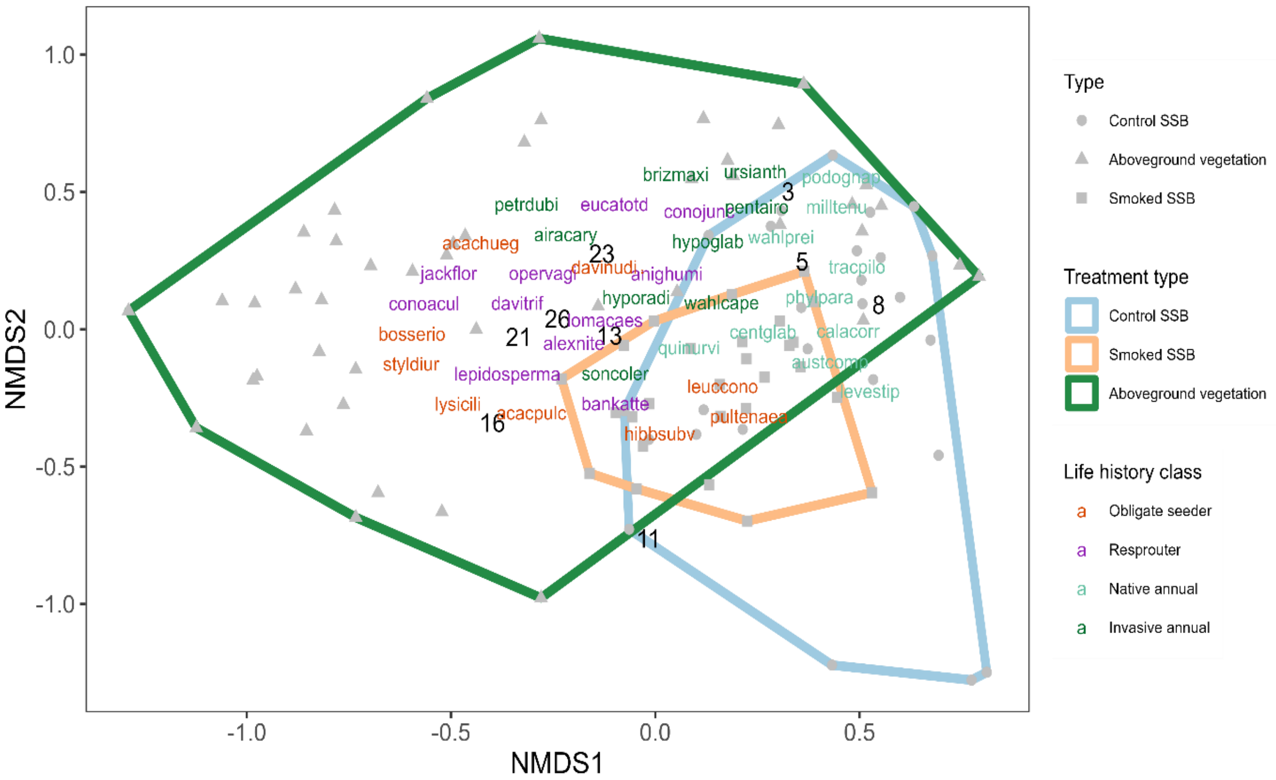

Figure 3.1: Axis 1 and 2 of a 3D NMDS of the Wisconsin double-standardized Bray-Curtis similarity of treatment types (polygons), with a biplot of significant species (full names in Table S3.3) and restoration age centroids (years).

Aboveground vegetation and control SSB richness were similar across the chronosequence, while smoked SSB richness was higher across all ages, decreasing slightly with restoration age (Figure S3.5b). We found little change in perennial obligate seeder and resprouter SSB richness across the 23-year restoration chronosequence (mean of 6 vs 5 respectively; Figure S3.6a). Native annuals had the highest mean richness in the SSB which were highest in restoration ages 3–8 years (Figure S3.6b).

Native perennial resprouters and obligate seeders SSB development

Perennial obligate seeder and resprouter density following smoke treatment increased from age 3 (46 vs 15 germinants m^{-2} respectively) to age 8 (123 vs 82) and then was broadly flat (Figure 3.2a). Mean densities of perennials ranged from 10–122 germinants m^{-2}, with similar resprouter and obligate seeder densities in most ages other than ages 16 and 21, where obligate seeder density was significantly higher based on lack of confidence interval overlap (Figure 3.2a). Modelling of abundance revealed the same pattern of greater obligate seeder individuals and no effect of restoration age or climate predictors (Table 3.2). There was little difference between obligate seeder and resprouter species richness in all ages except age 11 (Figure 3.2c). Native perennial richness following smoking was higher for obligate seeders than resprouters and lower with increased restoration age (estimate = 0.197, z value = 2.097, p=0.036 & estimate = -0.013, z value = -2.104, p=0.035; model R^2= 0.152; Table S3.5).

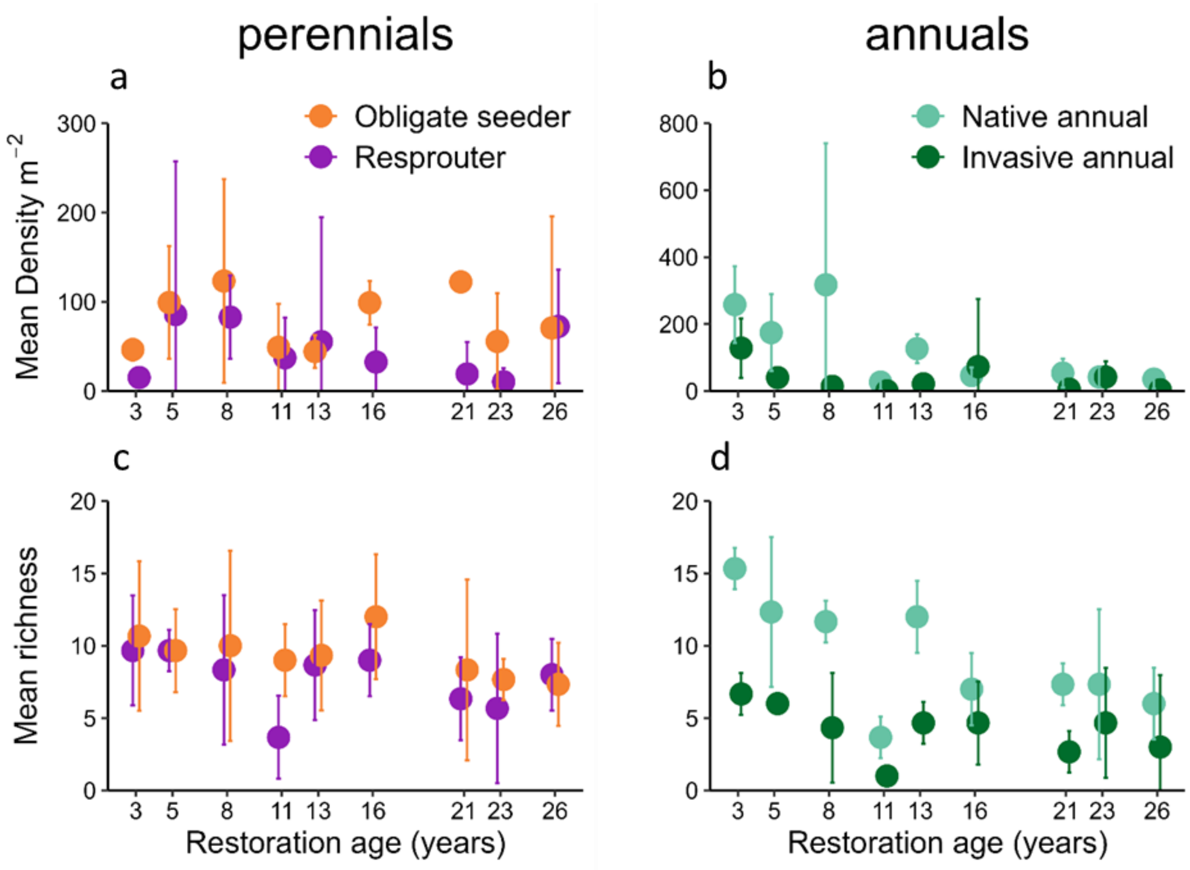

Figure 3.2: Mean and 95% CI perennials and annuals SSB germinant density (a,b) and richness (c,d) in n = 3, 4 m^2 smoked plots along a 23-year restoration chronosequence. Y axis scales differ.

Table 3.2: Effects of species trait and climate predictors on native perennial germinant density in smoked plots. Bolding of values indicates significance at *P*<0.05 level, × denotes an interaction. ICC = intra-class correlation and refers to the proportion of the variance explained by the grouping structure in the model, τ00 refers to individual random intercept variance explained.

Predictor	*Estimate*	*SE*	*Z value*	*P*
Intercept	**1.609**	**0.262**	**6.143**	**<0.001**
Restoration age	-0.048	0.147	-0.325	0.745
Fire response [obligate seeder]	**0.929**	**0.377**	**2.463**	**0.014**
Rainfall	0.164	0.127	1.291	0.197
Total number of heatwaves	0.272	0.158	1.720	0.085
Average max. Jan temp.	-0.188	0.163	-1.149	0.251
Age × fire response [obligate seeder]	0.036	0.124	0.292	0.770
Random effects				
$\tau_{00\ \text{smoke tent replicate:age}}$	0.014			
$\tau_{00\ \text{age}}$	0.075			
$\tau_{00\ \text{species}}$	1.251			
ICC	0.652			
Marginal R^2 / Conditional R^2	0.115 / 0.692			

Native annual SSB development

Following smoke treatment, native annual germinants were more abundant in ages 3–8 years compared to restoration ages >11 years, with species richness also highest in the three youngest ages (Figures 3.2b,d; Table 3.3). Richness peaked in age 3 and was consistently low for ages >16 years (Figure 3.2d) and declined significantly with age (estimate = -0.036, z value = -4.185, $p<0.001$, $R^2 = 0.435$; Table S3.5). Native annual densities ranged from 26–258 germinants m^{-2}, with restoration age significantly decreasing densities of native annual germinants following smoking (estimate = -0.561; z value = -4.260; p = <0.001; Table 3.3). No climate predictors significantly influenced native annual densities following smoking (Table 3.3).

Table 3.3: Effects of restoration age and climate predictors on native annual germinant densities in the smoked plots. Bolding of values indicates significance at *P*<0.05 level. ICC = intra-class correlation and refers to the proportion of the variance explained by the grouping structure in the model, τ00 refers to individual random intercept variance explained.

Predictor	*Estimate*	*SE*	*Z value*	*P*
Intercept	**2.429**	**0.332**	**7.315**	**<0.001**
Restoration age	**-0.561**	**0.132**	**-4.260**	**<0.001**
Rainfall	0.133	0.130	1.022	0.307
Total number of heatwaves	-0.143	0.159	-0.900	0.368
Average max. Jan temp.	0.006	0.159	0.040	0.968
Random effects				
$\tau_{00 \text{ smoke tent replicate:age}}$	0.089			
$\tau_{00 \text{ age}}$	0.052			
$\tau_{00 \text{ species}}$	1.718			
ICC	0.737			
Marginal R^2 / Conditional R^2	0.130 / 0.771			

Invasive annual SSB development

Invasive annual germinant density following smoke treatment was highest at age 3, and, after a small drop, relatively stable there-after (Figure 3.2b). The richness of invasive annuals in all ages, and their density in all but one age, was lower than that of native annuals (Figures 3.2b,d). Restoration age 11 was again an outlier, with both the lowest density and richness. Invasive annual densities ranged from 0–128 germinants m^{-2}, with only restoration age having a significant negative effect on their densities following smoking (estimate = -0.581, z value = -2.070, *p* =0.039; Table 3.4). Invasive annual richness following smoking significantly declined with restoration age (estimate = -0.025, z value = -1.966, *p=0.049*, R^2 = 0.148; Table S3.5).

Table 3.4: Effects of restoration age and climate predictors on invasive annual germinant densities in smoked plots. Bolding of values indicates significance at *P*<0.05 level. ICC = intra-class correlation and refers to the proportion of the variance explained by the grouping structure in the model, τ00 refers to individual random intercept variance explained.

Predictor	*Estimate*	*SE*	*Z value*	*P*
Intercept	**2.320**	**0.454**	**5.104**	**<0.001**
Restoration age	**-0.581**	**0.281**	**-2.070**	**0.039**
Rainfall	-0.049	-0.253	-0.191	0.848
Total number of heatwaves	-0.174	0.321	-0.542	0.588
Average max. Jan temp.	-0.161	0.311	-0.518	0.604
Random effects				
$\tau_{00\text{ smoke tent replicate:age}}$	0.148			
$\tau_{00\text{ age}}$	0.341			
$\tau_{00\text{ species}}$	1.442			
ICC	0.726			
Marginal R^2 / Conditional R^2	0.139 / 0.764			

Similarity of perennial SSB to aboveground vegetation

Using similarity as a measure of potential resilience to fire in the smoke-responsive SSB, we found that the similarity of smoked plots to aboveground vegetation among perennial obligate seeders had no linear trend and was highest in ages 16–26 years (Figure 3.3a). Smoking increased similarity to aboveground vegetation for perennial obligate seeders more than resprouters (Figures 3.3a,b). Resprouter similarity peaked at age 8, and then declined and remained stable in ages >16 years, except for age 11 (Figure 3.3b). Smoked SSB similarity to aboveground vegetation was significantly higher than that of the control SSB in most ages for both obligate seeders and resprouters (77 vs 34% of ages respectively) based on lack of confidence interval overlap (Figures 3.3a,b). Smoked SSB similarity to aboveground vegetation was higher for obligate seeders than resprouters across all ages (Figures 3.3a,b).

For the entire smoked perennial community (obligate seeders and resprouters combined), similarity slightly increased with restoration age and peaked at age 23, a pattern not observed for comparison of the control SSB and aboveground vegetation (Figure 3.3c). There was a significant positive interaction between restoration age and comparison type (smoked or control SSB to aboveground vegetation; estimate = 0.004, z value = 2.056; *p*=0.04, R^2= <1; Table S3.6). Removal of canopy stored and heat-responsive species (i.e., those unlikely to be stimulated by smoke; Table S3.4) did not change patterns of similarity with restoration age (Figure S3.7).

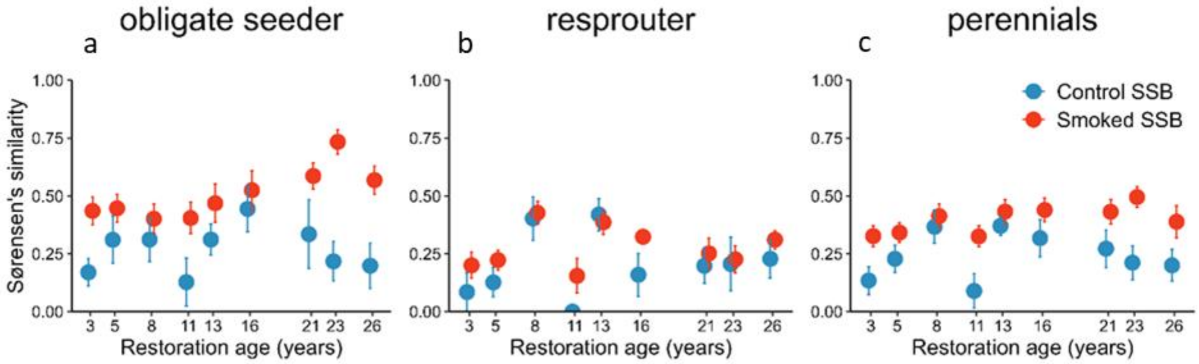

Figure 3.3: Mean similarity and 95% CI of smoked and control SSB to aboveground vegetation across the restoration chronosequence for a) native perennial obligate seeders, b) native perennial resprouters and c) entire native perennial community. n = max. 15 per age; three smoked or control plots compared to each of five plots of aboveground vegetation.

Indicator species analysis

Twenty-six indicator species associated with specific restoration ages were identified from SSB smoked plots. All native annual indicators occurred in ages 3–8, with most of these in the youngest age (Figure 3.4). Invasive annual indicator species were identified in restoration ages 3 and 16 years corresponding to ages with the highest invasive densities (Figures 3.2b,d, 3.4). Perennial indicators occurred across the entire restoration chronosequence, with 53% of perennials found in ages >16 years (Figure 3.4).

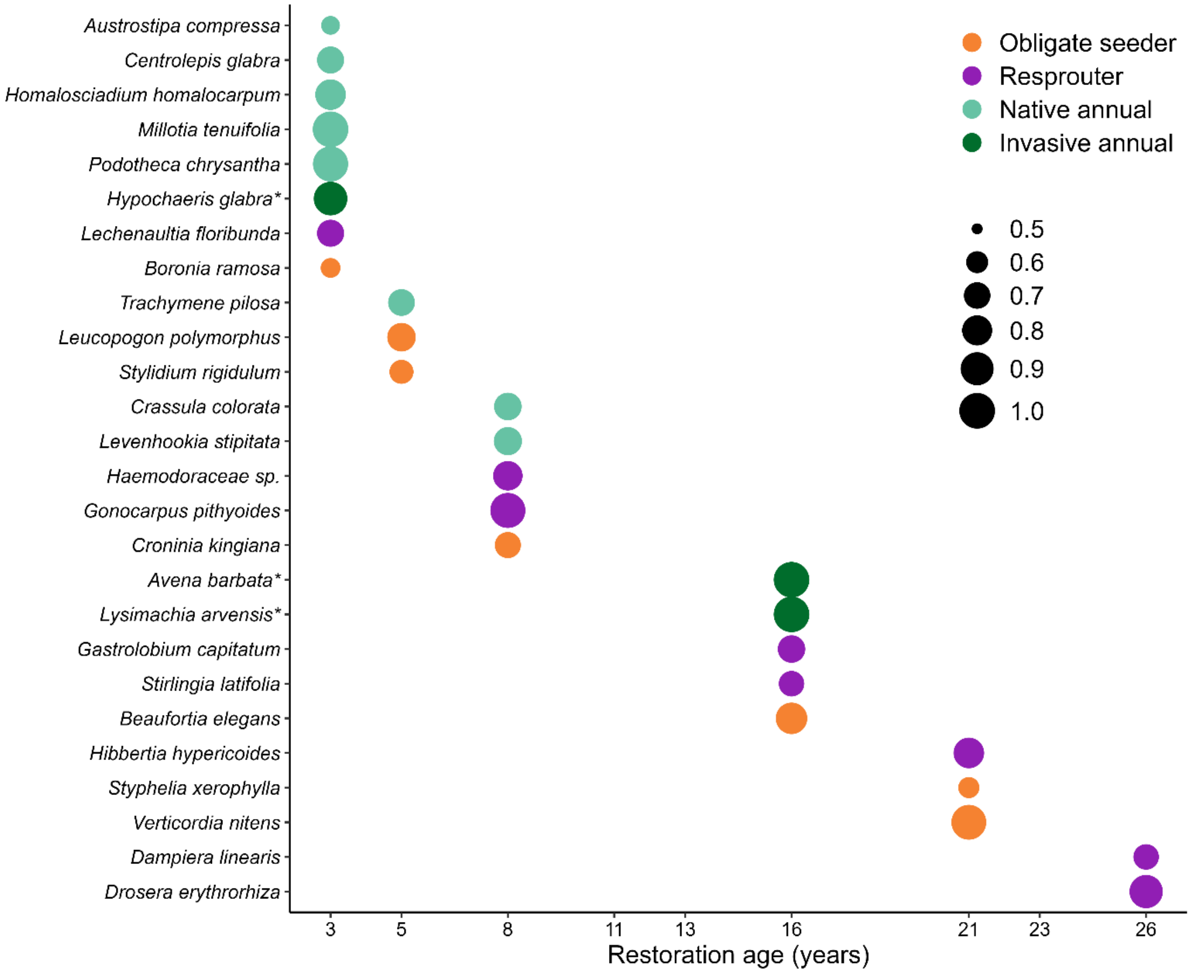

Figure 3.4: Indicator species in smoked SSB plots across the 23-year restoration chronosequence. Size of bubbles refers to indicator values, where 1 is most strongly associated with the restoration age (n=3).

Discussion

The density of native and invasive annuals, but not perennials, emerging from the smoke-treated SSB significantly decreased with restoration age, while richness significantly declined for all trait groups representing the initial floristics model of succession observed in Banksia woodlands (Hobbs and Atkins 1990; Mounsey et al., 2021). The similarity of the perennial species smoked SSB to aboveground vegetation slightly increased with restoration age, particularly for obligate seeders, suggesting that resilience to fire develops with time for these species. Further, while annual species dominated the SSB at the youngest ages assessed, smoke-responsive perennial species were represented too, suggesting restored Banksia woodland seedbanks could be resilient to fire from a young age. SSB development was evident due to shifts in species composition (as revealed by indicator species and NMDS analyses) rather than an increase in species richness and density with restoration age.

Perennials' SSB increases with time

Smoke application increased the richness and densities of both perennial resprouter and obligate seeder species germinants compared to controls reflecting the requirement of smoke for germination of many fire-prone species (Bell et al., 1993). Because resprouters generally take longer to mature and are less fecund (Pate et al., 1990; Clarke et al., 2013), their SSBs may develop more slowly. However, resprouters were the most speciose trait group in the smoked SSB and were present from age 5.

Age 3 perennial SSB density, but not richness, was substantially lower than age 5 and age 8 densities, potentially reflecting a period of reduced resilience over the first 3–4 years as plants establish, mature and the SSB re-develops. A positive relationship between perennial obligate seeder densities and restoration age of the smoke germinable SSB due to recruitment from seed being their only form of self-replacement was not supported by models. This finding is consistent with a study of intact Mediterranean climate woodlands in eastern Australia (Chick et al., 2015). The lack of clear development of SSB perennial density after 5 years could reflect seed inputs and seed losses with time, and varied seed persistence among species.

Annuals' SSB decreases with time

Both native and invasive annuals were most abundant in the smoke-germinable SSB in the younger restoration ages (3–8 years). This may be due to annuals favouring recently disturbed environments including newly restored sites (Ma et al., 2013). Additionally, native annuals may decrease in density with increasing canopy cover, which occurs with increasing time since disturbance (Wainwright et al., 2017). There was little change in the richness and density of annuals across both the smoke germinable and control SSB in sites older than eight years. The presence of some annual species in the SSB at 8 years and older is likely due to a combination of germinating fresh (from recent input) and persistent (from SSB) seeds. For example, we found *Austrostipa compressa* in both the smoked and control SSB of young restoration ages, but densities decreased drastically in the control SSB at ages older than 21 years, while high densities were found in the smoked SSB, consistent with their behaviour in Banksia woodland after fire (Smith et al., 1999). These dynamics are likely to be true of other species (e.g., *Centrolepis glabra, Podotheca gnaphalioides*) and reinforce the influence of seed input, seed loss, seed persistence and their interactions on SSB development for annual species, particularly for those that require smoke for germination.

Effect of climate and restoration practice

We expected climatic conditions during the first two years of restoration (when seedling mortality is highest) to influence plant establishment, seed deposition and consequently, SSB development. However, no climate predictors influenced native and invasive annuals, or native perennials SSB densities. This suggests that while climatic factors influence initial plant establishment and survival in restored Banksia woodlands, this effect does not influence SSB development.

Restoration practices influence plant density, cover and richness (Standish et al., 2015; Rokich 2016; Mounsey et al., 2021) and by extension, seed production and SSB composition. While we did not analyse the effects of restoration practices such as ripping depth, it is likely to have had effects on plant establishment and SSB development. The restoration aged 11 years was not ripped and this likely contributed to it being an outlier. It typically had lower SSB density, richness, and similarity than other ages within all treatment types. It also had the highest maximum January temperature, number of heatwaves, and lowest amount of rainfall across all restoration ages reflecting an extreme La Niña event that occurred in the region causing mortality of Banksia woodland plant populations (Ruthrof et al., 2018). These extreme conditions during establishment, coupled with reduced root and water penetrability in the unripped soil of this site was likely the cause of reduced plant density resulting in decreased SSB accumulation. This highlights how particularly unfavourable establishment conditions and restoration practices can have a long-lasting influence on restoration trajectories.

Varying resilience of smoke-responsive SSB to fire

Having data on both SSB and aboveground species composition may assist in understanding mechanisms driving community development (Hopfensperger 2007; Ma et al., 2021). We observed differences between obligate seeders and resprouters in similarity between the SSB and aboveground vegetation, highlighting the shortcomings of relying solely on aboveground vegetation to understand vegetation development.

Trends in similarity of smoked plots to aboveground vegetation differed with perennial trait group across the chronosequence. Similarity between the smoked SSB and aboveground vegetation increased with time in most ages >11 years for obligate seeders, potentially due to more species establishing, maturing and being able to deposit their seeds. A decrease in similarity in age 26 likely reflects the senescence of some species aboveground that are represented in the SSB (e.g., *Boronia ramosa, Calytrix fraseri and Kunzea glabrescens*). Lower similarity among resprouters than obligate seeders (mean similarity across the entire chronosequence of 27% vs 51% respectively) may reflect their slower time to reproduction, lack of SSB, or difficulty to establish in restoration (Pate et al., 1990; Daws and Koch 2015). Overall, a slight increase in similarity with restoration age for perennial species, peaking at 23 years, suggests resilience to fire develops with time. Native annuals were present early in the restoration chronosequence and for some species (e.g., *Austrostipa compressa*) their resilience to disturbance is likely supported by recruitment from a persistent SSB.

While it is not possible to determine the source of the seeds in the SSB (i.e., donor SSB from topsoil application, on-site seed rain or dispersal onto site), the majority of the SSB is likely from the donor SSB and seed rain, as dispersal onto site is rare in the study region, particularly for perennial species due to fragmentation of the region, unsuitable seed dispersal characteristics (e.g., ant-dispersed species) and seed predation (Standish et al., 2007). This emphasises the importance of using freshly transferred topsoil for restoration to maximise seedbank richness and seed viability to promote post-disturbance recovery of similar communities following fire. We found low levels of germination of heat-responsive Fabaceae species both in the smoked (seven species) and control SSB (six species), likely due to high soil temperatures and/or some SSB fraction became non-dormant through time as temperatures required to break dormancy may reduce with storage time (Liyanage and Ooi 2017).

Our data suggest that across all ages, but especially after 3–4 years, there is regeneration potential from restored Banksia woodland SSB, but its development is likely influenced by other factors including restoration treatments such as ripping. Invasive annual density declined with restoration age suggesting weed control may not be necessary following fire. The response of the perennial SSB to smoke across ages may suggest resilience of restored Banksia woodland to fire. Specifically, we infer that resilience of smoke-responsive native perennials to fire, the dominant vegetation in Banksia woodland, increases with time. Fire disturbance and comparison to reference Banksia woodland is needed to test these predictions and determine if species are missing from the restored SSB which could be added to restored sites. Overall, our study suggests that influences on SSB development are complex yet insightful for restoration practice and complement the usual measures of aboveground vegetation. While fire has not yet been observed in restored Banksia woodlands it should be expected: contemporary fire intervals between 8 and 20 years are common in intact Banksia woodlands. Burning closer to the maximum interval (~20 years) may promote ecological resilience of restored Banksia woodlands. Further research on seed inputs, seed losses and seed persistence would help to further understand SSB development in restoration projects and drivers of SSB change. Science-informed practice is essential to meet aspirational restoration goals in a time of global change.

Chapter Four

The following chapter has been drafted in accordance with *Austral Ecology*.

The current manuscript is published.

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The following authors contributed to this manuscript as outlined below.

Authorship order	Contribution (%)	Concept development	Data collection	Data analyses	Drafting of manuscript
Ebony Cowan	80	X	X	X	X
Joe Fontaine	7	X			X
Ben Miller	7	X			X
Rachel Standish	7	X	X		X

By signing this document, the Candidate and Principal Supervisor acknowledge that the above information is accurate and has been agreed to by all other authors.

ELCowan

Candidate

Principal Supervisor

Drivers of post-fire resprouting success in restored Banksia woodlands

Abstract

Disturbances can alter persistence trajectories of restored ecosystems. Resprouting is a common response of plants to disturbances such as fire or herbivory. Therefore, understanding a plant's resprouting response can inform successful restoration. We investigated patterns and drivers of resprouting following fire in fire-prone Banksia woodlands restored after sand mining in the Mediterranean-climate region of Western Australia. We applied experimental fire to samples of nine species with different resprouting types (rhizome, root crown, root sucker & lignotuber) across a 4–27 years old restoration chronosequence. We investigated the influence of pre-fire plant size, restoration age and soil conditions on resprouting success, defined by: i) the probability of resprouting (measured ~5 months after fire), ii) the probability of surviving the first summer and, iii) vigour (both measured ~12 months post-fire).

We found that the probability of initial resprouting was high across most species, but summer survival was lower but comparable to that in other post-mining restored ecosystems following fire. Generally, pre-fire plant size did not influence the probability of resprouting, while size and soil conditions were important for two species survival. Pre-fire plant size was a significant predictor of vigour for all species with soil conditions influencing four species. Restoration age significantly influenced survival of three species. However, as our models explained low amounts of variation in probabilities of resprouting and survival (R^2 =<0.11), other factors influencing resprouting success remain unidentified.

Resprouting response to fire disturbance in restored Banksia woodlands are species and resprouter type specific, with plant size and soil conditions potentially more informative for understanding responses to disturbances than restoration age alone.

Introduction

In Mediterranean-climate regions (excluding Chile), fire occurs at varying intervals of ~10–100 years (Cowling et al., 1996; Rundel et al., 2016) and drives ecosystem change, and has contributed to the high species diversity found in these regions (He et al., 2019). In these fire-prone ecosystems many plant species either survive (via resprouting), or are killed by fire and recruit from seeds (obligate seeding), with some species able to do both (facultative resprouters; Keeley et al., 2011; Clarke et al., 2015).

Following fire, resprouting from protected organs is common and promotes rapid plant growth (Clarke et al., 2013). Traits enabling resprouting include bud banks, their protection and resource availability, which are influenced by factors including plant size and age, and site environmental characteristics (Hodgkinson 1998; Vesk 2006; Clarke et al., 2013; Ott et al., 2019). For example, short fire intervals may result in smaller, younger plants which may not demonstrate strong resprouting ability due to insufficient bud bank size and stored energy resources, whereas extended fire intervals (which could result in larger, older plants) may prevent effective resprouting through declines in bud bank size due to bud senescence or burial (Keeley 2006; Enright et al., 2011). Impairment of resprouting capacity due to such factors can substantially reduce population persistence because seedlings of resprouting species often invest less in seed-based recruitment and take longer to reach reproductive maturity (Lamont and Wiens 2003; Clarke et al., 2013).

Following resprouting (after fire, for example) survival through the first summer drought can be low due to harsh summer conditions (Pratt et al., 2014; Enright et al., 2015) with drivers of survival variable. For example, survival may be influenced by factors such as changed water uptake due to altered functioning of stomata or bud availability (Pratt et al., 2014; Nolan et al., 2021), while other evidence suggests that access to nutrients is more important than pre-fire plant size (Moreira et al., 2012b; Marais et al., 2014). Additionally, resprouting vigour (biomass) is strongly positively related to pre-fire plant size or the concentration of carbohydrates which are crucial for the development of resprouts (Moreira et al., 2012b; Marais et al., 2014). The role of fire in degrading or enhancing biodiversity in intact, functioning ecosystems is well documented (e.g., Keeley et al., 2005; Enright et al., 2014; Le Stradic et al., 2018; Gallagher et al., 2021). However, we are unsure of the drivers of resprouting success of species with different resprouter organ types (Klimešová et al., 2021) and resprouting responses to fire in restored ecosystems (Chapter 2).

In ecosystem restoration projects, fire may elicit different resprouting responses compared to intact ecosystems. For example, in restoration projects where complete substrate reconstruction is undertaken, such as following mining, soil factors including compaction and field capacity may differ to that of intact ecosystems (Herath and Lamont 2009; Stevens et al., 2016). Such factors may reduce resprouting success due to impeded root development and/or architecture, and reduced water penetrability potentially reducing bud bank size (Rokich et al., 2001b; Herath and Lamont 2009).

Plant age can be an important driver of resprouting success (Keeley 2006; Enright et al., 2011). The age of resprouting individuals in intact ecosystems is unknown, and in plant populations with individuals of varying ages (years to decades or even centuries; Merwin et al., 2012), underground organ sizes and disturbance histories likely shape bud bank dynamics (depletion via resprouting or gain via growth following fire; Keeley 2006). In contrast, plants in restoration projects will either be even-aged (all established immediately) or uneven-aged with a truncated upper limit and often young relative to the species' lifespan. Restoration age is commonly used to understand ecosystem trajectories and predict plant responses to disturbances also (Chapter 2). Knowing the maximum plant age of individual resprouting plants provides an opportunity to assess how long resprouting capacity takes to develop, while the drivers of resprouting can be determined without being influenced by the effects of previous disturbances. Such complexities may pose a challenge for successful resprouting in fire-prone restoration projects in Mediterranean ecosystems, with restored sites providing a valuable opportunity to assess the drivers of resprouting success where fire is important for plant species regeneration (Clarke et al., 2013).

Here, we investigate the drivers of resprouting success of nine plant species from four resprouter types (root sucker, rhizome, lignotuber and root crown) in post-mine restored, fire-prone Banksia woodlands in southwestern Australia. We define resprouting success according to three response variables: i) resprouting probability, assessed ~5 months post-fire; ii) summer survival probability and; iii) resprouting vigour with the latter two both assessed ~12 months post-fire. Broadly, we expect responses of species within the same resprouter type to be influenced by similar variables. We expect pre-fire plant size (hereafter ‘plant size’) to influence both probability of resprouting and survival, with both responses to peak in intermediate sized and aged plants and to reduce in smaller, younger and larger, older individuals. We expect soil conditions (compaction and field capacity) to be more important for survival and vigour. Additionally, we test the effect of restoration age (as an indication of maximum plant age) on resprouting success and expect it to be important for resprouting and survival as bud development takes time.

Methods

Study region

Banksia woodlands are a highly speciose (>600 plant species) fire-prone ecosystem in southwestern Australia with a diverse sclerophyll understory (Stevens et al., 2016; Ritchie et al., 2021) and are listed as an endangered vegetation community by the Australian Commonwealth (Department of Environment and Energy 2016). Approximately 78% of species can resprout (Fontaine and Standish 2019), many of which are facultative resprouters. Pre-colonial fire intervals do not exist for Banksia woodlands, but estimates based on plant demography suggest a fire interval of 8–16 years for the maintenance of species diversity (Hobbs and Atkins 1990; Wilson et al., 2014; Valentine et al., 2014; Ritchie et al., 2021) corresponding with estimates of predicted fire frequency based on vegetation structure and fuel dynamics (i.e., fire hazard; Tangney et al., 2022).

Study site

This study was conducted at Hanson Heidelberg Construction Material’s sand mine, approximately 25 km northeast of Perth, Western Australia (lat. -31.76, long. 115.95). The mine is located on the Bassendean dune system (Bastian 1996) with nutrient-poor, acidic siliceous coarse sands with poor water-holding capacity (Salama et al., 2005) and experiences a Mediterranean climate. Between 1980 and 2020, mean annual precipitation at the climate station closest to the study site was 634 mm, maximum January (summer) and July (winter) temperatures average 33.5°C and 18°C respectively for the same period (Bureau of Meteorology 2021). We selected nine restoration ages at Hanson between 4–27 years since the beginning of restoration (Table 4.1).

Table 4.1: Management history and soil characteristics of restored Banksia woodland sites. All soils data are means, ripping depth: none = soils were not ripped, shallow = 10–15 cm, deep = 50 cm. See Figure S4.1 for relationships with age. mV = millivolts, VSW = volumetric soil water, MPA = megapascals.

Restoration age (years)	Year established	Soil moisture (mV / VSW%)	Soil compaction (MPa)	Soil field capacity (%)	Ripping depth	Soil profile composition
4	2017	122.070 / <1	1.061	20.91	Shallow	Sand
6	2015	133.468 / <1	0.968	24.22	Shallow	Sand
9	2012	101.571/ <1	0.728	20.87	Shallow	Sand
12	2009	96.980/ <1	0.664	29.20	None	Sand
14	2007	109.874/ <1	0.784	20.67	Shallow	Sand
17	2004	142.560 / 1.6	0.952	22.58	Shallow	Sand
22	1999	124.544 / 1.3	1.044	18.52	Shallow	Sand
24	1997	101.852 / <1	0.800	19.26	Deep	Overburden
27	1994	157.892 / 2.3	1.100	16.35	None	Overburden

Hanson has rehabilitated sand mine pits to restore Banksia woodlands in most years since 1991. Before mining, land clearing occurs with removal of the first 10 cm of topsoil, and separately, overburden, followed by mining of the soil profile (Stevens et al., 2016). After mining, transferred topsoil is deposited either directly on the pit surface (still comprised of sand), or on top of a layer of spread overburden (sand with a higher proportion of organic matter; B. Fruin & D. Hardy, pers. comm., November 2021) and is then ripped to reduce soil compaction (Stevens et al., 2016; Table 4.1). Seeding and planting of difficult-to-establish species, including some resprouters, usually occurs within four years of topsoil application. Restoration practices including ripping depth and soil profile composition can influence plant establishment and vegetation development (Stevens et al., 2016; Mounsey et al., 2021), and have been largely consistent since 1999 (Table 4.1).

Study species

Nine native facultative resprouting species common in Banksia woodlands were studied to understand resprouting responses to fire (Table 4.2). All species resprout basally, but from different organs (stem or root) or modifications to the root. Species selected had an even spread of sizes across the restoration chronosequence and were from common resprouter types observed in Banksia woodlands: root suckers (3 species, n = 243), rhizomes (3 species, n = 155), root crown (1 species, n = 51) and lignotubers (2 species, n = 333). Sample sizes per species ranged from 25–233 individuals (Table 4.2). These four resprouter types are characterized by varying bud bank size and protection characteristics (Clarke et al., 2013; Pausas et al., 2018). Data on resprouter types was sourced from Wilson et al., (2010), Pausas et al., (2018) and field observations (W. Veber, unpublished data, 2019; E. Cowan, pers. obs., 2021). All focal species recruited from seeds in the topsoil except for *Gastrolobium capitatum* which was seeded.

Table 4.2: Plant species surveyed. Resprouter types are listed by increasing aboveground plant size and defined according to Clarke et al., (2013) and Pausas et al., (2018). Maximum rooting depth was determined when plants were harvested, † = rooting depth may be underestimated. Sample size refers to number of individuals burnt.

Resprouter type	Species	Family	Growth form	Max. rooting depth (cm)	Sample size
Root sucker	*Dampiera linearis*	Goodeniaceae	Herb	29	49
	Gonocarpus pithyoides	Haloragaceae	Herb	20	55

	Lechenaultia floribunda	Goodeniaceae	Shrub	11	139
Rhizome	*Conostylis aculeata*	Haemodoraceae	Graminoid	33	84
	Conostylis juncea	Haemodoraceae	Graminoid	17	25
	Patersonia occidentalis	Iridaceae	Graminoid	24	46
Root crown	*Gastrolobium capitatum*	Fabaceae	Shrub	21	51
Lignotuber	*Scholtzia involucrata*	Myrtaceae	Shrub	93†	233
	Stirlingia latifolia	Proteaceae	Shrub	90†	100

Response variables data collection

To determine resprouting success of nine Banksia woodlands species in restored Banksia woodlands, we tagged plants across the 23-year restoration chronosequence (Table 4.1), species were not all present in every restoration age (Table S4.1). We collected data pre-fire in March 2021, applied fire in May 2021, and monitored individual plant responses at two intervals within the year after burning. We defined resprouting success as:

1- Resprouting probability, indicated by green shoots emerging from burnt plant remnants (yes or no; measured in October 2021 ~5 months following fire);

2- Survival probability of the first summer, plants visibly still alive and had living resprouts (yes or no; measured in May 2022 ~12 months following fire);

3- Resprouting vigour of surviving plants, defined as length of longest resprouted stem (cm; Enright et al., 2011; measured in May 2022 ~12 months following fire).

Burning treatment

We used experimental fire to elicit a fire response in resprouting species. Before burning, plant size was recorded for each tagged plant. On May 16th, 2021, low-severity fires were conducted in sites aged 14 to 27 years by the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA). The fires that were implemented were patchy and did not burn all tagged individuals. Therefore, within 9 days prior or 3 days after experimental fires, we used a hand-held weed burner (a low-intensity gas-fired blowtorch) to burn tagged resprouter individuals that would not burn or had not burnt in the experimental fires due to lack of nearby fuel (permit number LFABP_82; City of Swan). Experimental fires were not attempted in ages 4–12 years because fuel loads were deemed too low to carry fires and sufficiently burn vegetation (DBCA, pers. comm., June 2019). Therefore, individual plants in these sites were burnt with a hand-held weed burner. The effects of fire on individual plants were similar regardless of delivery method. In both cases, the leaves of burned plants were combusted, leaving a scorched rootstock at the soil surface for rhizome species due to quick combustion of their leaves, while remnants of woody and/or herbaceous branches and stems remained but were scorched for other resprouter types.

Explanatory variables

We expected root biomass to influence resprouting success due to its influence on stored bud and resource reserves, which can develop with plant growth (Clarke et al., 2013; Pausas et al., 2018). Therefore, we assessed relationships between measures of above-ground plant size (plant height, width, canopy volume, estimated resprout organ size; Supplementary text S4.1; Table S4.2; Figure S4.2). Legacy effects of the restoration process may impact post-fire responses (Herath and Lamont 2009; Riviera et al., 2021). Therefore, we measured soil compaction, moisture and field capacity (water holding capacity after excess water has drained; Supplementary text S4.2) as explanatory variables of resprouter survival and vigour.

Data analysis

We sought to understand how resprouting success (resprouting probability, survival probability and vigour) following fire varied between species and resprouter types and was explained by potential drivers. Using a combination of summary statistics, generalized linear (GLM) and generalized additive (GAM) modelling, we quantified the relationship between plant size and restoration age on the probability of resprouting, and plant size, restoration age and soil conditions on the probability of survival and vigour, reflecting our hypotheses. Analysis was conducted in R Studio (version 4.0.4; R Core Team 2020), with figures made using the R package *ggplot2* (Wickham 2016) and *cowplot* (Wilke 2020) and correlations assessed using *corrplot* (Wei and Simko 2021). Models subsets were determined using *FSSgams* (Fisher et al., 2018) with model summaries fitted using *mgcv* (GAMs; Wood and Wood 2015) and “glm()” in base R. Visualizations of model effects were created with the packages *visreg* (Breheny and Burchett 2017) and *sjPlot* (Lüdecke 2022).

To determine if responses differed among resprouter types, we used GLMs to model each measure of resprouting success against resprouter type only. We found substantial heterogeneity within resprouting type (Table S4.4; Figures S4.4, S4.5), so therefore modelled species separately to allow us to look for consistent explanatory variables across resprouter types.

Modelling plant and soil attributes

We modelled the probability of individual plants resprouting after fire and summer survival with a binomial distribution whereas vigour (longest resprout length) was modelled using a gaussian distribution (Zuur et al., 2009). We standardized soil covariates to improve model interpretability by subtracting the mean of each value and dividing by the standard deviation (Schielzeth 2010).

For the probability of resprouting and survival, plant size and restoration age were modelled as continuous smoothers to allow for non-linear relationships as hypothesized (GAMs). The smoothing parameter was limited to a simple spline ($k = 3$) to prevent overfitting. All predictors for vigour models were linear (GLMs).

We expected plant size to drive probability of resprouting, so we modelled each species' resprouting probability against smoothed plant size only. To understand factors driving survival and vigour, for each species we constructed a set of possible GAMs using size and soil variables as predictors. We compared these models using Akaike's Information Criterion corrected for small sample size (AICc) and model weights (ωAICc), which represent the probability for each model (Hurvich and Tsai 1989; Burnham et al., 2011). We did not model restoration practices (ripping depth and soil profile composition; Table 4.1) as these were highly correlated with soil compaction, moisture and field capacity. Furthermore, when correlations were accessed per species, soil moisture and compaction were highly correlated ($r > 0.77$), so we modelled soil compaction only as it had low correlations with field capacity for most species (Figure S4.6).

Predictor variables that were correlated with other predictor variables ($r > 0.28$) were dropped from models to avoid overfitting and bias in parameter estimates (Graham 2003). Variance explained was estimated as adjusted R^2 and log-likelihood was determined using the R function "loglik()". Due to a-priori hypotheses of plant size being important for resprouting success, we modelled all species responses against plant size, even when size was not in the top-ranked model (i.e., lowest AICc model). For species where the top-ranked model included size and another predictor, these predictors were modelled. We did not model one species originally thought to be a resprouter, *G. capitatum* (root crown), due to its poor resprouting (6%) and survival (4%) compared to other species (54–98% & 28–91% respectively). *Conostylis juncea* and *P. occidentalis* probability of resprouting and *P. occidentalis* survival were not modelled as model convergence was not possible likely due to high resprouting success and low sample size. *Conostylis juncea* vigour was not modelled due to small sample size (n = 7; Table S4.1).

Modelling restoration age

Plant community development usually occurs with time, so land managers may assume the development of certain characteristics based on restoration age. Here, we might expect plant size to increase with restoration age. Surprisingly, it did not (r =-0.13–0.14), so we modelled restoration age separately to understand its potential influence on resprouting success. We only modelled species observed in >75% of restoration ages (*C. aculeata, S. involucrata* and *S. latifolia*; Table S4.1). We excluded soil variables due to high correlations with restoration age (Figure S4.6). Restoration age was fitted with a smoother for resprouting and survival probabilities but was linear for vigour.

Results

Following burning, across all species and resprouter types, 541 individuals (69% of those measured) resprouted in spring, but only 394 (50%) individuals of all measured individuals survived their first summer. Among individual species and across resprouter types, resprouting ability was high and ranged from 54–98%, except for *G. capitatum* (root crown type) which only had 6% of individuals resprout (Figure 4.1). Both species and resprouter types had lower and more variable summer survival rates compared to their resprouting abilities (Figure 4.1).

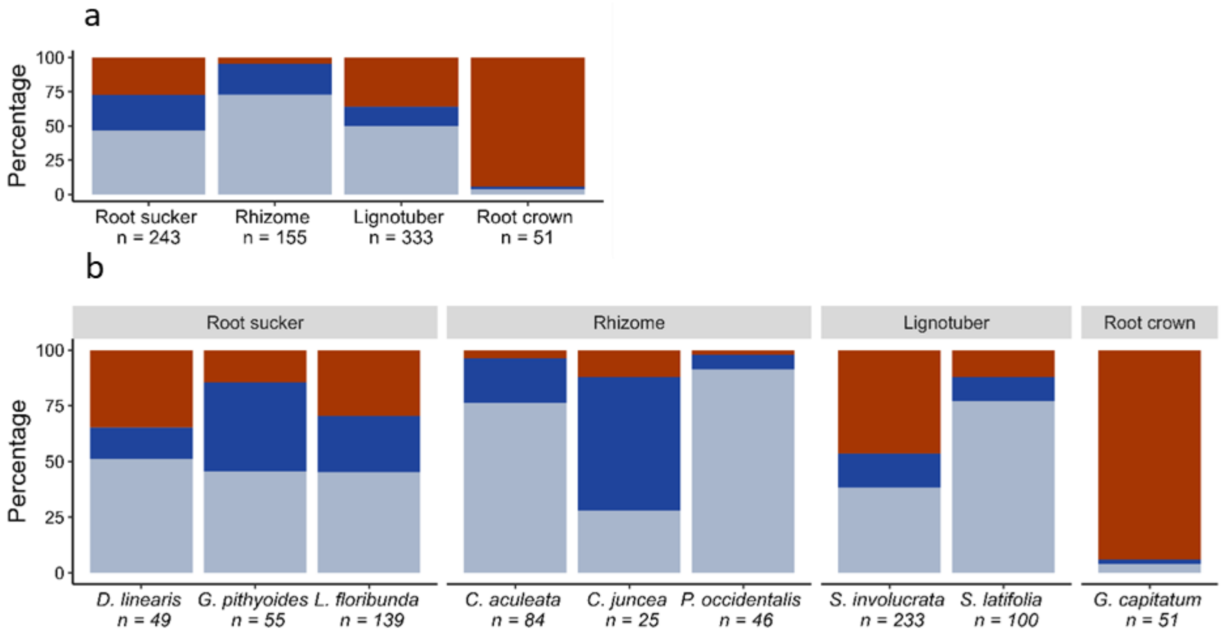

Figure 4.1: Percentages of responses to fire separated by a) resprouter type and b) species. Red = did not resprout after fire, dark blue = resprouted at 6 months following fire but did not survive, light blue = survived 12 months following fire.

Influence of plant size on probability of resprouting

Predicted relationships between plant size and resprouting probability varied widely among species (Figure 4.2). Probability of resprouting increased with plant size and remained high in large *C. aculeata* and *S. latifolia* individuals but decreased slightly with increasing plant size for *G. pithyoides* and *L. floribunda* (Figure 4.2). Both *D. linearis* and *S. involucrata* probability of resprouting varied with plant size (Figures 4.2a,c). However, despite varied relationships with probability of resprouting, plant size did not have a significant effect on any species' probabilities of resprouting and explained low amounts of variance (R^2=-0.018–0.068; Table S4.5).

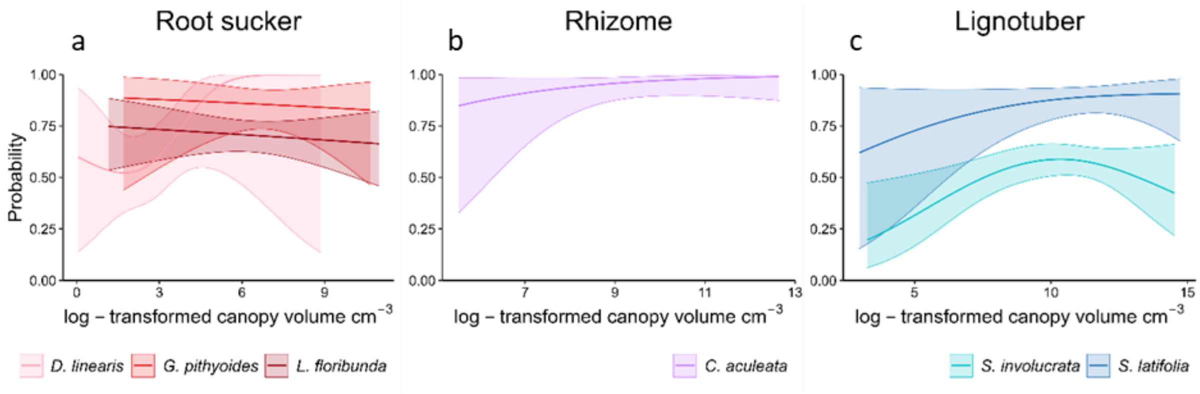

Figure 4.2: Predicted effect of smoothed log-transformed plant size (cm^{-3}) on probability of resprouting for a) root sucker, b) rhizome and c) lignotuber species. Graphs have 95% CI, x axes vary. Log-transformed plant size did not have a significant effect on any species resprouting probabilities (Table S4.5).

Plant and soil attributes influencing survival and vigour

Using a model subset approach, we determined what measures of size and soil attributes correlated with survival and vigour at 12 months following fire. Across some species' survival and vigour, multiple models had similar log-likelihood, ωAICc, R^2 and ΔAICc <2 from the top-ranked (lowest AICc) model (Tables S4.6–S4.8). Top-ranked models of survival explained low levels of variation ($R^2 = 0$–0.171; mean = 0.066), while vigour models typically explained more variation ($R^2 = 0.11$–0.707; mean = 0.307; Table 4.3).

Table 4.3: Predictors (shaded boxes) and their significance (indicated by number of *) in the species top-ranked model (lowest AICc) with model ωAICc and R^2. See Tables S4.6–S4.8 for full model subsets. Plant size is modelled with a smoother for survival, but linear for vigour. Models without plant size in the top-ranked model are indicated by †, those with the intercept only are indicated by ‡. * refer to *P* values: *** = <0.001, ** = <0.01, * = <0.05.

			Individual	Soil			
Response	Resprouter type	Species	Plant size	Compaction	Field capacity	ωAICc	R^2
Survival	Root sucker	*Damperia linearis* †		▨	▨	0.684	0.171
		Gonocarpus pithyoides †‡				0.425	0
		Leschenaultia floribunda	*	*		0.388	0.060
	Rhizome	*Conostylis aculeata* †			▨	0.541	0.073
		Conostylis juncea †‡				0.373	0
	Lignotuber	*Scholtzia involucrata*	▨	▨	*	0.431	0.045
		Stirlingia latifolia	*		**	0.827	0.110
Vigour	Root sucker	*Damperia linearis*	*			0.287	0.153
		Gonocarpus pithyoides	*			0.428	0.155
		Leschenaultia floribunda	**			0.544	0.110
	Rhizome	*Conostylis aculeata*	***	*		0.704	0.270
		Patersonia occidentalis	***	***		0.988	0.422
	Lignotuber	*Scholtzia involucrata*	***		**	0.963	0.332
		Stirlingia latifolia	***		***	1	0.707

Plant and soil attributes influence on probability of survival

We found similar relationships between plant size and probability of survival within some resprouter types (Figure 4.3). Both *G. pithyoides* and *L. floribunda* (root suckers) survival probability increased with plant size, while *D. linearis* survival increased with size then rapidly decreased in larger individuals (Figure 4.3a). Both *S. latifolia* and *S. involucrata* (lignotuber species) survival probability increased with increasing plant size until plants were mid-sized, then decreased (Figure 4.3c). Trends were not similar for rhizome species; *C. aculeata* probability of survival slightly increased with plant size and remained relatively high, while *C. juncea* survival increased with plant size but reduced in larger individuals (Figure 4.3b).

A range of predictors were found in the top-ranked model influencing probabilities of surviving the first summer (Table 4.3). Size was in the top-ranked model for 43% of species, however only two of these species (*L. floribunda* & *S. latifolia*) had moderate evidence of size significantly influencing survival (Tables 4.3, S4.9). Field capacity had a significant negative effect on *S. involucrata* and *S. latifolia* (both lignotuber species; Table S4.9).

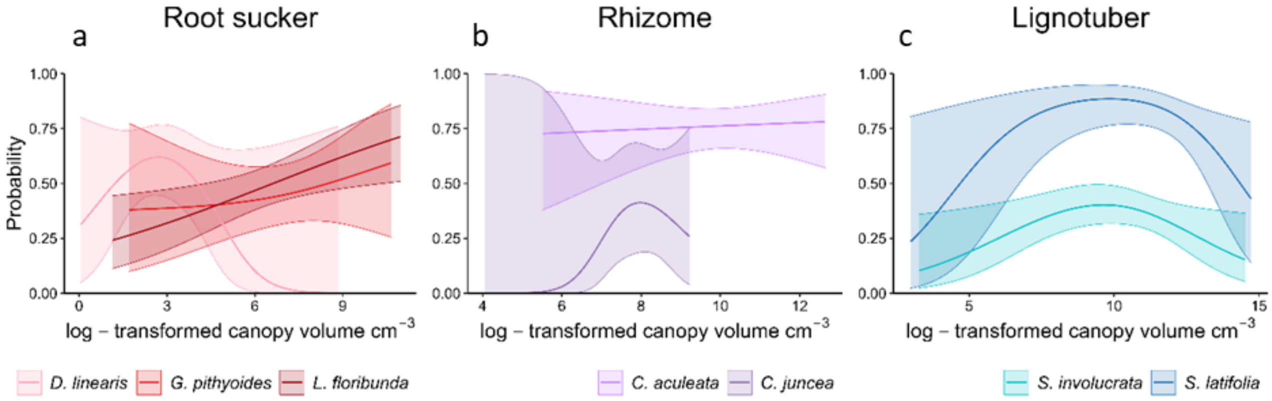

Figure 4.3: Predicted effect of smoothed log-transformed plant size (cm^{-3}) on probability of surviving the first summer for a) root sucker, b) rhizome and c) lignotuber species. Graphs have 95% CI, x axes vary.

Plant and soil attributes influence on resprouting vigour

Predictors in the top-ranked models of vigour, measured as longest resprout length, were consistent across all resprouter types; models of root suckers had size only, rhizomes had size and compaction, and lignotubers had size and field capacity (Tables 4.3, S4.10; Figure 4.4). All species had moderate evidence of resprouting vigour increasing with plant size, while soil compaction and field capacity significantly decreased vigour for rhizome and lignotuber species respectively (Figure 4.4; Table S4.10).

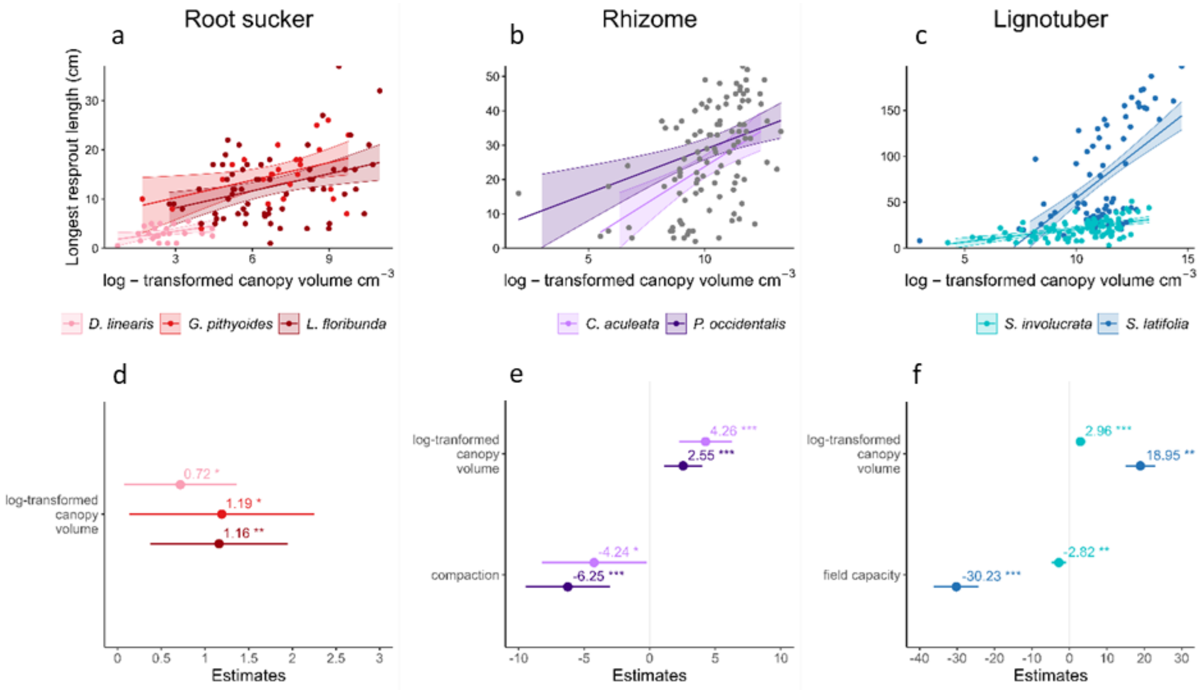

Figure 4.4: Predicted effect of the top-ranked model for all species vigour (longest resprout length cm) against (a-c) log-transformed plant size (cm^{-3}) with (d-f) estimates of predictors per resprouter type. Colours in a-c reflect species in d-f. Graphs have 95% CI, x axes vary. Raw vigour points are plotted. See Table S4.10 for model summaries.

Restoration age effects on resprouting success

Resprouter survival was similar across all restoration ages (33–63%), except for age 14 (80%; Figure 4.5a). When separated by resprouter type, root suckers and rhizomes in restoration age 4 had lower resprouter survival to ~12 months (32 & 34%; Figure 4.5b). Despite all three rhizome species being found in ages 4 and 24, both ages had the highest rates of resprouter mortality between ~5 and ~12 months compared to the rest of the chronosequence (62 & 48% vs 0–10%; Figure 4.5b; Table S4.1). Conversely, restoration ages 9 and 27 years had the highest numbers of root suckers, but survival varied among these ages (33 vs 61% respectively; Figure 4.5b). Ages 9 and 22 had similar counts of each lignotuber species and high counts across the chronosequence, yet different resprouter survival rates (42 vs 75% respectively; Figure 4.5b).

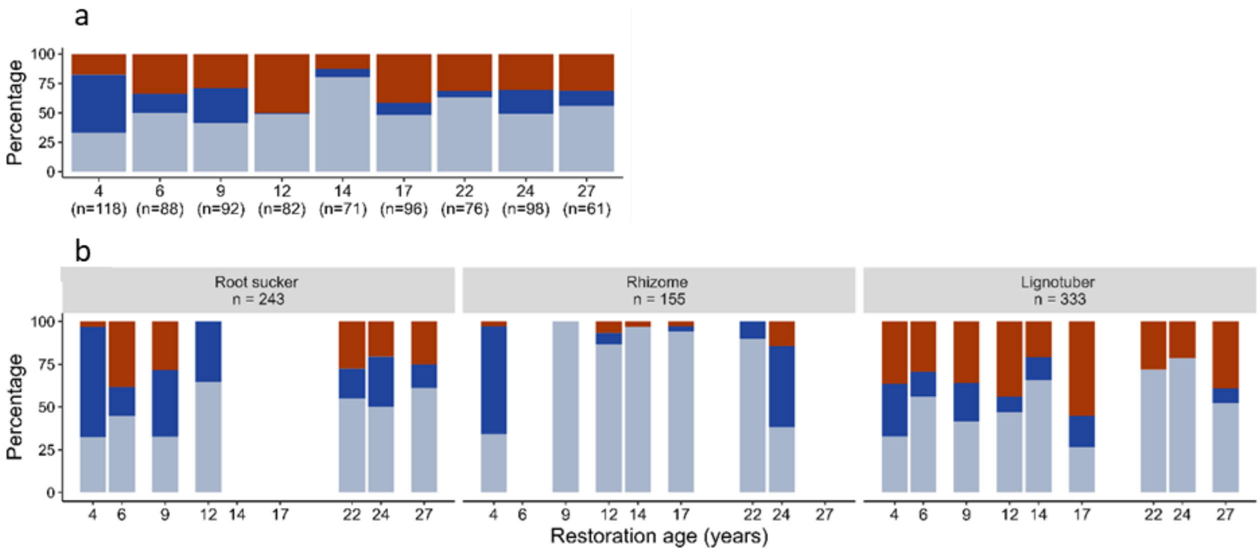

Figure 4.5: Percentages of responses to fire separated by a) resprouter type and b) species per restoration age. Red = did not resprout after fire, dark blue = resprouted at 6 months following fire but did not survive, light blue = survived 12 months following fire. Numbers in brackets for a) are sample sizes, sample sizes for b) ranged from 7–52.

For species found across 75% of all restoration ages, probability of resprouting did not vary with restoration age for any species, while probability of survival increased with age for both *S. involucrata* and *S. latifolia* (lignotuber species) and a hump-shaped response for *C. aculeata* peaking at age 9–14 (Figure 4.6). Age had a significant effect on all species survival (Table 4.4). Vigour increased with age for *S. involucrata* and *S. latifolia*, but slightly decreased for *C. aculeata* (Figure 4.6c; Table 4.4).

Table 4.4: Effect of restoration age on resprouting success. Bolding of values indicates significance at $P<0.05$, (s) denotes a smoother added to the predictor. A negative R^2 indicates the model is not explaining the variability of the dependent variable more effectively than a horizontal with an R^2 of 0, demonstrating poor model performance.

Response	Species	Predictor				
Resprout	*C. aculeata*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**3.376**	**0.633**	**5.336**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(age)	1	0.474	0.491	
		Adjusted R^2	-0.007			
	S. involucrata	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	0.146	0.131	1.113	0.266
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(age)	1.001	0	0.994	
		Adjusted R^2	-0.004			
	S. latifolia	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**2.023**	**0.318**	**6.381**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(age)	1	0.809	0.368	
		Adjusted R^2	-0.002			
Survival	*C. aculeata*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**1.497**	**0.335**	**4.466**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(age)	**1.945**	**17.95**	**<0.001**	
		Adjusted R^2	0.276			
	S. involucrata	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**-0.498**	**0.138**	**-3.615**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(age)	**1**	**7.579**	**0.006**	
		Adjusted R^2	0.029			
	S. latifolia	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**1.325**	**0.264**	**5.015**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(age)	**1**	**5.238**	**0.022**	
		Adjusted R^2	0.046			
Vigour	*C. aculeata*	*Linear terms*	*Estimate*	*SE*	*t value*	*P*
		Intercept	**29.495**	**5.037**	**5.856**	**<0.001**
		Age	-0.556	0.374	-1.488	0.142
		R^2	0.034			
	S. involucrata	*Linear terms*	*Estimate*	*SE*	*t value*	*P*
		Intercept	**17.073**	**2.336**	**7.309**	**<0.001**
		Age	0.239	0.142	1.686	0.095

	R^2	0.032			
S. latifolia	*Linear terms*	*Estimate*	*SE*	*t value*	*P*
	Intercept	13.056	9.108	1.434	0.156
	Age	**4.718**	**0.614**	**7.691**	**<0.001**
	R^2	0.441			

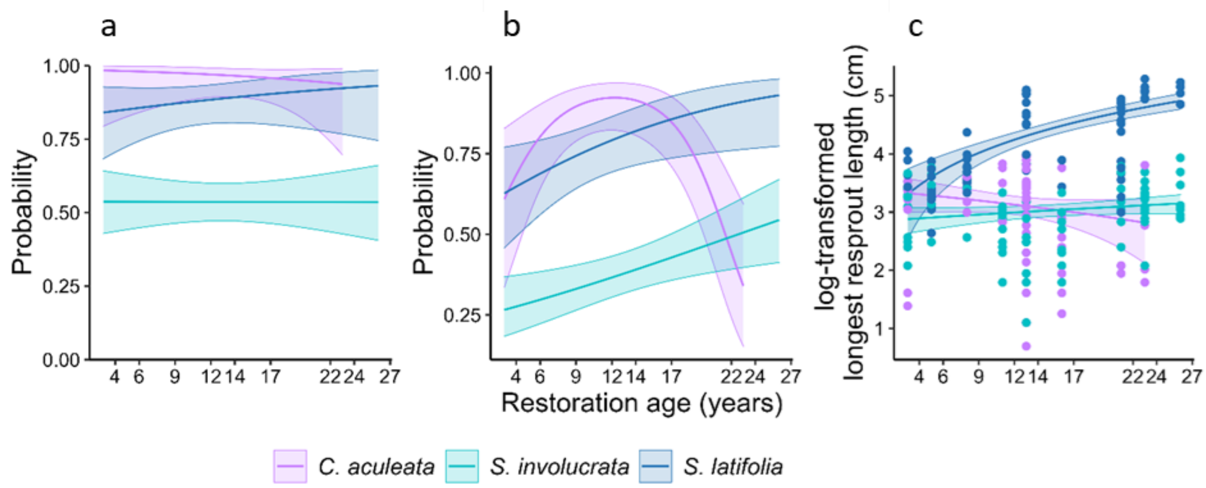

Figure 4.6: Predicted effects of restoration age on species a) probability of resprouting, b) probability of survival and c) log-transformed vigour at 12 months. Graphs have 95% CI. Vigour was transformed when graphing to allow for predicted relationships to be easily visualized.

Discussion

Following experimental fire in post-mining restored Banksia woodlands, we found that most species demonstrated high resprouting ability at ~5 months post-fire with survival reducing following the first summer (~12 months post-fire). Additionally, we found that pre-fire plant size and soil conditions influenced some species' survival and vigour, while restoration age influenced survival. Influences of resprouting success varied among resprouter types. Our results demonstrate that restoration age is important for resprouter survival, but attributes of plant size and soil conditions may be more informative for overall resprouting success. This calls into question the use of restoration age solely as a surrogate of resilience or stability.

Overall resprouting success

Following fire in restored Banksia woodlands, most species demonstrated high resprouting ability at ~5 months post-fire (54–98%). This is more variable than that observed in burnt revegetated woodlands in south-eastern Australia where resprouting ability across 12 native species at ~6 months following fire was lower in direct seeded plots (~85%) compared to both tubestock planted and remnant woodlands (both ~90%; Pickup et al., 2013). Differences in resprouting ability may reflect site establishment legacies (agriculture vs mining) further highlighting the potential impacts of site establishment on resprouting.

Post-fire survival rates (to ~12 months following fire) ranged from 28–91% (average = 57%; excluding *G. capitatum*), which is comparable to resprouter survival in post-mining restored Kwongan (diverse shrublands which share a similar set of species to Banksia woodlands) where 11–93% (mean = 52%) of individuals from ten lignotuberous species survived to one year following fire (Herath and Lamont 2009). However, resprouting success was higher in unmined Kwongan for the same set of species (79–100%, mean = 96%; Herath and Lamont 2009). Restored Kwongan resprouting rates for lignotuberous species is similar to post-fire survival rates in this study (survival = 50%).

Plant size influenced survival and vigour, but not resprouting probability

We hypothesized that plant size (assessed through log-transformed pre-fire canopy volume) would be important for the ability to resprout because buds, resources, and organ protection necessary for resprouting may develop with size (Clarke et al., 2013; Ott et al., 2019). Instead, we found that size does not significantly influence probability of resprouting and species relationships between size and resprouting success vary. For example, as hypothesized *S.*

involucrata resprouting probability increased with size, then reduced for larger individuals, potentially due to insufficient bud development in smaller individuals, or bud senescence in larger individuals (Hodgkinson 1998; Clarke et al., 2013). In contrast, *G. pithyoides, L. floribunda* and *C. aculeata* resprouting probabilities changed slightly with size, and size explains low amounts of variation for this response (R^2=-0.018–0.068). Minimal influence of plant size on initial resprouting after fire or coppicing has also been found by Vesk (2006) and Moreira et al., (2012b) in some species and growth forms studied, but not all.

We found reduced survival of the first summer following fire in larger individuals for four plant species, specifically both lignotuber species, one root sucker and one rhizome species. This reduction may be due to reduced resource availability in the summer resulting in larger individuals being unable to sustain their resprouts, potentially due to increased bud-senescence, burial or low stem counts preventing resource uptake (Keeley 2006; Enright et al., 2011; Clarke et al., 2013). For 43% of species, plant size was found in the top-ranked model (lowest AICc), demonstrating that other factors have a greater influence on survival than plant size. Conversely, we found that survival increased with plant size for three species (although not significantly for two species). In forest stands in Mediterranean Iberia (Casals et al., 2018) and thickets in South Africa (Strydom et al., 2023), post-fire resprouting success was higher in larger plants, or resprouting success varied with plant size (Giddey et al., 2022).

Vigour following fire is indicative of future plant persistence. For example, a vigorously resprouting individual may have more photosynthetic material available allowing greater resource gain (Marais et al., 2014). We found evidence of plant size increasing post-fire resprouting vigour in all species in this study, potentially due to increased resources in larger plants promoting quicker growth following fire. Similar evidence of vigour increasing with plant size has been found following fire and coppicing for resprouting individuals in intact ecosystems (Moreira et al., 2012b; Casals et al., 2018; Strydom et al., 2023).

Soil conditions influenced resprouter survival and vigour

Legacy effects of restoration establishment may influence soil characteristics such as compaction and field capacity which may impact responses to fire (Herath and Lamont 2009; Mounsey et al., 2021; Riviera et al., 2021). As hypothesised, soil characteristics influenced survival or vigour of most species, potentially due to individuals needing to rely on resources influenced by soil conditions over summer when water is limited. While we are unsure of resprouting success in intact Banksia woodlands, resprouter survival was higher in burnt intact than mined Kwongan (79–100%, mean = 96% vs 11-93%, mean = 52%; Herath and Lamont 2009). Due to differences in site attributes, and plant development between restored and intact sites, we may expect resprouting success to be higher in intact Banksia woodlands also.

We found consistent soil attributes effects on resprouting vigour among resprouter types. Specifically, soil compaction significantly reduced vigour in resprouting rhizome species which are shallow-rooted (<33 cm), likely due to limited root penetrability and changed soil and root architecture potentially influencing soil nutrient and water absorption (Rokich et al., 2001b; Herath and Lamont 2009). Furthermore, increasing field capacity significantly decreased survival and vigour for lignotuberous species. Field capacity may increase with soil depth in compacted soil profiles, which may promote water logging, thereby reducing resprouting success in plants with deeper root systems. This may explain the negative effect of field capacity on lignotuber species in this study. Differences in resource absorption of root structures among different plant types may help to explain the differences in the importance of soil conditions also (Wang et al., 2019) but further studies across a wider range of species and resprouter types are needed. Continued assessment of soil conditions as an influence on post-fire responses would also be valuable.

Increased importance of soil conditions on resprouter survival and vigour, as well as reduced survival may be partly due to the extreme weather conditions experienced in the first summer after burning when plants were ~8–11 months old. Post-fire maximum summer temperatures were ~0.9°C higher than the previous long-term average, with a record number of days over 40°C (Logan 2022). Such extreme climatic events are becoming more common (Breshears et al., 2021) and have led to substantial mortality of plants in the region (Challis et al., 2016; Ruthrof et al., 2018).

When fires occur during or after drought and/or heatwave conditions, resprouting success may be reduced (Pratt et al., 2014; Bendall et al., 2022a but see Enright et al., 2014; van Blerk et al., 2021). Reduced water availability had varied impacts on resprouting success in severely water stressed *Quercus* species (Resco de Dios et al., 2020), while Pratt et al., (2014) found variable plant survival following drought and fire among chaparral shrubs. Gower et al., (2015) found poorer resprouting success (measured using number and length of resprouts) following severe hail and fire events, which suggests a lack of carbohydrates drove poor resprouting success that could not be overcome by increased amounts of water. Alternatively, analysis of post-fire survival of the four most common Kwongan woody species in Enright et al., (2014) found resprouter survival did not change with different amounts of summer rainfall in the first year following fire suggesting that access to rainfall was not a limiting factor for survival. However, other studies suggest plant characteristics such as resprout organ protection, location and/or development are more important than drought intensity at driving resprouting success (Pausas and Paula 2019; Bendall et al., 2022b). This may partially explain the different survival rates between the resprouter types as plant characteristics differ. With only one summer drought of observations, it is not possible to determine what had a greater influence in our study (e.g., reduced water availability or plant characteristics). Due to uncertainty of the effects of extreme post-fire weather conditions on resprouting, post-fire responses following “average” summer conditions should not be expected to be different.

Restoration age is important for plant survival after fire

We investigated the effect of restoration age (as an indication of maximum plant age) on the three resprouting species that were found across most of the 23-year restoration chronosequence. Restoration age is often used to assume vegetation development and responses to disturbances (Chapter 2). We found that restoration age did not influence probability of resprouting. However, survival did increase with restoration age for the two lignotuberous species examined where fire tolerance may peak at intermediate fire intervals (Enright et al., 2011). Alternatively, *C. aculeata* (rhizomatous resprouter) survival reduced in ages >14 years potentially due to bud senescence (Fidelis et al., 2014). Similarly, Herath and Lamont (2009) found mixed effects of restoration age on lignotuberous species resprouter survival in post-mining restored Kwongan: survival was lowest in the youngest restoration age for five species, with three and two species having highest survival in the oldest or two oldest sites respectively. Where highest survival was observed in oldest restoration ages, survival was still substantially less than that in intact (unmined) Kwongan for the same species (Herath and Lamont 2009).

While we cannot be certain of the age of the resprouting plants, it is most likely that individuals recruited from seeds during the topsoil application processes which can trigger germination of these smoke-responsive species (Dixon et al., 2009). While low levels of inter-fire recruitment of these species do occur (Chapter 3), seedling establishment is limited (Stevens et al., 2016).

Other potential drivers of resprouting success

Our models of probability of resprouting and survival explain low amounts of variation suggesting other drivers influence resprouting success such as plant carbohydrates and nutrient reserves, water relations and competition (Moreira et al., 2012b; Matula et al., 2019; Resco de Dios et al., 2020), which we did not measure. These variables can be influenced by plant age and/or size further complicating potential resprouting responses. Furthermore, soil fungal communities typically develop with restoration age and can be difficult to return to their reference state in restoration (Hart et al., 2019). Altered fungal community composition may prevent the uptake of essential nutrients to promote plant survival (Ott et al., 2019). Additionally, all species are facultative resprouters which can influence bud and resource development trade-offs and survival. For example, facultative resprouters have been found to have reduced survival and shorter shoots than obligate resprouters following fire (Marais et al., 2014) while other studies report no differences between seed and resprout-based reproductive output in facultative resprouters (Cruz and Moreno 2001).

Drivers of resprouting success vary widely across the eight species we studied, and therefore we recommend a species-level approach to considering responses to fire in restored Banksia woodlands. Most species demonstrated high initial resprouting success with reduced survival of the first summer highlighting the importance of monitoring following the first summer post-disturbance. Plant size is an important determinant of resprouting success and yet did not correlate with restoration age in the species we examined, suggesting restoration age cannot be used as a proxy for resprouting success in restored environments. Despite wide interest in the development of a plant trait-based approach to restoration (e.g., Laughlin 2014; Carlucci et al., 2020; Coutinho et al., 2023), we found little consistency in responses among species with shared traits. We invite future research of species responses to disturbances in ecological restoration to inform vegetation development.

Chapter Five

The following chapter has been drafted in accordance with *Ecological Monographs*

The current manuscript is prepared for submission.

The following authors contributed to this manuscript as outlined below.

Authorship order	Contribution (%)	Concept development	Data collection	Data analyses	Drafting of manuscript
Ebony Cowan	80	X	X	X	X
Joe Fontaine	5	X	X		X
Ben Miller	4	X	X		X
Rachel Standish	4	X	X		X
Russell Miller	4		X	X	X
Willa Veber	4		X	X	X

By signing this document, the Candidate and Principal Supervisor acknowledge that the above information is accurate and has been agreed to by all other authors.

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Candidate

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Ecological resilience of restored Mediterranean-climate woodlands to experimental fire

Abstract

The ability of restored sites to recover from disturbances is a key component of restoration success. In fire-prone ecosystems, plant communities have adapted to fire, but the drivers of post-fire responses and resilience to fire in restored ecosystems are under-explored, particularly using experimental approaches. This understanding could indicate potential resilience of restored ecosystems to disturbance.

We implemented fine-scale experimental fires in a post-mining restoration chronosequence 14–27 years of age in Banksia woodlands, Western Australia. We sought to understand the effects of restoration age, fire impact, and soil conditions on post-fire regeneration and survival of Banksia woodland plant species in sites restored after mining. To assess early-stage resilience to fire, we calculated four metrics to describe ecosystem state: plant species density, species diversity, rarefied richness and functional redundancy, and compared how these changed following fire across the chronosequence of restoration ages and in comparison to near-by intact 'reference' Banksia woodlands. Additionally, we used ordinations and indicator species analyses to compare restored and reference sites.

In restoration sites, post-fire resprouting and seedling recruitment success was consistent across all ages, and was not influenced by fire impact or soil conditions. For obligate seeders, post-fire plant density, species diversity, rarefied richness and functional redundancy was not influenced by restoration age and were typically similar to reference sites. In contrast, resprouter species diversity decreased following fire in restored sites, and was significantly less than that observed in reference Banksia woodlands. Changes in diversity, rarefied richness and functional redundancy pre- to post-fire in restored sites were typically similar or less than that observed in reference sites. However, community composition of resprouters differed as resprouters were dominant in reference sites but not restored sites.

Our findings suggest that for restored sites able to sustain fire, resprouters demonstrated poor resilience to fire. More broadly, change following fire often did not reflect that observed in reference sites. Resilience metrics and comparisons of pre-disturbance restored and reference states yielded different interpretations of resilience, highlighting the importance of utilizing reference data and a broad range of metrics to fully understand responses of restored ecosystems to fire.

Introduction

Ecological restoration to improve the condition of degraded ecosystems is crucial for biodiversity conservation, with responses to disturbances being an important determinant of restoration success (Standish et al., 2014; Miller et al., 2017; Buisson et al., 2021; Young et al., 2022; Chapter 2). Determining an ecosystem's ability to absorb changes in state variables, and persist after a disturbance (i.e., ecological resilience; Holling 1973) is vital to understanding ecosystem dynamics and can help restoration practitioners determine successional trajectories. After a disturbance, resilient sites may be characterized by the maintenance of species and ecosystem structure and function (Walker et al., 2004). However, quantifying resilience is difficult, partly due to the vagueness of the term and differentiating between desirable and undesirable changes to ecosystem states (Standish et al., 2014). This is particularly true in ecological restoration projects because resilience may develop over time, meaning that newly restored sites may revert to a degraded state after disturbance rather than following a desirable successional trajectory towards a reference state. Comparisons to reference sites are required to assess the restored site's responses to disturbance and specifically, if responses of restored ecosystems are desirable, and if resilience is attained (Ross et al., 2004; Miller et al., 2017; McKenna et al., 2019; Harries et al., 2023).

Fire is a common disturbance globally that can substantially alter ecosystem development through changing species composition, ecosystem structure and function, which can impact ecological resilience (Keeley et al., 2011; Pausas and Keeley 2014; Pausas and Keeley 2019). In fire-prone environments, plant species have developed strategies to promote their regeneration and resilience following fire (Pausas and Keeley 2014). Key strategies include resprouting from surviving plant biomass (where species are referred to as resprouters; Clarke et al., 2013), or regeneration from fire-responsive seedbanks following complete adult mortality (obligate seeders) with seeds often requiring exposure to heat or smoke for germination (Keeley et al., 2011). Development of these fire-response mechanisms is typically shaped by fire intervals; appropriate intervals allow sufficient development of seedbanks and resprouting capacity, whereas seeding and resprouting may be compromised if fire intervals are shorter than the time to reproductive or resprouter maturity (immaturity risk) or longer than the lifespan of mature plants, seedbanks and resprouting organs (senescence risk; Clarke et al., 2013; Enright et al., 2014; Pausas and Keeley 2014; Agne et al., 2022). Initial (pre-disturbance) ecosystem states, and ecological (e.g., soil) and fire legacies (e.g., previous fire severity and coverage) also influence these responses and may be important for post-fire resilience (Johnstone et al., 2016; Newman 2019). More generally, the effects of legacies of the restoration process on disturbance responses are underexplored in ecological restoration despite their importance for restoration success (Chapter 2).

Restoration projects may have their own set of unique complexities that may not be observed in comparable reference ecosystems, and vice versa. For example, in fire-prone restored ecosystems, the development of resprouting and recruitment capacities may differ from that of intact ecosystems. In intact ecosystems, established resprouters are capable of resprouting shortly after disturbance, whereas restoration projects established from transferred topsoil are reliant on seedbanks until resprouting species have had time to develop root-stock and necessary buds (Ross et al., 2004; Herath and Lamont 2009; Waryszak et al., 2021; Gerrits et al., 2023). Intact ecosystems also contain structural elements that may contribute to their recovery such as facilitation of seedling establishment due to beneficial microclimates created by large trees or leaf litter (Enright and Lamont 1989; Dimson and Gillespie 2020). Additionally, legacy effects of the restoration process such as soil compaction or altered soil profile composition may influence vegetation structure and development, or plant species responses to fire by reducing seedling establishment and altering rooting patterns (Carrick and Krüger 2007; Herath et al., 2009; Rokich et al., 2016; Riviera et al., 2021; Figueiredo et al., 2023). The impact of such factors has mixed effects on resprouting success (Chapter 4) and may influence soil seedbank composition (Chapter 3), highlighting their potential impacts on the resilience of restoration projects.

Here, we implemented fine-scale experimental fires to investigate early-stage (~17 months post-fire) resilience to fire in Banksia woodlands restored after sand mining in southwestern Australia. This region has a Mediterranean-type climate where plant traits adapted to fire are dominant (e.g., resprouting, fire-stimulated flowering, and fire-cued seed germination), reflecting the historical occurrence of fire in the landscape (He et al., 2016; Lamont and He 2017). Understanding thresholds of resilience soon after a disturbance can allow for the early identification of an undesirable development trajectory and the consideration of appropriate management strategies that may encourage restoration success (Chapter 2). Using a chronosequence of restored sites aged between 14–27 years since the onset of restoration (ages <13 years were not burnt due to insufficient biomass limiting fire spread), we sought to determine the effect of restoration age on: i) fire impact, which we expect to influence the ii) post-fire regeneration and its drivers (measured ~5 months following fire) and survival (measured ~17 months following fire) for seedlings and resprouts, and iii) the early-stage resilience to fire. We expected restoration age to be a key driver of ecosystem development and response to fire, and age is commonly used to assess restoration development and success (Chapter 2). We quantify early-stage resilience to experimental fire through assessments of plant density, Shannon-Weiner species diversity, rarefied richness, and functional redundancy (hereafter collectively 'resilience metrics'). We also compare changes in resilience metrics both pre- and post-fire (after Holling 1973) and between restored and reference (i.e., intact native) Banksia woodlands to infer resilience in the context of ecosystem development along a restoration trajectory towards a desired state. We also utilize species composition analyses (ordination, indicator species analysis) to provide an additional assessment of resilience based on plant community similarity between restored and reference sites.

Methods

Study region

Banksia woodlands are a highly speciose (>600 plant species) fire-prone ecosystem with 2–3 co-dominant *Banksia* tree species and a diverse sclerophyll understory (Stevens et al., 2016; Ritchie et al., 2021). They predominantly occur on the Swan Coastal Plain in the southwest of Western Australia, where minimum tolerable fire intervals are estimated at 8–16 years based on plant demography and fuel accumulation (Burrows and McCaw 1990; Hobbs and Atkins 1990; Wilson et al., 2014; Valentine et al., 2014; Ritchie et al., 2021; Tangney et al., 2022) reflecting the influence of fire on plant adaptations. Post-fire resprouting and obligate seeding are common traits among plant species (~78 and 22% of species respectively; Fontaine and Standish 2019) with many species able to both resprout and recruit from seeds following fire (i.e., facultative resprouters). Most species store their seeds in the soil (~70%; Rokich et al., 2001b; Stevens et al., 2016) with seedbanks typically persistent (>1–40 years; Onans and Parsons 1980) and usually triggered for germination by smoke or heat (Bell et al., 1993; Turner et al., 2022). Canopy seed storage (serotiny) and release following fire is also present (e.g., *Banksia* species).

Study site

This study was conducted at a sand mine operated by Hanson Heidelberg Construction Materials (hereafter ‘Hanson’), approximately 25 km northeast of Perth, Western Australia (lat. -31.76, lon. 115.95). The mine is in the Bassendean dune system (Bastian 1996) which has acidic, nutrient-poor coarse sands with poor water-holding capacity (Salama et al., 2005). The study site experiences a Mediterranean-type climate. At the nearest climate station (~10 km NE of the study site), maximum and minimum summer (January) temperatures averaged 33.5 and 17°C respectively, with average winter (July) temperatures of 18 and 8.3°C between 1980 and 2020 (Bureau of Meteorology 2021). Mean annual precipitation was 634 mm for the same period (Bureau of Meteorology 2021).

Hanson has restored open-cut sand mine pits to Banksia woodlands most years since 1991. Before mining, vegetation is cleared and the top 10 cm of topsoil (which contains most of the soil seedbank) is removed and stored (typically <3 months to maximize seed viability) with this topsoil essential for plant species recruitment during restoration (Gerrits et al., 2023). During mining, the top 5–50 m of the soil profile is removed and once complete, sites are filled with sand or overburden (low vs high amounts of organic matter respectively; B. Fruin & D. Hardy, pers. comm., November 2021) to a depth of 2–4 m, with the 10 cm layer of topsoil deposited on top (Stevens et al., 2016). To reduce compaction, sites are generally ripped to 10 cm depth (after topsoil deposition; Table 5.1) which may influence future soil conditions. Subsequent seeding and planting of difficult-to-establish species, including resprouters and serotinous species, often occurs within 4 years of topsoil deposition. Typically, germination of smoke-responsive species occurs within the first year after topsoil application, potentially due to the release of the same active ‘smoke’ chemical during topsoil transfer and ripping (Merritt et al., 2006; Daws et al., 2014).

Table 5.1: Age, soil conditions and restoration practices of restored Banksia woodlands sites surveyed.

Restoration age (years)	Year established	Soil compaction (MPA)		Soil field capacity (%)	Ripping depth	Soil profile composition
		10 cm	30 cm			
14	2007	0.64–0.88	1.28–1.48	14–26	Shallow	Sand
16	2005	0.7–1	1–2.16	19–24	None	Clay
17	2004	0.76–1.16	1–1.48	19–26	Shallow	Sand
18	2003	0.64–0.82	0.84–1.48	20–24	None	Sand
22	1999	0.9–1.18	1.18–2.26	9–23	Shallow	Sand
24	1997	0.68–0.88	0.78–1.14	11–25	Deep	Overburden
27	1994	0.86–1.44	2.4–4.4	9–20	None	Overburden

Soil compaction data is the range of averages per plot, while field capacity is the range of plot values (n=5). Ripping depth: shallow = 10–15 cm, deep = 50 cm. mV = millivolts, VSW = volumetric soil water, MPA = megapascals.

Restored Banksia woodlands data collection

In October – November 2019 (spring), we measured plant species composition in seven restoration ages between 14–27 years since the beginning of restoration and the placement of topsoil (Table 5.1). We established five 4×4 m (16 m^2) plots per restoration age, with plots at least 20 m apart. In each 4×4 m plot, we counted the number of established individuals (> 2–3 years old) for all perennial species. In two 0.7×0.7 m subplots nested in the southwest and northeast corners of each 4×4 m plot, we also counted all individuals of all species, including annuals and seedlings of perennial species.

In May 2021 (autumn), restoration sites were burnt in experimental prescribed burns by the Western Australia Department of Biodiversity, Conservation and Attractions (DBCA). Fire was applied directly to plants and combustible litter in plots using drip torches to ensure that plots were burnt. Fire was not attempted in sites <13 years old given that the high cover of bare ground was likely to prevent fire spread (DBCA, pers. comm., June 2019; Figure S5.1).

Fire impact was assessed within three days of the burns. To do so, we estimated fire coverage as the percentage area of each subplot burnt (largely based on the presence of burnt litter) and fire severity as the proportion of plants scorched within each 4×4 m plot. For trees, the estimated percent of crown burnt and height of charring on stems were also recorded.

In October 2021 (spring; ~5 months following fire) we assessed initial post-fire regeneration in the burnt plots. Mature perennial plants in the 4×4 m plots were again counted by species and recorded as either survivors (not impacted by fire, still alive) or established resprouts (individuals which had been burnt by fire and subsequently resprouted). In the 0.7×0.7 m subplots, all individuals were counted and classed as follows: seedlings (individuals which had germinated within the first five months following fire), survivors or established resprouts (defined as above). Due to low numbers of smoke and/or heat-responsive species seedlings in some plots, particularly plots with little fire coverage, additional 0.7×0.7 m subplots were added in the other corners (southeast and northwest) of the 4×4 m plots until at least 50 perennial seedlings were recorded in total for each plot. Twelve (34%) 4×4 m plots had two subplots, 20 (57%) had four subplots and three (9%) had eight subplots. In October 2022 (spring; ~17 months post-fire) we assessed the survival of seedlings and resprouts by re-counting individuals in the burnt plots using the same methods.

Reference Banksia woodlands data collection

Data in reference (i.e., intact, native) Banksia woodlands were collected from sites 1.3–8.5 km from the Hanson mine (Table S5.1). Two sites (10 and 22 years since last fire) were measured one year following fire (hereafter post-fire reference sites), with nine sites measured at varying intervals from 4–49 years since fire (hereafter pre-fire reference sites). Each site had 5–7 replicate 4×4 m plots. All perennials were measured in spring using the same methods as above.

In the two sites monitored one year following fire, plants were recorded as survivors or established resprouts as per above, with seedling regeneration assessed in two replicate subplots, the same size as those used in restored plant data collection (0.7×0.7 m). Fires in reference Banksia woodland plots were conducted as part of DBCA's prescribed burning program. Data was collected as part of a broader project investigating fire interval effects in intact Banksia woodlands.

Explanatory environmental variables in restored sites

To determine the effect of soil conditions on seedling establishment and resprouter vegetation regrowth, we assessed soil compaction in dry soils in November 2021 (late spring). We measured soil compaction (25 replicates per age) using an Eijkelkamp Penetrologger 6.08. We did not expect field capacity (water holding capacity after excess water has drained) to be as variable as compaction due to soil profiles being established in the same manner within each restoration age (Table 5.1). Therefore, we collected one replicate per plot to 6 cm in the soil profile to measure field capacity. In the laboratory, soils were wet until saturation occurred, drained for 24 hours and oven-dried at 80°C until constant weight was achieved.

Data processing

Post-fire states and early trajectories are driven by initial responses to fire (i.e., regeneration and initial survival). To capture potential differences in the drivers of these responses, we used different plant community assemblages to assess i) drivers of post-fire responses (regeneration and survival) and ii) early-stage resilience to fire (Figure 5.1).

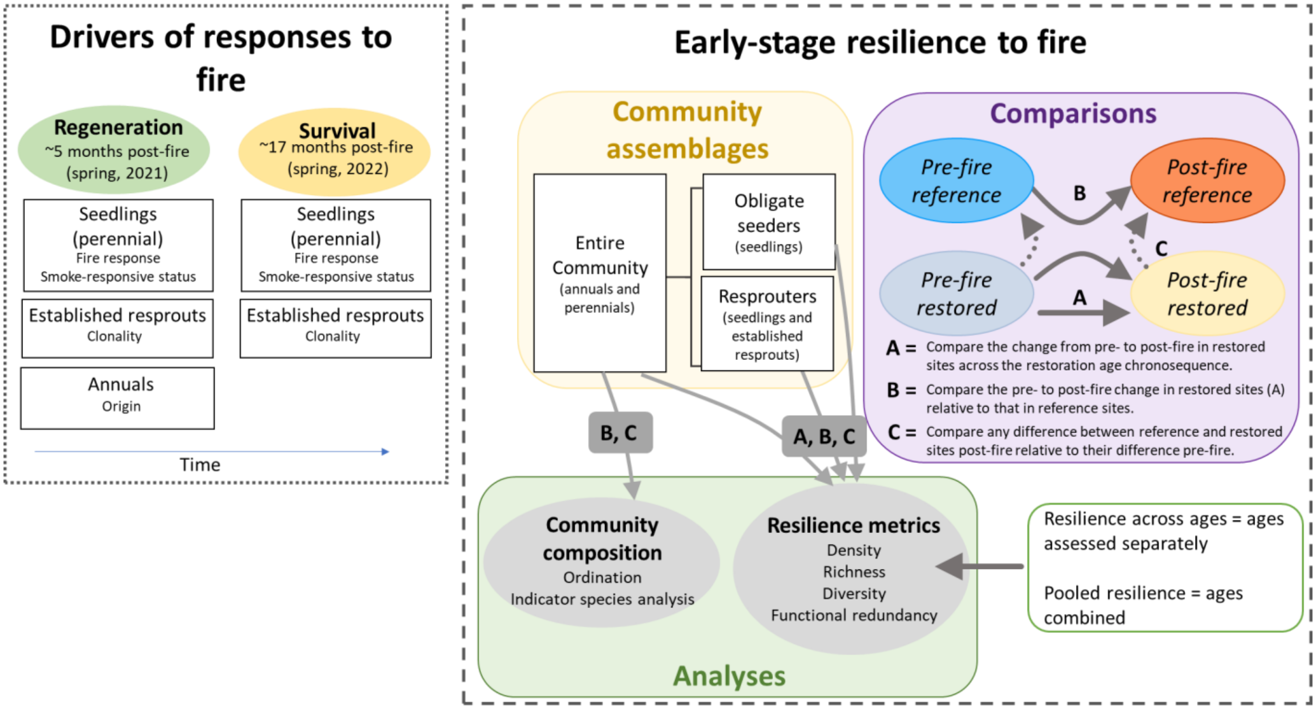

Drivers of responses to fire
Regeneration
~5 months post-fire
(spring, 2021)
Survival
~17 months post-fire
(spring, 2022)
Seedlings (perennial)
Fire response
Smoke-responsive status
Seedlings (perennial)
Fire response
Smoke-responsive status
Established resprouts
Clonality
Established resprouts
Clonality
Annuals
Origin
Time
Early-stage resilience to fire
Community assemblages
Entire Community
(annuals and perennials)
Obligate seeders
(seedlings)
Resprouters
(seedlings and established resprouts)
Comparisons
Pre-fire reference
Post-fire reference
Pre-fire restored
Post-fire restored
A
B
C
A = Compare the change from pre- to post-fire in restored sites across the restoration age chronosequence.
B = Compare the pre- to post-fire change in restored sites (A) relative to that in reference sites.
C = Compare any difference between reference and restored sites post-fire relative to their difference pre-fire.
B, C
A, B, C
Community composition
Ordination
Indicator species analysis
Resilience metrics
Density
Richness
Diversity
Functional redundancy
Analyses
Resilience across ages = ages assessed separately
Pooled resilience = ages combined

Figure 5.1: Simplified diagram of plant community responses and separation of plant communities used in this study. Ovals refer to response variables while rectangles with a white background represent plant community groups. Investigations of the drivers of responses to fire (enclosed by the grey dotted rectangle) assess the regeneration and survival of different community groups based on regeneration mode and plant trait types using mixed models. Assessments of early-stage resilience to fire (enclosed by the grey dashed rectangle) utilise comparisons of both pre-fire and post-fire data, at restored and reference sites (purple box), for different community assemblages (yellow box). Analyses (green filled box) are conducted for these comparisons and community assemblages as specified by the arrows and comparison type (A, B or C). Comparison type 'A' compares both resilience across restoration ages and pooled resilience for the resilience metrics (i.e., compares restored pre-to-post only), while comparison type 'B' (bent grey arrows) compares pre and post-fire change for both restored and reference Banksia woodlands. Early-stage resilience to fire is grouped by resilience across ages (where ages are analysed separately), or pooled resilience (where ages are combined; unfilled green box). For regeneration responses, resprouts are analysed separately based on mode of regeneration (i.e., seedlings vs established resprouts), while for early-stage resilience, community assemblages are separated by species trait types, so resprouter seedlings and established resprouts are combined.

We expected drivers of post-fire responses (i.e., regeneration and survival) to vary among dominant fire-response mechanisms (seedling vs resprouting). Therefore, we assessed the regeneration response separately for these two mechanisms: seedling recruitment of annuals and perennials, and resprouting of pre-fire established individuals (hereafter 'established resprouts'; Figure 5.1). Survival of ~5-month post-fire individuals to ~17 months was assessed for perennial seedlings and established resprouts, but not annuals due to their short life cycles and germination response being more influenced by climatic conditions than fire (Saatkamp et al., 2011; Dwyer and Erickson 2016). Separation of plant community assemblages was based on species-level traits that are expected to have a strong influence on fire response; seedlings were separated by the smoke-responsive status of their seedbank and their fire-response type (obligate seeder vs resprouter), while established resprouts were separated based on clonal vs non-clonal growth habit (Supplementary text S5.1; Figure 5.1). Data on plant traits were collated from relevant databases (Table S5.2) and supplemented with field observations (E. Cowan, pers. obs., 2021-2022).

To assess early-stage resilience to fire, we compared the ~17 month post-fire restored sites to pre-fire Banksia woodlands in both restored and reference sites (reference post-fire data collected 12 months following fire). Early-stage resilience to fire was assessed with ~17 month post-fire data as plants were established and reflected the successional trajectory. Because plants (particularly obligate seeders) senesce over time, density and richness decline with increasing fire intervals (Hobbs and Atkins 1990; Enright et al., 2014) or time since the onset of restoration (Standish et al., 2021, 2023). Therefore, we separated our reference sites into groups based on their fire intervals for comparison with pre- and post-fire restored sites. For post-fire reference sites, we used two sites for analysis which were burnt at different fire intervals (10 vs 22 years since last fire; Table S5.1). Due to substantial differences in density (Figure S5.2a) we assessed these sites separately. For pre-fire reference sites, we grouped sites into three ages classes: 4 years post-fire (two sites), 10–24 years since fire (six sites) and 49 years since fire (one site) as density and richness were similar among these age groups (Table S5.1; Figure S5.2). Among these different ecosystem types (restored vs reference, pre- vs post-fire), we separated the plant community into three assemblages based on mode of regeneration: 1) the entire community (all annuals and native perennials), 2) obligate seeders (perennial) and 3) resprouters (perennial; Figure 5.1). Resprouters are composed of both seedlings and established resprouts to allow us to assess their resilience based on plant trait groups. Annuals were not assessed on their own for the reasons mentioned above.

Data analysis

For all analyses, we removed ephemeral species (i.e., Orchidaceae and *Drosera* species; making up <2% of counts) as variation in yearly weather patterns influenced the timing of their aboveground presence. We also removed invasive perennials due to their low abundance across the study (<6% of counts). Plants unaffected by fire (individuals not burnt) were removed from the dataset so we could quantify the effect of fire on burnt plants only. Analysis was conducted in R Studio (R Core Team 2020) with data visualisations created using *ggplot2* (Wickham 2016), *cowplot* (Wilke 2020) and *ggnewscale* (Campitelli 2022). We interpreted a lack of overlap in 95% confidence intervals (CI) as evidence of a statistical difference at $p<0.05$ (Ramsey and Schafer 2002).

Quantifying drivers of post-fire seeding and resprouting responses in restored Banksia woodlands

To assess post-fire regeneration and survival in restored Banksia woodlands, we first modelled different plant community groups (Figure 5.1) of restored Banksia woodlands against restoration age, fire impact, and soil variables. However, due to similar responses across the restoration chronosequence and little impact of plant traits, fire impact, and soil conditions, we pooled species counts per plot and restoration age to provide an assessment of post-fire seedling and resprouting responses. See Supplementary text S5.2 for detailed modelling procedures.

Assessments of early-stage resilience to fire

We assessed early-stage resilience to fire using three approaches: 1) resilience across restoration ages (restoration age analysed individually), 2) pooled resilience (restoration ages combined) and, 3) changes in community composition pre- and post-fire, and compared with reference sites

(Figure 5.1). Approaches one and two quantified resilience using ‘resilience metrics’, see below; while changes in community composition were assessed using ordinations and indicator species analyses. All of these measures are commonly used to quantify resilience and changes following disturbances (Chapter 2).

Resilience across restoration ages

We expected restoration age to influence early-stage resilience to fire due to reproductive or resprouting capacity potentially developing with time. Analysis of seedbank development (Chapter 3) and resprouter responses to fire (Chapter 4) at Hanson has revealed mixed importance of restoration age, and we sought to determine its effect on the responses of the entire plant community to fire. Therefore, for our first assessment of resilience, we assessed the impact of fire on ecosystem states at the chronosequence level (i.e., assessed pre- and post-fire states per restoration age; hereafter ‘resilience across ages’; Figure 5.1). For each restoration age, we compared if restored states were similar to reference states by calculating means and 95% CIs of the previously mentioned community assemblages and reference site groups (Table S5.1). We considered restored site states to reflect reference site states if 95% CIs overlapped. For the reference sites summaries, ages were combined within pre- and post-fire groupings due to little difference in the values of most metrics.

Pooled resilience

To provide a broader overview of restored sites resilience to fire, means and 95% CIs for restored pre- and post-fire, and reference pre- and post-fire states across all restoration ages (here-after ‘pooled resilience’) were calculated. Using these data, we assessed the resilience of the restored sites in comparison to reference sites (Figure 5.1). This approach permitted the quantification of change post-fire in restored sites versus that of reference sites. These comparisons were based on the amount and direction (positive vs negative) of change in states of resilience metrics, and asked: A) how did restored sites change following fire (compared restored pre- vs post-fire states), B) is resilience in restored sites similar to that of reference sites (i.e., has restored sites resilience to fire been restored; compared change from fire in restored vs reference), and C) are restored sites on a trajectory towards reference states following fire (compared any differences in post-fire restored and reference states, versus pre-fire restored and reference states; Figure 5.1).

Resilience metrics

We assessed both resilience across restoration ages and pooled resilience using four metrics (i.e., resilience metrics; Figure 5.1). The metrics were: density per species, Shannon Weiner diversity, rarefied richness and functional redundancy of the plant community. Density per species, Shannon Weiner diversity, and rarefied richness are commonly used metrics to assess resilience and responses to disturbances in both restored (Chapter 2) and intact ecosystems (Albrich et al., 2020; Nikinmaa et al., 2020), while assessments of functional redundancy are used less but provide an alternative view of resilience that incorporates traits (Chapter 2; Walker 1994; Standish et al., 2014).

Metrics were calculated for each community assemblage. Density measures were assessed within smoke-response classes (smoke-responsive vs unlikely smoke-responsive) to investigate the different responses to fire, but diversity, rarefied richness and functional redundancy were not, as some ages had low replication of species in trait groups, preventing the calculation of metrics. Shannon Weiner diversity is based on the number of species and relative abundances, while rarefied richness provides an indication of expected richness based on sample sizes (Hurlbert

1971; Oksanen et al., 2020). Rarefied richness was calculated to account for varying sample sizes between pre- vs post-fire and restoration vs reference sites. Both rarefied richness and diversity were calculated in the R package *vegan* using the functions “rarefy” and “diversity” respectively (Oksanen et al., 2020).

Functional redundancy measures the level of redundancy in an ecosystem based on species counts and their trait values (Walker 1992; Díaz and Cabido 2001) and may be a proxy measure of resilience (Standish et al., 2014; Chapter 2). Theory suggests that communities with more redundant species (i.e., more species occupying a similar functional role to each other) should be buffered against the loss of ecosystem functioning and future resilience even if individual species are lost (Díaz and Cabido 2001; Oliver et al., 2015; Biggs et al., 2020). Lower functional redundancy typically means that a greater portion of species are performing functions not performed by other species, which may alter persistence pathways, future ecological functioning, and resilience following a disturbance (Walker 1992; Biggs et al., 2020). We calculated functional redundancy using a variety of plant traits that may influence community responses to fire, including: fire-response, longevity, species origin, growth form, smoke-responsive status, seed storage location, microbial associations, seed mass and specific leaf area (Table S5.3). Functional redundancy was calculated by first determining species similarity in trait space using Gower distances in the *FD* package (Laliberté and Legendre 2010; Laliberté and Legendre 2014). Gower distances can tolerate missing trait data (Brown et al., 2012). Next, using trait similarity and species density, in the *adiv* package (Pavoine 2022) we calculated functional redundancy using the “uniqueness” function. Removal of traits where a high proportion of species had missing trait data had minimal influence on functional redundancy values (Figure S5.3), so we kept all traits in the analyses.

Assessments of resilience based on community composition

In restoration projects, a common challenge is restoring a similar community (typically in terms of the number of species and their abundance) to that in reference ecosystems (e.g., Herath et al., 2009; Mounsey et al., 2021; Riviera et al., 2021). Therefore, an important component of resilience in restored ecosystems is determining the similarity between restored and reference sites (Chapter 2). Using data on the entire plant community in restored and reference sites across pre- and post-fire states, we conducted an indicator species analysis, and nonmetric-multidimensional scaling ordination (NMDS). We separated our sites by age to determine potential successional trajectories in restored sites and changes with fire, and how this compares to reference ecosystems.

To understand how species trait dominance contributes to resilience and change between sites and their age, we conducted an Indicator Species Analysis (ISA). Species with high indicator values suggest high frequency and abundance within a given age (De Cáceres and Legendre 2009). We combined indicator species by trait type within ecosystem type (restored vs reference) and site age for ease of visualization due to the high number of indicator species. ISA was conducted in the R package *Indicspecies* (De Cáceres and Legendre 2009). We report indicator species where $p<0.05$.

To assess ecological resilience based on the return of sites to their pre-disturbance state or a reference state, we conducted a 3D NMDS using the Hellinger transformed Bray Curtis similarity of pre-fire and ~17 month post-fire restoration, and reference (pre- and post-fire) Banksia woodlands. The Hellinger transformation divides all values in a row (site) by the row sum, and then square root transforms these values and is appropriate for datasets with many zeros, such as the dataset used here (Legendre and Gallagher 2001; Legendre and Legendre

2012). NMDS was conducted for the entire community (annuals and native perennials) in the R package *vegan* (Oksanen et al., 2020). We added polygons for each ecosystem type (restoration vs reference, pre- vs post-fire), and centroids for each age for ease of visualization. We also connected pre-fire to post-fire restoration age centroids using arrows to show how these communities have shifted following fire. Due to density differing between plant trait types and ecosystem types, and the potential impact on similarity in composition, we added a biplot of the proportion of individuals per plot for the previously defined plant trait classes (i.e., native obligate seeder, native resprouter, native annual and invasive annual) using the “envfit” function (Oksanen et al., 2020). We used analysis of similarity (ANOSIM) between ages and ecosystem type in *vegan* (Oksanen et al., 2020) to determine if groups were different.

Results

Characterising Banksia woodlands

Across the entire restoration chronosequence, we found 113 species including 5 invasive perennial species. Of these 108 species (excluding invasive perennials), 49 were resprouters, 26 obligate seeders, 19 native annuals and 14 invasive annuals. Of the native perennial species, 19 (73%) obligate seeders and 36 (73%) resprouters were smoke-responsive (Table S5.4). For species capable of resprouting, there was 24 clonal and 25 non-clonal species respectively in restored sites. Twenty-seven species found pre-fire were not found post-fire and 63% of these were resprouters, with 16 species found in post-fire only (63% of these were native annuals; Table S5.4).

Of the 108 species found in restoration sites (excluding the 5 invasive perennial species), 93 (86%) were also found in reference Banksia woodlands (Table S5.4). There were an additional 65 species found in reference sites only, with the majority of these being perennial species (38 perennial resprouters, 15 perennial obligate seeders; Table S5.4). Eleven species were found in restored sites but not reference sites (6 invasive annuals, 4 resprouters; Table S5.4).

Fire impact in restored Banksia woodlands

Fires were not attempted in restoration ages <13 years due to high amounts of bare ground restricting fire spread (DBCA, pers. comm., June 2019; Figure S5.1). Fire severity (percentage of shrubs scorched) in restoration plots was highly variable and generally increased with restoration age (55–91%), although not significantly based on lack of confidence interval overlap (Figure 5.2a). Similarly, fire coverage (i.e., the amount of each subplot burnt) generally increased with restoration age and was highest in the oldest site (65% in age 27 vs 5–30% in ages 14–24; Figure 5.2b).

Experimental burns had little impact on tree canopies as 85% of plots had >90% unburnt tree canopies, and no plots had >50% tree canopy unburnt. Forty percent of plots had charring on tree stems, with 25% of plots having char heights <25% of the total tree height (typically <20 cm high) on at least one tree. One plot had charring at 50% of the height of one tree.

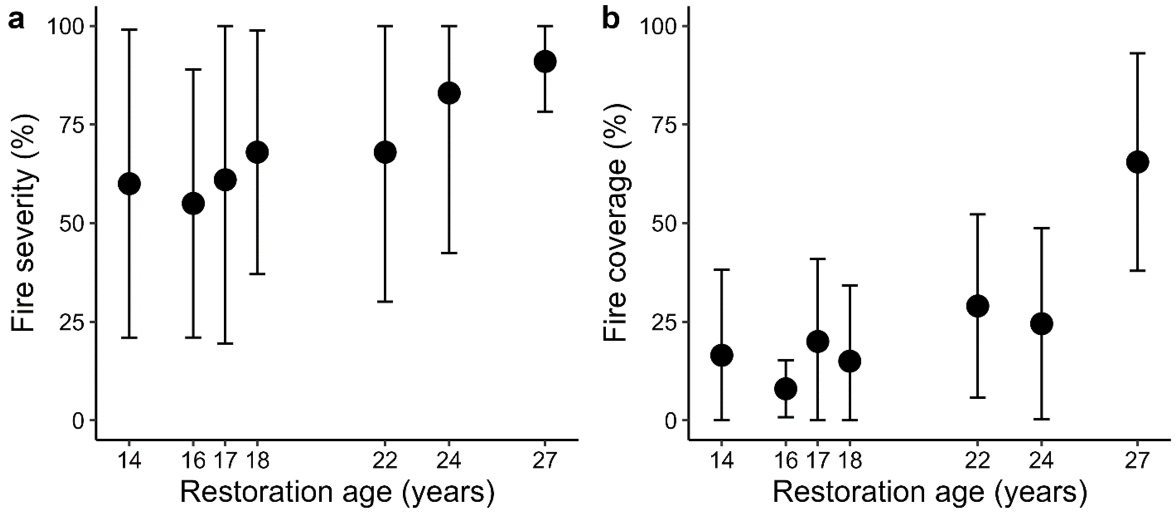


Figure 5.2: Mean±95% CI of percentage of fire a) severity and b) coverage across the restoration chronosequence.

Post-fire regeneration and survival

At ~5 months post-fire, there was evidence of recruitment from the seedbank for both perennial and annual species with substantial seedling density across most restoration ages (Figures S5.4a-c). When pooled across restoration ages, density of smoke-responsive perennials were more variable than those of unlikely smoke-responsive species (Figure 5.3a). Across the restoration chronosequence, restoration age, native vs invasive origin (assessed for annuals only), fire-response type (assessed for perennial seedlings only), and fire coverage had no clear effect on seedling density (Figures S5.4a-c; Table S5.5).

Following fire, persistence via resprouting occurred across the restoration chronosequence. The proportion of pre-fire established resprouters (those capable of resprouting) that had resprouted and survived fire varied widely (Figure S5.4d). Mean resprouting proportions was similar between non-clonal (0.47) and clonal (0.31) resprouters (Figure 5.3b), with resprouting proportions also similar across most restoration ages (Figure S5.4d). Restoration age and fire severity (the proportions of plants scorched) did not have a significant effect on the proportion of plants that resprouted, nor did interactions between age or severity with clonality (Table S5.5).

The proportion of seedlings and resprouts of perennial species present at ~5 months that survived to ~17 months was variable across the restoration chronosequence (Figure S5.5). The average survival of perennial seedlings was similar regardless of a species' smoke-responsive status or fire-response type (mean proportions = 0.15–0.20; Figure 5.3d). For established resprouters, survival from ~5 to ~17 months was relatively high and did not differ among clonal and non-clonal species types (proportions = 0.75 vs 0.76; Figures 5.3e, S5.5c). When separated by restoration age, both perennial seedlings and established resprouts survival was not influenced by restoration age, soil compaction or field capacity (Table S5.6). On average, 43% of resprouters present pre-fire were alive at ~17 months post-fire.

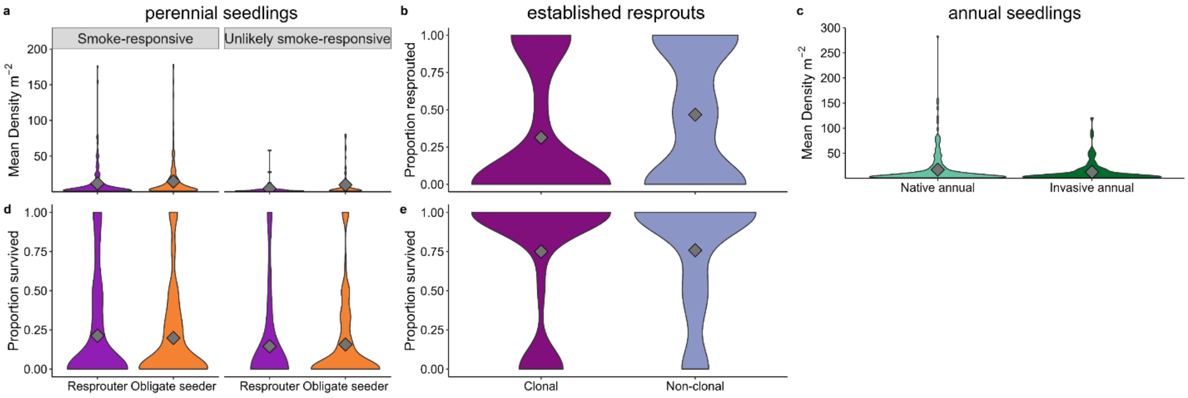


Figure 5.3: Violin plots for regeneration at ~5 months post-fire of a) perennial seedlings, b) established resprouts (proportion of pre-fire individuals that had resprouted at ~5 months following fire) and c) annual seedlings, and ~17 month survival proportions (of ~5 month data) of d) perennial seedlings and e) established resprouts. Data are species counts (a,c) or proportion (b,d,e) per plot and restoration age combination. Grey diamond = mean. n = 31–243.

Resilience across restoration ages

For the entire community (annuals and native perennials), the average density of individuals per species pre-fire were typically lower in restoration ages 14–22 years compared to reference sites, while ages 24–27 were similar to reference sites (Figure 5.4a). Following fire, density significantly increased in all restoration ages, with restoration ages 22—27 having higher density compared to restoration ages 14–18 years (5.8–9.7 vs 12.2–17.5 individuals m^{-2}; Figure 5.4a; Table 5.2). Post-fire density in restoration ages 14–18 years were similar to reference sites, but density in ages 22–27 were higher than reference sites (Figure 5.4a; Table 5.2).

Post-fire diversity and functional redundancy of the entire community were similar to pre-fire restored values across most of the restoration chronosequence, but rarefied richness was consistently lower (although not significantly; Figures 5.4d,g,j; Table 5.2). For these metrics, in most cases, restored sites both pre- and post-fire met reference values for the resilience metrics, except for post-fire diversity in ages 16 and 24, and post-fire rarefied richness in age 24 which were all significantly lower than reference sites (Table 5.2).

Across all restoration ages, obligate seeder density were higher following fire regardless of smoke-responsive status, while only the density of smoke-responsive resprouter species increased following fire (i.e., non-smoke responsive resprouters did not increase; Figures 5.4b,c, Table 5.2). For both resprouters and obligate seeders, the density of smoke-responsive species was higher than that of unlikely smoke-responsive species (2–7 vs 0–4 seedlings m^{2} per species respectively; Figures 5.4b,c). For obligate seeders, despite significant increases in smoke-responsive density following fire in four restoration ages, post-fire density in three of these restoration ages were significantly less than that of reference Banksia woodlands following fire

(Table 5.2). Resprouters had significantly lower unlikely smoke-responsive density post-fire in all ages except 17 and 18 years compared to reference sites (Figure 5.4c; Table 5.2).

Across the entire restoration chronosequence, obligate seeder diversity, rarefied richness and functional redundancy did not significantly change following fire and were similar to that of reference sites (Figures 5.4e,h,k; Table 5.2). For resprouting species, diversity and rarefied richness decreased following fire in all restoration ages (although only the decline in diversity in Age 14 was significant; Figures 5.4f,i; Table 5.2). Functional redundancy for resprouters was similar pre-to-post fire across most restoration ages (Figure 5.4l; Table 5.2). Post-fire resprouter diversity in all restoration ages was significantly lower than that observed in reference Banksia woodlands, with post-fire rarefied richness in restoration Age 14 significantly less than that in reference Banksia woodlands (Figures 5.4f,i; Table 5.2).

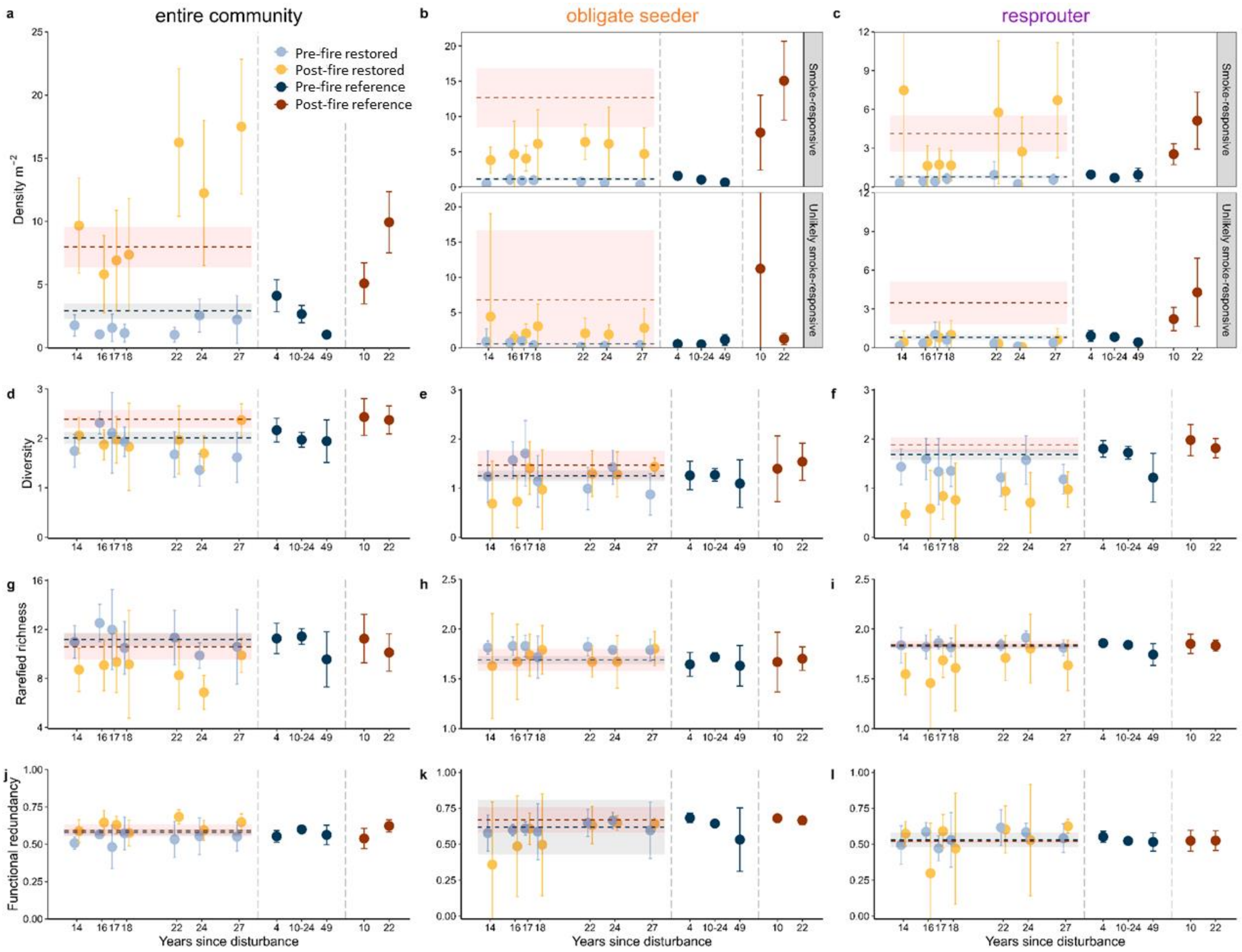
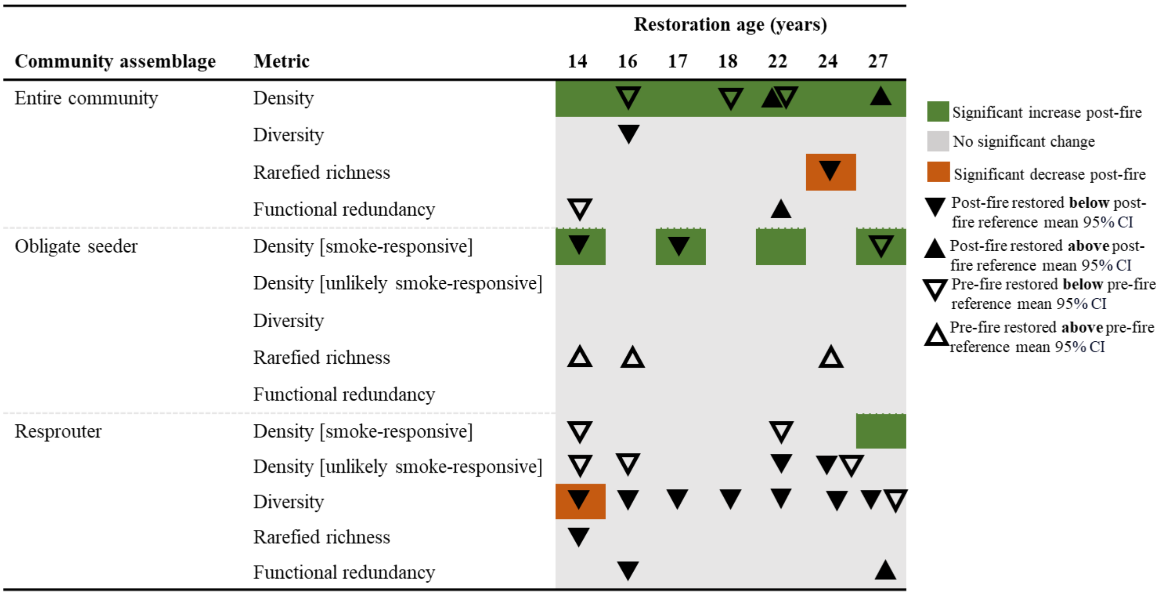
a
entire community
b
obligate seeder
c
resprouter
Pre-fire restored
Post-fire restored
Pre-fire reference
Post-fire reference
Density m^{-2}
Smoke-responsive
Unlikely smoke-responsive
d
e
f
Diversity
g
h
i
Rarefied richness
j
k
l
Functional redundancy
14
16
17
18
22
24
27
4
10-24
49
10
22
Years since disturbance

Figure 5.4: Mean±95% CI values for entire community (annuals and native perennials) and perennial obligate seeder and resprouter density, diversity, rarefied richness and functional redundancy against years since disturbance in Banksia woodlands. Years since disturbance refers to restoration age in restoration sites and years since fire in reference sites. Colours reflect ecosystem types and state (pre-vs-post fire). Bands and dotted lines over restoration data refer to means (dotted line) and 95% CI of post-fire (red) and pre-fire (blue) reference Banksia woodlands data. Post-fire restoration data was measured ~17 months post-fire, post-fire reference data was measured ~12 months following fire. n = 5–42 plots.

Table 5.2: Summary table for each metric describing the change between post-fire and pre-fire restored states (colours) and how post-fire restored states compare to reference intact sites (symbols). The table is based on significant differences in Figure 5.4.



		Restoration age (years)						
Community assemblage	**Metric**	**14**	**16**	**17**	**18**	**22**	**24**	**27**
Entire community	Density	🟩	🟩 ▽	🟩	🟩 ▽	🟩 ▲▽	🟩	🟩 ▲
	Diversity		▼					
	Rarefied richness						🟧 ▼	
	Functional redundancy	▽				▲		
Obligate seeder	Density [smoke-responsive]	🟩 ▼		🟩 ▼		🟩		🟩 ▽
	Density [unlikely smoke-responsive]							
	Diversity							
	Rarefied richness	△	△				△	
	Functional redundancy							
Resprouter	Density [smoke-responsive]	▽				▽		🟩
	Density [unlikely smoke-responsive]	▽	▽			▼	▼▽	
	Diversity	🟧 ▼	▼	▼	▼	▼	▼	▼▽
	Rarefied richness	▼						
	Functional redundancy		▼					▲

🟩 Significant increase post-fire
⬜ No significant change
🟧 Significant decrease post-fire
▼ Post-fire restored **below** post-fire reference mean 95% CI
▲ Post-fire restored **above** post-fire reference mean 95% CI
▽ Pre-fire restored **below** pre-fire reference mean 95% CI
△ Pre-fire restored **above** pre-fire reference mean 95% CI

Pooled resilience

Following fire in restored sites (restoration ages combined), density either increased or did not change (unlikely smoke-responsive resprouters only) across all community assemblages (Figures 5.5a-c, 5.6a). However, the change following fire in restored Banksia woodlands was less than that in reference sites for unlikely smoke-responsive density for both resprouters and obligate seeders (Figures 5.5b-c, 5.6b). Similarly, while smoke-responsive obligate seeder density significantly increased following fire in restored sites, this amount of change was less than that observed in reference sites (Figures 5.6a,b).

Comparisons of change following fire in restored sites found that fire either had little effect or decreased diversity, rarefied richness and functional redundancy for all community assemblages, with particularly high losses observed in the rarefied richness of the entire community and resprouter diversity (Figures 5.5d-l, 5.6a). This is reflected when comparisons of change in restored sites are considered relative to those in reference sites, where the amount of change in restored sites was similar to, or less than that in reference sites (Figure 5.6b). High losses in resprouter diversity following fire in restored sites was also reflected by restored sites changing less than reference sites, where reference sites increased while restored sites significantly decreased (Figures 5.5i, 5.6b).

Following fire, the difference in density between restored and reference sites for the entire community and smoke-responsive resprouters was less than that observed pre-fire (i.e., fire shifted resprouter density closer to reference states; Figure 5.6c). The difference in unlikely smoke-responsive density of both obligate seeders and resprouters following fire was more than that pre-fire (i.e., fire shifted density further from reference states; Figure 5.6c). The amount and direction of change in pre-fire and post-fire restored and reference sites were similar for most measures of diversity, rarefied richness and functional redundancy (Figure 5.6c). However, despite this, key metrics (e.g., diversity and density values) were significantly lower in post-fire restored states than that of reference states for 50% of metrics for the entire community, 40% for obligate seeders and 60% for resprouters (Figure 5.6c).

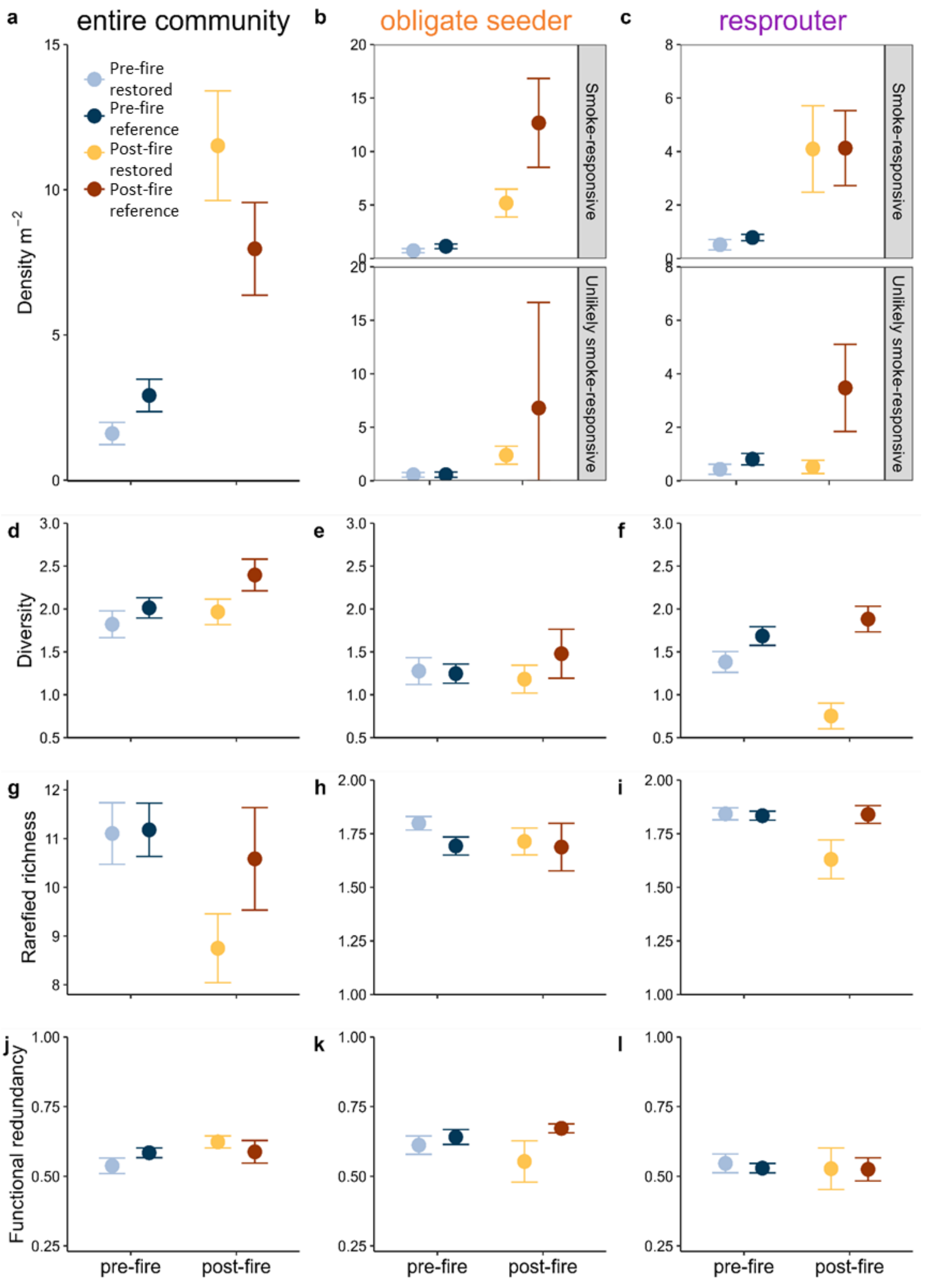

a
entire community
b
obligate seeder
c
resprouter
Pre-fire restored
Pre-fire reference
Post-fire restored
Post-fire reference
Density m^{-2}
0
5
10
15
20
8
6
4
2
Smoke-responsive
Unlikely smoke-responsive
d
e
f
Diversity
0.5
1.0
1.5
2.0
2.5
3.0
g
h
i
Rarefied richness
8
9
10
11
12
1.00
1.25
1.50
1.75
2.00
j
k
l
Functional redundancy
0.25
0.50
0.75
1.00
pre-fire
post-fire

Figure 5.5: Means±95% CI values for pooled resilience for the entire community (annuals and native perennials) and perennial obligate seeder and resprouter density, diversity, rarefied richness and functional redundancy in Banksia woodlands.

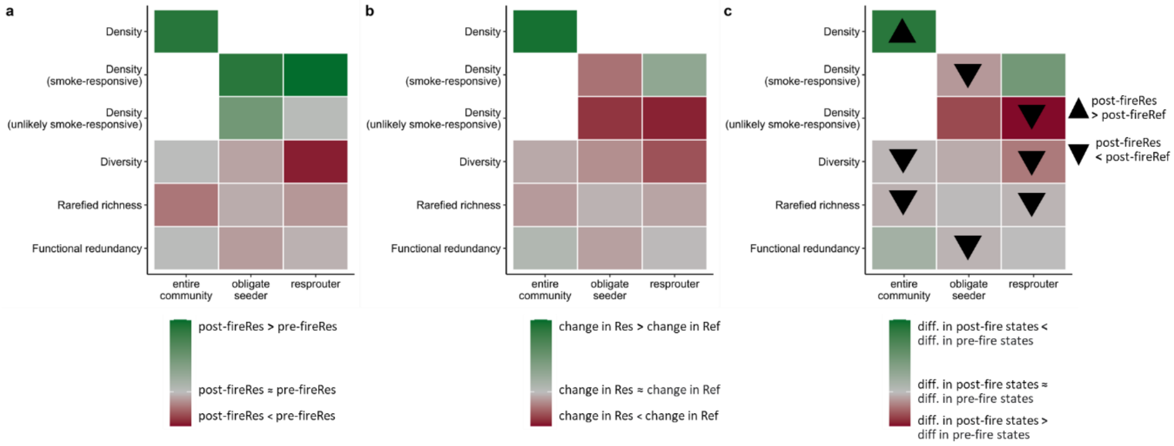


Figure 5.6: Amounts of change for pooled resilience (Figure 5.1) for the three pairwise assessments: a) change in restored sites from fire, b) change in restored sites in regards to reference sites following fire, and c) difference in post-fire states (for restored and reference sites) compared to pre-fire states (i.e., has fire shifted restored states closer to reference et states). Arrows in c) show whether post-fire restored states significantly differ from that in reference, based on Figure 5.5. Specific interpretations differ among the three comparisons (see legends), but broadly, green tiles demonstrate a desirable response of restored sites, while red suggests an undesirable response of restored sites regarding resilience. Res=restored, Ref=reference, diff. = difference. Panels refer to A, B and C comparisons in Figure 5.1.

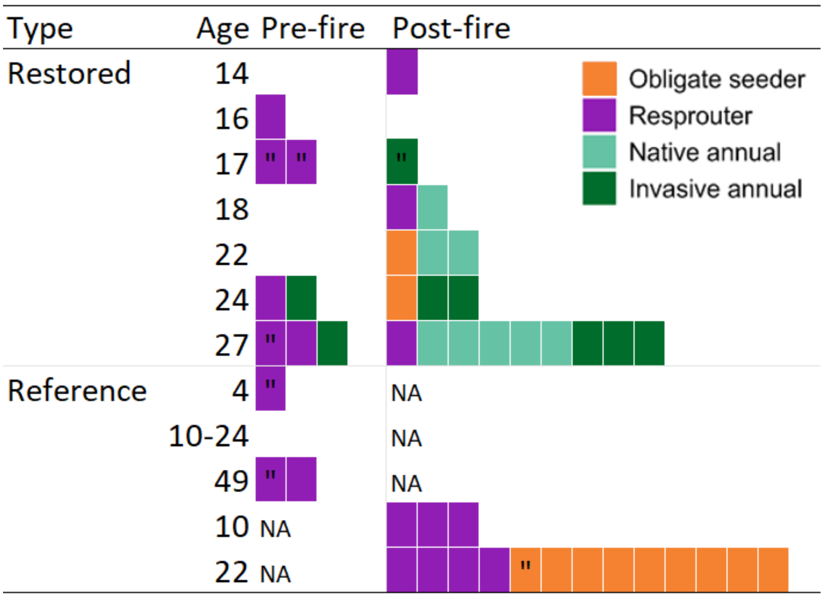
Consistency of pooled resilience assessments

Across the three comparisons used to assess pooled resilience, comparisons utilising reference sites (Figures 5.6b,c) revealed differing levels of resilience compared to comparisons utilising change in restored sites only (Figure 5.6a), particularly for assessments of density. For example, obligate seeder smoke-responsive density were found to increase post-fire in restored sites (Figure 5.6a), but comparisons utilising reference data demonstrate that relative change in restored sites was substantially less than that of reference sites, while fire made restored and reference states more different than pre-fire states (Figures 5.6b,c). For most assessments of diversity, rarefied richness and functional redundancy, resilience comparisons were typically similar, as demonstrated by similar colours (representing the amount and direction of change) among the three comparisons (Figure 5.6).

Resilience based on community composition

For some resilience metrics, restored states were more similar to reference states after fire than before fire (Figure 5.6c). Yet community composition analyses revealed that post-fire restored and reference sites were distinct in species composition (as indicated by lack of overlap in polygons; Figure 5.7). This was largely driven by differences in perennial species abundance (Figure 5.7; Table 5.3). ISA revealed that post-fire reference sites were entirely differentiated by perennial indicator species while post-fire restored sites were mostly differentiated by annual indicator species (74% of indicator species were annuals; Tables 5.3, S5.7). Similarly, NMDS revealed that perennial resprouters and obligate seeders were correlated with reference site composition, while annuals were correlated with restored sites (Table 5.3; Figure 5.7). Overall, significant differences were observed among both restoration ages and between restored and reference site species composition (ANOSIM R = 0.28, $p = <0.001$ & R = 0.34, $p = <0.001$ respectively). The high density of the entire community in restoration age 27 are likely due to five native and three invasive annual species found as indicators in this age (Table 5.3).

Table 5.3: Counts by trait types of indicator species across the site ages. NA = group not assessed for reference sites as age not present, " = species found in restored or reference sites only. See Table S5.7 for species associated with each age and ecosystem type. Each coloured box refers to one species.



Type	Age	Pre-fire	Post-fire
Restored	14		🟪
	16	🟪	
	17	🟪" 🟪"	■"
	18		🟪 🟩
	22		🟧 🟩 🟩
	24	🟪 ■	🟧 ■ ■
	27	🟪" 🟪 ■	🟪 🟩 🟩 🟩 🟩 🟩 ■ ■ ■
Reference	4	🟪"	NA
	10-24		NA
	49	🟪" 🟪	NA
	10	NA	🟪 🟪 🟪
	22	NA	🟪 🟪 🟪 🟪 🟧" 🟧 🟧 🟧 🟧 🟧 🟧 🟧 🟧

🟧 Obligate seeder
🟪 Resprouter
🟩 Native annual
■ Invasive annual

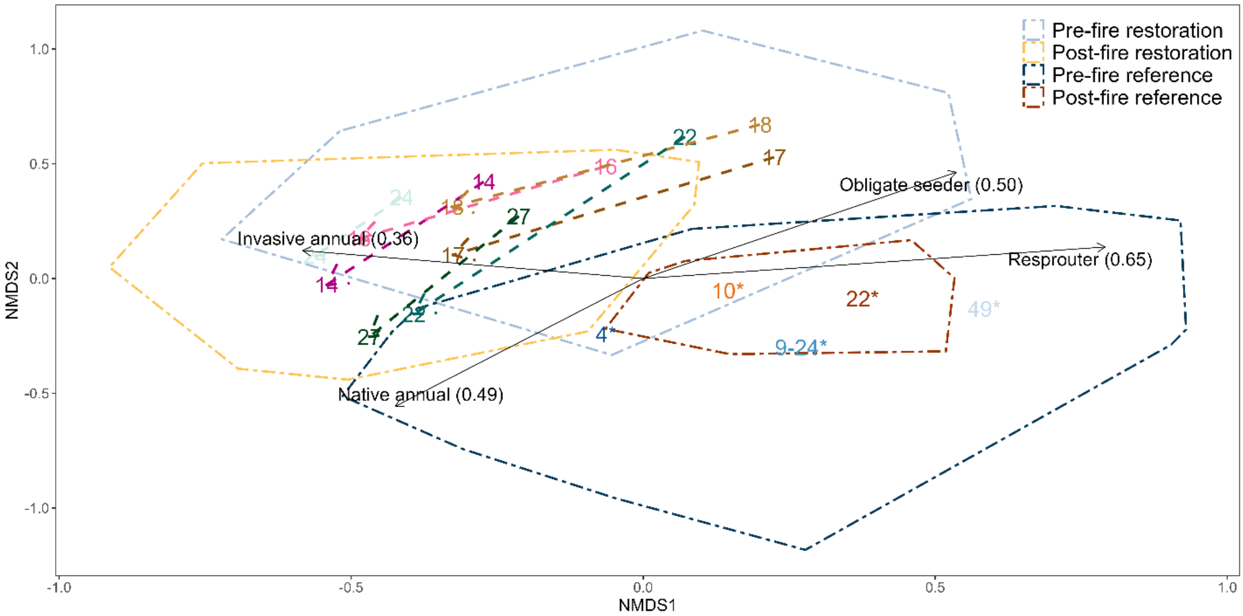


Figure 5.7: Axis 1 and 2 of a 3D NMDS of Hellinger transformed Bray-Curtis similarity of ecosystem types (polygons), age centroids and a biplot of proportions of individuals per trait. Arrows link the pre-fire community to the post-fire community for each restoration age. Ages with * are reference Banksia woodlands plots, numbers in brackets for species trait biplot are R^2 values. Ecosystem type polygons surround all plots for that state, individual plots are not shown for ease of visualization. Stress = 0.18. Axis three revealed more similarity of the reference et and restored Banksia woodlands compared to Figure 5.7.

Discussion

Experimental fires across a 13-year chronosequence of restored Banksia woodlands resulted in fire impact increasing with restoration age likely reflecting reduced bare ground cover in older sites. Post-fire regeneration (at ~5 months) and survival (to ~17 months) of seedlings and established resprouts (individuals which had been burnt by fire and subsequently resprouted) were not influenced by restoration age, fire impact or soil conditions, with high amounts of unexplained variability. Density of obligate seeders and both density and diversity of resprouters typically demonstrated little resilience to fire as the amount and direction of change in restored sites did not always reflect that of reference Banksia woodlands. However, entire community diversity, rarefied richness, and functional redundancy suggested community-level resilience to fire was present given similar changes across restored and reference Banksia woodland sites. Comparison of changes using reference site data was key to assessing the resilience of restored sites to fire, with pre- and post-fire restored sites distinct from reference sites due to differing species composition and trait dominance. Specifically, annuals dominated restored sites while perennials dominated reference Banksia woodlands.

Post-fire recruitment and resprouting survival was not influenced by restoration age or legacies

Following fire, resprouting and seedling recruitment occurred across all restoration ages in restored Banksia woodlands. We found that survival rates of perennial species seedlings ranged from 16–20%. This is similar to survival rates following direct seeding of six species to investigate plant facilitation at the same site (survival across all species =18.2–21.6%; species level survival =0.8–54.3%; Svejcar 2020) following the first summer post-fire. Slightly higher survival values following the first summer post-fire have also been found in Banksia woodlands following restoration (~20–55%; Standish et al., 2012) and following fire in post-mining restored Kwongan (sclerophyllous species-rich shrublands ~250 km north of Hanson; survival = ~24%;) which shares a similar subset of species (Herath et al., 2009). While these studies assessed survival ~12 months following fire, the comparison captures the first summer after fire where germinant mortality rates are typically high. Low mortality rates between autumn and spring due to winter rains mean that these studies are relevant to contextualize our findings, despite being measured at different times since fire.

Resprouting species were the most speciose trait group in restored sites, and we found that approximately 43% of resprouter individuals present before fire had resprouted and survived to ~17 months post-fire. While resprouting rates following fire are not well documented in intact Banksia woodlands, we found lower established resprouter survival than post-fire studies in post-mining restored and intact Kwongan (mean = 52 vs 96 & 85% respectively; Herath and Lamont 2009; Enright et al., 2011). Similarly, in Chapter 4 we found restored sites resprouter survival to range from 3–92%, further highlighting the variation in resprouting success among species and resprouter types.

Across the restoration chronosequence, we found that overall perennial seedling emergence was not significantly influenced by restoration age. This result is consistent with findings in Chapter 3 and intact Mediterranean climate woodlands in southeastern Australia (Chick et al., 2015), potentially due to variable seed input, losses, and persistence with time and among species unrelated to restoration age. We found no evidence of increased resprouting success in older restoration ages, consistent with research in mine site restored and intact Kwongan where resprouter survival varied with fire intervals (Herath and Lamont 2009; Enright et al., 2011). Species-specific responses and other factors including pre-fire plant size may be more important for resprouting success than restoration age (Chapter 4).

We found no effect of fire impact and soil composition (compaction and field capacity) on drivers of post-fire responses (regeneration and survival) despite their effect on post-fire responses observed in Chapter 4 and other restoration projects (e.g., Herath et al., 2009; Herath and Lamont 2009; Riviera et al., 2021). While soil composition variables have been found to influence plant establishment following restoration (e.g., Holmes 2001; Rokich et al., 2001a; Le Stradic et al., 2014; Pauw et al., 2018; Timsina et al., 2022), they seem to have inconsistent effects on responses to fire: this manuscript found no effect at the plant community scale but effects on the plant population scale were identified in Chapter 4. Therefore, we suggest further investigation of the effects of soil composition on plant responses to fire, potentially through measurement at finer scales.

Resprouters demonstrated variable early-stage resilience to fire

The development of resprouter organs and resprouting success following fire is complex, with plant age having variable effects on resprouters resilience (Herath and Lamont 2009; Enright et al., 2011; Chapter 4). When comparing pre- vs post-fire states, we found reduced resilience of resprouters in restoration ages 14 and 16 (the youngest ages we were able to assess here) compared to reference sites, demonstrated by the significant loss of diversity in age 14 and multiple metrics being lower than reference states compared to other restoration ages. For some plant species, 14–16 years could be too short of a time to develop resilience to fire via seeding and resprouting mechanisms in restored sites, with such ages substantially younger than plants in intact sites which may be centuries old (Merwin et al., 2012). While we found high resprouting success in restoration age 14 (~80% resprouter survival to 12 months post-fire) for a subset of Banksia woodland resprouting species (Chapter 4), it appears this is not reflected across a broader range of species. Post-fire resilience of resprouters ~14 years since fire in intact Banksia woodlands is not well documented, but Enright et al., (2014) found high resprouter survival rates in intact Kwongan ~14 years after fire, but this was not reflected in post-mining sites of a similar age in the same region (Herath and Lamont 2009).

We also found reduced resilience of resprouters in our assessments of pooled resilience (restoration ages combined). We found that the density of unlikely smoke-responsive resprouters and resprouter diversity change following fire in restored sites did not reflect that of reference sites, and fire appeared to shift restored states further from reference states, resulting in significantly lower values in restored states than reference states. These responses demonstrate that resprouter resilience in restored Banksia woodlands did not mimic that in reference Banksia woodlands for these metrics. However, restored sites rarefied richness decreased following fire but the change was mostly similar to reference sites, and fire did not appear to shift restored and reference states further from each other. This highlights the complexity of assessments of resilience and the importance of utilizing multiple metrics.

To better understand resprouter resilience to fire, additional research should further explore drivers of resprouting success by considering factors including carbohydrate storage and bud-bank availability (Clarke et al., 2013; Ott et al., 2019) using a trait-based or species-specific approach (Chapter 4) depending on goals and findings. Additionally, this study revealed that the perennial species (particularly resprouters) found in restored Banksia woodlands were only a subset of those found in reference Banksia woodlands. For restoration goals based on achieving similar species and trait composition to reference sites, further knowledge is needed to promote successful establishment and survival of resprouters following topsoil transfer, as regeneration success from existing plant material in the topsoil is mixed (e.g., Koch 2007; Tozer et al., 2012; Daws and Koch 2015; Pilon et al., 2019). Planting of difficult-to-establish resprouting species may also improve compositional similarity to reference woodlands.

Resprouter species in restoration ages 14 and 16 demonstrated poor resilience to fire, suggesting that resprouters in these (and younger) ages are not ready for fire as substantial changes in resilience metrics occurred or change did not reflect that of reference sites. This is likely due to a combination of inadequate resprouting and reproductive capacity. Depending on restoration goals, subsequent management may be required to ensure the persistence and development of resprouter populations (regardless of the age when they are burnt). For example, planting and seeding may be required (ideally during or a few years after topsoil transfer when baseline surveys have been able to determine if community composition differs) to promote similar species composition between restored and reference sites if this reflects restoration goals. While goals that aim for no substantial change in restored states following fire, excluding sites from fire for a long period of time may be required to allow existing plants to develop their resprouting and reproductive capacity.

Obligate seeders typically displayed resilience to fire for most metrics

We found that restoration age typically did not impact the resilience of obligate seeders to fire for any resilience metric suggesting seedbanks were adequate for species replacement post-fire, potentially due to high seedbank density and richness in restoration ages >13 years (Chapter 3). Assessments of both resilience across restoration ages and pooled resilience (restoration ages combined) found that obligate seeder density post-fire was less than that in reference Banksia woodlands, but this did not result in substantial losses of diversity, rarefied richness, or functional redundancy in restored sites following fire. Change following fire was similar in restored and reference sites for rarefied richness and slightly dissimilar for diversity and functional redundancy, but fire did not shift obligate seeder states further from reference states, thereby suggesting resilience.

For obligate seeder populations to self-replace, they need adequate seedbanks, while resprouters have more complex requirements including both seedbank reserves and resprouter organ presence and functioning (Pausas and Keeley 2014). These differences in fire-response mechanisms and their associated complexities may explain the increased resilience of obligate seeders compared to resprouters in restored sites. Additionally, higher seed quantities and quicker growth rates in obligate seeders compared to resprouters (Pate et al., 1990; Lamont and Wiens 2003; Chapter 3) may promote greater post-fire resilience of obligate seeders as their ability to successfully produce seedbanks occurs earlier in the restoration trajectory. Drought tolerance may also differ among the fire-response types and influence resilience (e.g., Vilagrosa et al., 2014; Parra and Moreno 2018; Cooper et al., 2018), but this was not observed in this study as survival was similar among resprouter and obligate seeder seedlings. These differences among obligate seeders and resprouters may also explain their altered resilience to fire following mining disturbance.

Analyses of the entire community highlighted the complexities of assessing resilience in restoration projects

In this study, assessments of the entire community (i.e., perennials and annuals) using resilience metrics often found that restored sites were similar to reference sites for all resilience metrics and restoration ages. Assessments of pooled resilience suggested this also, as changes following fire in restored sites usually reflected those in reference states, thereby suggesting early-stage resilience to fire. However, despite resilience metrics suggesting early-stage resilience to fire in some cases, the entire community composition (assessed through ordinations and ISA) differed between restored and reference sites. In particular, restored sites were dominated by annuals, while reference sites were dominated by perennials which were not apparent in analyses of resilience metrics. This also explains the higher overall plant density of the entire community in post-fire restored sites (i.e., dominated by annuals).

The greater dominance of annuals in restored sites may be due to their favouring of sites with less competition from perennial plants (as observed in some restored sites with lower perennial density in restored compared to reference sites) or their favouring of recently disturbed environments (Fowler et al., 2015; Wainwright et al., 2017). Annual density is likely to decrease with time since disturbance (Keeley et al., 2005; Bates et al., 2014; Fowler et al., 2015; Chapter 3). Regardless, perennial community assemblages in restored sites vs reference sites are likely to remain distinct throughout vegetation development.

Important considerations for the assessment of resilience in restored ecosystems

Despite resilience being widely acknowledged as an important component of restoration success, its quantification remains difficult (Standish et al., 2014; Chapter 2), so we assessed resilience using three approaches, four resilience metrics and two levels of biological organisation (communities vs species populations, and grouped by traits). Broadly, we found most resilience metrics (i.e., change in diversity, rarefied richness or functional redundancy) often suggested resilience as there was little change pre-to-post fire, and restored states were often comparable to reference states, except for resprouters. Analysis of community composition (using ordination and ISA) however, revealed more distinct changes between restored and reference sites that were not apparent in the resilience metrics. Due to the difficulty in successfully establishing all plant species in restoration projects (e.g., Riviera et al., 2021; Shackelford et al., 2021; De Vitis et al., 2022; Gerrits et al., 2023), it is important to incorporate assessments of community composition comparing restored and reference (i.e., reference) states. Community-level analyses can help to identify specific species and trait groups that may respond poorly to a disturbance and streamline future research and management (Chapter 2). Therefore, we suggest a multifaceted approach using a variety of different assessments is necessary when assessing resilience.

The inclusion of reference Banksia woodlands data was also essential for understanding if resilience was similar in restored and reference sites. Specifically, assessments of pooled resilience revealed that while values changed following fire in restored sites, the amount of, and direction of change did not reflect that of reference sites in some cases (e.g., density). Fire caused a substantial decrease in restored sites, but the inclusion of reference data reveals that fire did not shift restored sites further from reference sites (i.e., the difference in post-fire and pre-fire states was similar). This is apparent in the rarefied richness of both the entire community and resprouter group, and functional redundancy among obligate seeders. Where possible, we suggest the inclusion of both pre-and post-disturbance reference data to allow for assessments of resilience in restored sites, as similarity in states (e.g., density, diversity) and change following fire are key elements of resilience in restoration projects. We also acknowledge that the inclusion of a wider range of reference sites may have demonstrated more variability in reference Banksia woodlands and influenced interpretations of the resilience of restored sites.

Resilience proxies including those that are based on species functions are proving powerful at assessing resilience as they allow for further assessment of changes in ecosystem function and future resilience (Biggs et al., 2020; Standish et al., 2021; Chapter 2). Through our assessment of functional redundancy, we typically found little change following fire in restored sites and reference sites. This was true for resprouters also: despite their losses and differences in density, diversity and rarefied richness compared to reference states, ecosystem functioning was maintained (i.e., species lost were not performing specialized functions). This aligns with research by Carrick and Forsythe (2020) and Standish et al., (2021) that found species composition alone accounts for very little of the variation of ecosystem function, which may be more apparent in highly diverse sites where species share functional roles (Holmes and Richardson 1999; Gallagher et al., 2013; Araújo and Conceição 2021). While our findings broadly suggest resilience of functional redundancy following fire, it is important to note that such indices are heavily dependent on the trait data used which can be difficult to obtain and may not account for high levels of trait variability (e.g., Moreira et al., 2012a; Mitchell et al., 2020; Westerband et al., 2021). Therefore, we advise caution regarding the development of restoration goals and management plans based solely on functional proxies due to the mixed importance of species' roles and the importance of functional redundancy for high levels of ecosystem functioning in diverse ecosystems (Hautier et al., 2018; Le Bagousse-Pinguet et al., 2019).

It is important to note the potential effects of the unfavourable weather conditions observed during the first summer after fire in this study (when plants were ~8–11 months old). During this period, maximum summer temperatures were ~0.9°C higher than the average, and a record number of days over 40°C occurred (Logan 2022), which may have increased the mortality of seedlings and established resprouts (Pratt et al., 2014; Stewart et al., 2021; Nolan et al., 2021; Bendall et al., 2022a; Salesa 2022) but see Enright et al., (2014) and Parra and Moreno (2018). Increased mortality in the established but unburnt restoration was observed at Hanson following this extreme summer also (E. Cowan, pers. obs., March 2022), highlighting the potential vulnerability of these restored sites to drier and warmer conditions. Uncertainty of the effects of extreme post-fire weather conditions on plant responses makes it difficult to determine to what extent our results were influenced, so post-fire responses following "average" summer conditions should not be expected to be different. Furthermore, resilience to wildfire (i.e., fire not deliberately initiated) may differ from that of experimental fires, with higher fire intensity and younger ages potentially being burnt during wildfire than what occurred in this study. Additionally, assessments of younger or older restoration ages than what was surveyed may have yielded different interpretations of resilience, particularly in reference to minimum or maximum tolerable fire intervals of restored sites.

Resilience to experimental fire was typically demonstrated in restored Banksia woodlands for entire community measures although these were frequently sustained by the contributions from annual species. For obligate seeder and resprouter species groups, density and diversity measures of resilience in restored sites did not reflect that of reference sites. Additionally, resprouters demonstrated losses of diversity and rarefied richness after fire in restoration ages 14 and 16, and more broadly had lower levels of resilience in most metrics than reference Banksia woodlands. Due to resprouters being the most speciose component of Banksia woodlands, we suggest avoiding deliberate fire in restoration ages ≤16 years, with careful consideration of fire in restored sites in ages >17 acknowledging resprouting species losses are likely to occur. Community composition differed substantially as annual species drove patterns in restored sites, and perennials drove reference Banksia woodlands. Resprouters in restored Banksia woodlands were a subset of those in reference Banksia woodlands due to initial restoration establishment rather than fire responses. Therefore, research and management focus on promoting the successful establishment of perennial plants, and drivers of post-fire resprouting may assist to increase similarity in the composition of perennial species. The inclusion of reference data is necessary to interpret if changes in restored sites are desirable or not, with continuous monitoring of ecosystem states key to understanding successional changes. Assessing resilience using a variety of metrics is encouraged to refine restoration goals and identify the nature of the disturbance response of restoration projects.

Chapter Six

General discussion

To understand how resilience to fire develops in restored Banksia woodlands, my research combined concepts of both restoration ecology and disturbance ecology (particularly fire ecology). To do so, I conducted studies on community and population levels of ecology based on species functional traits (typically fire-response type and longevity) as I expected these traits to influence the development of Banksia woodland resilience to fire (e.g., Pate et al., 1990; Lamont and Wiens 2003; Clarke et al., 2013; Enright et al., 2014). Additionally, legacies of the restoration process may influence restored sites establishment and resilience (e.g., Foster et al., 2003; Hilderbrand et al., 2005; Crouzeilles et al., 2016), so attributes relating to soil condition were assessed as potential drivers of resilience also. My findings are relevant to the successful restoration of other disturbance-prone restoration projects (e.g., those in Mediterranean-climate regions where fire is common), particularly following disturbances where substantial amounts of biomass are lost and recovery is dependent on the development of key disturbance response mechanisms.

My research evaluated resilience to fire in Banksia woodlands restored after sand mining using a chronosequence approach. This approach permitted consideration of the importance of time for the development of resilience: a notion that is likely still common within the field of restoration ecology (Hilderband et al., 2005). For perennial species, I found that resilience rarely developed linearly (Chapters 3 and 4), with high variation in species responses to fire often having a larger effect than restoration age (Chapters 3 and 5). For annual species, the dominance in recently disturbed sites (younger ages) reflects their successional pathways (i.e., preference of recently disturbed sites) rather than their resilience.

Here, I discuss the key findings of my research and explore how my different approaches may assist in understanding resilience in restored ecosystems. I separate my response variables into leading indicators (processes such as recruitment, and survival) and lagging indicators (ecosystem states at a single point in time such as density, and diversity; Ota et al., 2021) as per Chapter 2.

I would like to acknowledge research by McKenna et al., (2017) and McKenna et al., (2019) that was accidentally omitted in my literature review. The inclusion of these studies would have added additional insights to the measurement of fire disturbance in restored grasslands and open woodlands aged 19–21 years following coal mining in Queensland, Australia. Attributes assessed included cover, biomass, species richness, density, fuel loads and fire behaviour, with sites compared to pre-disturbance restoration and reference sites. A range of statistical analysis types were used including summary statistics, variance of means, regression and ordination. Their inclusion however does not alter the key findings of my literature review, as the effects of disturbances in restoration projects still require more research globally.

Table 6.1: Summary of response and explanatory variables used to assess plants' responses to fire and implications for resilience in my thesis. Attribute types are lagging (demonstrate a system state at a single point in time), leading indicators (demonstrate rates of change) and proxy (infer resilience and often relate to a leading or lagging indicator; see Figure 2.5 for further explanations). Explanatory variables listed are those that differed for perennial species only, as perennial species are commonly used to evaluate restoration success as they dominate Banksia woodlands. Explanatory variables identified in Chapters 3 and 4, and regeneration and survival responses in Chapter 5 were found to be significant (*$p<0.05$*) for perennials in at least one case. Chapter 5 response variables with an * were not modelled against a range of predictors, so explanatory variables listed in Table 6.1 varied for perennial species, even if not consistently. SSB density and richness was identified as a leading indicator as it was used to predict plant establishment following a disturbance (Chapter 2). Functional redundancy was identified as a proxy measure of resilience (i.e., may indicate potential resilience) in Chapter 2, but I used it as a lagging indicator by comparing states in Chapter 5. Traits refer to plant traits, usually fire-response type for perennial species, age = restoration age, SSB = soil seedbank.

Chapter	Response variable	Attribute type	Explanatory variables where results differed
3	SSB density and richness	Leading	Traits, age
	SSB similarity to above-ground	Lagging	Age
4	Resprouting ability	Leading	None
	Resprouter survival	Leading	Age, soils, pre-fire plant size
	Resprouter vigour (resprout growth)	Leading	Age, soils, pre-fire plant size
5	Regeneration and survival	Leading	None
	Density, diversity, rarefied richness*	Lagging	Traits, age
	Functional redundancy*	Proxy (Lagging)	Traits
	Community compositional similarity	Lagging	Traits, age

Overview of major findings

Using a range of analyses and metrics to assess resilience, my research found that regeneration via resprouting and seedling recruitment (the two dominant responses of plants to fire) can occur after experimental fire in restored Banksia woodlands aged between 3–27 years since the onset of restoration. Restoration age had varied influence on post-fire responses, specifically, resilience was lower in ages 14–16 years compared to those >17 years due to a range of metrics declining or being less than reference sites following fire (Chapter 5). Lower resilience was also observed in Age 3 due to reduced SSB density (Chapter 3). Drivers of resprouting success varied and were largely unable to be quantified by the models I used.

Restoration age had mixed influence on leading indicators following fire

Throughout my thesis, I sought to determine the effect of restoration age on leading indicators. Leading indicators typically measure processes and relate to rates of change (Chapter 2; Manero et al., 2020; Ota et al., 2021). In my research, the key processes I assessed were seedling recruitment (Chapters 3, 5), persistence via resprouting (Chapters 4, 5), and survival of seedlings and/or resprouts (Chapters 4, 5). I typically found restoration age influenced the development of these responses (Table 6.1), potentially due to fire intervals being a key element of fire regimes that influence species responses to fire (e.g., Enright et al., 2014; Turner et al., 2019; McColl-Gausden et al., 2022).

Recruitment from soil seedbanks following fire is necessary for the establishment of approximately ~70% of Banksia woodland plant species (Rokich et al., 2001b; Stevens et al., 2016). In both Chapter 3 (smoke tents) and Chapter 5 (experimental burns), linear modelling found no evidence of restoration age between 3–26 years influencing regeneration (assessed through the germination response) from the SSB for perennial species. This may be due to ongoing changes in SSB composition due to seed losses, accumulation and dispersal which are typically species-specific. Annual species were found to dominate soon after disturbance (both in younger restoration years and the first ~5 months following fire), which reflects their preference for recently disturbed sites (Saatkamp et al., 2011; Dwyer and Erickson 2016). In some systems, the annual-dominated state can persist and is resilient to disturbances, but here the annual state tends to be replaced by the perennial-dominated state.

Approximately 78% of perennial species can resprout following fire in Banksia woodlands (Fontaine and Standish 2019). Species used to assess drivers of resprouting responses differed among chapters: resprouting was assessed for three species separately that were found across most of the restoration chronosequence (individual scale; Chapter 4), while in Chapter 5, all species capable of resprouting were pooled by age and plot (community scale; Table 1.1). Despite different biological organization levels measured (i.e., individual plants, plant populations and plant communities) and statistical methods used (GAM vs GLM), restoration age did not influence whether a species had resprouted ~5 months post-fire. Resprouter survival was measured at different times since fire for the two studies (Chapter 4 = ~12 months post-fire vs Chapter 5 = ~17 months post-fire) with the importance of age differing among Chapter 4 and Chapter 5. Similar to the seedling recruitment responses, differences in the importance of age may reflect the length of the restoration chronosequence (23 vs 13 years) or scale (individual vs community) where variation in species responses is substantial.

Restoration age was important for some lagging indicators, but not all

Lagging indicators quantify states at a particular point in time (Chapter 2), so their measurement following key events driving succession (e.g., after disturbance) can help to infer resilience. Lagging indicators are also commonly used to quantify restoration success

(Ruiz-Jaen and Aide 2005; Wortley et al., 2013; Chapter 2). To determine both the impact of the disturbance and if post-disturbance states were desirable, I compared post-fire lagging indicators to either an unburnt restored control (Chapters 3, 5), or burnt and unburnt reference Banksia woodlands (Chapter 5; Table 6.1).

In Chapter 3, for each restoration age, I compared the similarity in composition of the smoked SSB to the above-ground vegetation for the same restoration age to understand how resilience to fire may change among the restoration chronosequence. Specifically, resilience was considered to be greater where similarity between the above-ground and smoke-treated vegetation was higher. This suggests a greater ability to return to its prior state, and therefore demonstrate resilience. Similarly, post-fire density of both the entire community and obligate seeders was higher and had more change in older restoration ages (>22) than younger ages (14–18; Figure 5.4; Chapter 5), also suggesting that densities resilience to fire increased with age. This may be due to the initial floristics model of succession (Egler 1954) that is observed in both restored and intact Banksia woodlands (Hobbs and Atkins 1990; Mounsey et al., 2021), where senesced individuals in older ages are replaced via seedling recruitment or resprouting following fire. However, this pattern was not reflected in assessments of diversity, rarefied richness and functional redundancy, so further assessment of successional change in these metrics is needed.

Limitations

The development of post-fire responses and resilience was hypothesized to be driven by restoration age, so I used a space-for-time chronosequence design to assess the development of these attributes with time (Figure 1.2). Such approaches are common in restoration projects and facilitate the evaluation of restoration success and responses to disturbances when long-term monitoring is not possible (Wortley et al., 2013; Chapter 2). The space-for-time approach assumes that all variables other than time are constant so that differences observed are due to time (Pickett 1989; Johnson and Miyanishi 2007). However, this is difficult to achieve in practice due to continuous learning and the adoption of improved practices shaping how restoration is conducted (Rokich 2016; Stevens et al., 2016). Therefore, ripping depths and soil composition varied among the restoration ages I studied, particularly in ages >22 years (Tables 3.1, 4.1 and 5.1). Due to poor replication among site restoration procedures, it was not possible to determine the exact effects of this variation on resilience to fire. However, topsoil storage time is an important driver of restoration success (e.g., Rokich et al., 2001a; Koch 2007; Pauw et al., 2018) and this was consistent across all ages studied (except age 16 in Chapter 5 – a site not studied in Chapters 3 and 4), so topsoil quality which drives plant community development should have been similar among ages. Age 16 in Chapter 5 had similar responses to fire and SSB composition as other restoration ages, so it appears this did not influence my study results. Overall, these slight differences in soil reconstruction are not likely to significantly impact the conclusions of my research.

Assessments of different restoration ages than those I studied would potentially improve the understanding of resilience to fire in restored Banksia woodlands. Specifically, quantifying SSB composition in ages <3 years could have determined if SSB composition was due to germination following topsoil transfer rather than seed deposition from plants, as assumed in Age 3 (Chapter 3). Monitoring of both SSB and resprouting responses in ages >27 years may have allowed for maximum tolerable fire intervals to be determined though identifying when recruitment from the SSB is not possible due to a lack of viable seeds, or if there is a reduction in resprouting success of longer-lived species (i.e., *Scholtzia involucrata* and *Stirlingia latifolia*). Assessing fire impact and resilience in older restoration ages may have yielded higher fire severity which likely influences post-fire responses. Determining how post-fire restored sites <12 years compared to reference Banksia woodlands of the same age after fire may have provided additional information regarding successional trajectories. For example, it would determine if reference vegetation <12 years since fire is unable to carry fire, so fire should be avoided. Comparing seedbank development (Chapter 3) and resprouting drivers (Chapter 4) to reference Banksia woodlands would have provided additional insights as to if the resilience of restored sites reflects that of reference sites.

In my research, post-fire conditions were characterized by the hottest summer on record for the Perth region (Logan 2022), which potentially influenced survival responses in Chapters 4 and 5. In autumn 2022 (immediately after the extreme 2022 summer), I observed high levels of mortality of established plants in unburnt restoration ages (particularly in ages <10 years; E Cowan, pers. obs., March 2022), so I expect increased mortality of post-fire recruits and resprouts was possible too. Given the inconsistency of the effects of drier conditions on post-fire responses (see Chapters 4 and 5 for further discussion), assuming that survival outcomes would be higher under "typical" summer conditions is unwise. Instead, perhaps the observed outcomes could be considered as an indication of future post-fire responses due to expected warming and drying in the region (Andrys et al., 2017). Additionally, each fire is unique (e.g., severity, timing, behaviour) which likely influences interactions with factors including post-fire weather conditions.

Fire in restored Banksia woodlands

The implementation of fire in restored communities may provide biodiversity maintenance or enhancement, fuel hazard reduction, or assist in understanding potential responses to unplanned wildfire. If sites are ready for fire, this suggests that their regenerative capacity is sufficient to prevent changes to an altered, potentially degraded state following fire.

Initially, when considering implementing prescribed fire in restoration projects, likely responses to fire of high conservation value species in the restored sites (e.g., threatened and/or keystone species) should be considered. However, at the Hanson Gaskell sand mine (thesis study area), there were no threatened species present and keystone species (e.g., *Banksia* spp.) persisted and regenerated following fire (i.e., were not top-killed and some seed germination was present). Therefore, my recommendations for when to implement fire are based on: 1) fire risk, 2) post-fire responses of resprouters (as resprouters dominated the restored community and were more negatively impacted by fire than obligate seeders and annuals), 3) soil seedbank composition, and 4) soil condition, with consideration of reference sites (Figure 6.1).

If fire spread is not possible, then a site resists fire and it cannot demonstrate resilience as it will not burn. Therefore, I consider sites where experimental fire can spread may be potentially resilient to fire. I found resilience to fire was greater in older ages which corresponds with higher fire severity, so experimental fires may be best limited to these ages. Additionally, the inclusion of reference sites is important to contextualize the resilience of restored ecosystems. The following recommendations for restoration practice at the Hanson sand mine (thesis study site) are largely based on lagging indicators of resilience, these being Shannon Weiner (plant) diversity, rarefied richness, functional redundancy and community similarity, and comparisons between restored and reference sites (Chapter 5). Key results from Chapters 3 and 4 will be used to validate my suggestions.

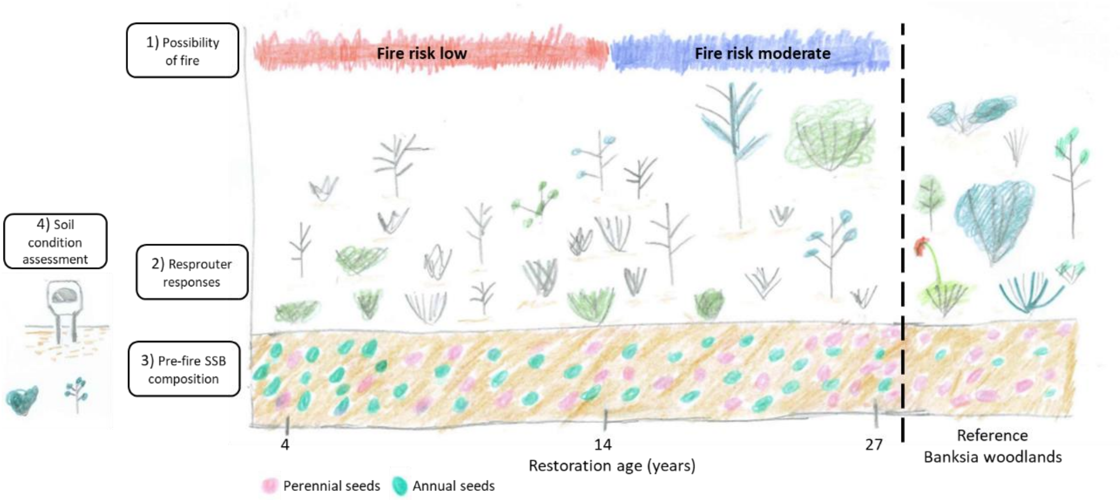


Figure 6.1: Simplified diagram showing the development of key attributes suggested by my research for assessing resilience to experimental fire. Numbers reflect attributes in order of importance (1 = most important, 4 = least important). Resilience to experimental fire can not be assessed in sites where fire risk is low (1). Resprouter responses to fire (2) is an important consideration as they are the most speciose fire-response plant type at Hanson and their resprouting success is estimated as a rough proportion of species that resprouted after fire (green plants) vs those that did not (grey plant skeletons). Pre-fire SSB composition (3) is important for considering recruitment capacity for species. Soil condition assessment (4) may be more appropriate on a per-species scale or scale smaller than species pooled together. The composition of all post-fire restoration ages differs to reference Banksia woodlands as demonstrated through different resprouter species and seedbank composition.

Initially, testing resilience to experimental fire is not possible in ages <14 due to experimental fire being unlikely to occur or be successfully implemented due to high amounts of bare ground (Figures S5.1, 6.1). However, species may still demonstrate some elements of desirable post-fire responses (e.g., seeding and resprouting). Additionally, resprouting species in ages 14 and 16 had the worst outcomes following fire compared to older restoration ages as demonstrated by more metrics that were significantly lower in restored sites following fire and when compared to reference sites (Table 5.2). Therefore, experimental fire should be avoided in these restoration ages.

While post-fire metrics in restored and reference Banksia woodlands were typically similar among restoration ages 17–27 years (Table 5.2), fire impact (severity and coverage) was slightly higher in ages 22–27 years (Figure 5.2). In these older ages (≥22 years), fire implementation is likely easier due to increased fire spread thereby promoting enough fire for plants to initiate their post-fire responses. Therefore, I advise careful consideration of experimental burning in restoration ages 22–27, and post-fire differences in species assemblages (particularly resprouters) compared to reference sites are to be expected (Figure 5.7; Table 5.3), and subsequent management actions may be required.

Implications

The following are key implications identified from my research that are explored in more detail below:

Future research is necessary to understand:

- Drivers of resprouting success and methods to promote resprouter establishment as I found their resilience to fire was poorer than other plant functional types.
- The effect of soil properties on post-fire resilience as I found their effects were varied.
- The utility of trait-based approaches since my research consistently suggested variation among species within trait groups.
- The effect of restoration practices and ecosystem functions on resilience.

Future study design elements should include:

- The use of a range of complimentary statistical and data summary approaches to identify periods of varying resilience, as resilience often did not develop in a linear manner.

- Resilience of restored ecosystems should be quantified using a range of metrics as I found different metrics typically yielded different results.
- Comparison of resilience between restoration and reference sites to understand restoration success and identify beneficial management strategies to promote resilience in restoration sites.

Potential actions at Hanson (the study site) to further understand and/or improve resilience to fire may include:

- Continual short and long-term monitoring of post-fire responses.
- Measurement of resilience to an unplanned wildfire.
- Potential actions to improve post-fire plant survival if desired.

Future research

I typically found poorer resilience of resprouters compared to obligate seeders and the drivers of their responses were variable. Future research in successfully establishing resprouters during the first few years of restoration (after topsoil transfer) may assist in increasing the similarity of restored Banksia woodlands to reference sites both pre- and post-fire (Chapter 5). Determining constraints to resprouter survival may also promote their future persistence (i.e., no resprouting may suggest organ development is poor while mortality over summer may suggest weather conditions were too extreme).

Soil factors such as compaction and field capacity may differ in restored sites which can influence plant establishment and potential resilience (e.g., Holmes 2001; Rokich et al., 2001a,b; Carrick and Krüger 2007; MacDonald et al., 2015; Timsina et al., 2022). Soil compaction and field capacity influenced resprouter survival and vigour at the individual plant scale for 63% of species surveyed (Chapter 4) but not at the community scale (species pooled together) for seedling and resprouter survival (Chapter 5). The lack of difference at the community scale may reflect mixed species responses to soil conditions within community models. As there is little evidence of the impacts of such soil factors on responses to fire in restored ecosystems (but see Herath et al., 2009; Herath and Lamont 2009), I suggest soil parameters continue to be considered as a potential driver of small-scale differences, but finer-scale measurement (e.g., more replicates, or measured on a per-species scale) may be appropriate.

More research is needed to assess the utility of trait-based approaches to understand species responses. Therefore, study designs should consider if species-specific studies are best, or if grouping species by traits and/or calculating trait-based indices is appropriate, as both may yield differing interpretations of resilience and explanation of variance. Having a deep understanding of restoration goals and reference site successional pathways is important. For example, if keystone or threatened species are desired in restoration then species-level analyses may be appropriate. While less studied in restoration sites (Chapter 2), utilizing trait-based indices such as functional redundancy may provide a useful assessment of resilience than more traditionally used measures of resilience like species diversity or richness. These metrics allow for an assessment of changes to ecosystem functioning following disturbance, which can also influence future resilience (Walker 1992; Díaz and Cabido 2001). I suggest consideration of the inclusion of functional targets for assessing restoration success if species trait values are well documented, and to be mindful of intra-specific trait variation within species (Moreira et al., 2012a; Mitchell et al., 2020; Westerband et al., 2021). These may be more useful in areas of high biodiversity where it may not be possible to return all species through restoration.

My thesis is an important contribution to understanding the drivers of post-fire responses and resilience to fire in restored Banksia woodlands, however, this is only the tip of the iceberg. In many cases, my models explained low amounts of variance suggesting that other factors are more important in driving the development of resilience in restored Banksia woodlands than the ones I measured. This is likely due to resilience being dynamic and multifaceted. Restoration practices such as ripping depth and soil composition should be considered due to their potential effects. Additionally, various ecosystem functions are likely important for resilience to fire and may include fauna, pollination, nutrient cycling and connectivity (Standish et al., 2014; Miller et al., 2017; Chambers et al., 2019).

Future study design elements

Different statistical methods complement each other, and I typically modelled restoration age as a continuous variable in regression-based analyses. While I typically found restoration age didn’t have a consistent effect on responses, through utilizing summary statistics describing variability around means (i.e., means and 95% confidence intervals), I was able to pick up ages of reduced resilience that models could not. Including site age in ordination analyses of similarity promotes understanding of community change with age too (Harries et al., 2023; Chapter 2). Additionally, my work suggests that changes with age are rarely linear, so linear regression alone is not sufficient to understand post-fire responses and resilience.

A range of variables should be considered when assessing resilience, as they all detail different results. Consideration of how these may be used to define resilience in restored ecosystems should occur. These may include further investigation of how reference sites may assist in understanding acceptable and/or historical range of variation (Brudvig et al., 2017; Erskine et al., 2019; Oliver et al., 2023) or through the lens of state-and-transition models (Hernandez-Santin et al., 2020). Guidance on the development of restoration goals that are specific to resilience would benefit this also (E. Cowan, unpublished data, 2023).

The inclusion of reference data (i.e., reference intact Banksia woodlands) is essential for determining if post-fire states are desirable (Herath and Lamont 2009; McKenna et al., 2019;

Oliver et al., 2023). In Chapter 5, I compared restored sites to reference Banksia woodlands sites which typically yielded different interpretations of resilience as while restored and reference states were similar in parameters like diversity and functional redundancy, their composition was substantially different. Additionally, determining if the amount of, and direction of ecological change was similar despite differences in community composition and states (e.g., density, diversity) which is common in restoration projects allowed me to determine if responses are desirable and should be completed where pre-and-post-fire data of reference sites is available.

Potential actions at Hanson (the study site)

Following fire, ongoing monitoring is necessary to determine the successional pathways of restored Banksia woodlands and their long-term (>~17 months) resilience to fire as changes in community states are likely. Monitoring should be relatively frequent after fire until there is little change among ecosystem states between monitoring periods. Quantifying how much change occurs in early post-fire stages may determine if early intervention is needed to ensure that future plant communities can meet restoration goals. Repeated monitoring at older times since fire is needed also to determine senescence timeframes for individual species which can assist in promoting their persistence following future fire. It can also provide valuable information regarding when there may be a state change, potentially reflecting changed resilience (Chapter 2).

It is important to note that the experimental fire occurred during a time with increased fuel moisture, so wildfire (unplanned fire) risk was lower. Therefore, if wildfires were to occur, conditions would likely be drier, and fire would likely be more severe and potentially burn a wider range of restoration ages. This may have led to different responses and inferences of resilience. Expected differences may include higher germinant density and richness due to potentially higher fire temperatures and smoke lingering on the soil for longer. It is difficult to predict resprouter responses as fire severity might be higher which may promote or prevent resprouting. In regards to restoration age, if younger sites are burnt, there may be a stronger effect of age due to resilience being poorly developed in younger ages, as suggested for perennials in Chapter 3 and some species in Chapter 4.

I found that post-fire survival of the first summer (a key persistence bottleneck) was similar across the restoration chronosequence for both seedlings and established resprouts (~18 vs 43% survival respectively; Chapter 5). Survival rates were similar to those observed in restored Banksia woodlands and other sites restored after mining (Herath and Lamont 2009; Herath et al., 2009; Standish et al., 2012). If higher survival rates are desired, actions to promote seedling survival may include watering over the summer, which can promote survival by ~1–30% following topsoil transfer in Banksia woodlands (Standish et al., 2012). Or, canopy cover and litter could be altered, but the effects of this are mixed (e.g., Enright and Lamont 1989; Lloret 1998; Silva et al., 2015; Figueiredo et al., 2023) and unknown for established resprouter survival. Additionally, planting of individuals from warmer climates (i.e., climate-adjusted provenances) may assist in improving restoration success and plant survival under climate change (Prober et al., 2015; Bush et al., 2022), if consistent with restoration objectives.

Conclusion

My thesis considered resilience to fire in restored Banksia woodlands — are our current restoration strategies restoring resilience? Broadly, my research suggests that in older restoration sites, if resilience is considered based on a site's ability to return to its prior state, then largely resilience is present. However, this fails to investigate if restored sites are similar to reference sites, which is a key goal of successful restoration. Through the inclusion of reference sites, my research found that for some metrics, post-fire responses in restored sites reflect those of reference sites. However, regardless of restoration age burnt, restored sites were dissimilar to reference sites both before and after fire, suggesting that the successful establishment of plants during the initial restoration phase (i.e., during topsoil transfer) is necessary. Improving the establishment of perennial species and understanding resprouting responses to fire will likely enhance the similarity of restored and reference Banksia woodlands and is a top priority for future research. Overall, my thesis provides insights into the complex range of factors driving resilience to fire and highlights how a multifaceted understanding is necessary for restoration success.

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Appendices

Chapter 2 supporting information

Table S2.1: Key details associated with references used in the review.

ecosystem	location	pre-restoration land use	disturbance type	used reference or control	Evidence number	Study
Grasslands	Illinois, USA	NA	Drought	yes - reference	1	Allison 2008
Grasslands	Nebraska, USA	agriculture	Drought	yes - control	2	Carter et al., 2012
Grasslands	Northern Territory, Australia	mining	Fire	yes - both	3	Cook 2012
Grasslands	Tennessee, USA	agriculture	Fire	yes - control	4	Holcomb et al., 2014
Grasslands	Wisconsin, USA	agriculture	Fire	yes - control	5	Howe 1994
Grasslands	Arkansas, USA	NA	Fire	yes - control	6	Sparks et al., 1998
Shrublands	Western Australia, Australia	mining	Fire	yes - reference	7	Herath & Lamont 2009
Shrublands	Western Australia, Australia	mining	Fire	yes - reference	8	Herath et al., 2009
Temperate forests	Western Australia, Australia	mining	Fire	yes - reference	9	Grant et al., 1997
Temperate forests	Western Australia, Australia	mining	Fire	yes - both	10	Grant and Loneragan 1999
Temperate forests	Western Australia, Australia	mining	Fire	yes - both	11	Grant and Loneragan 2001
Temperate forests	Western Australia, Australia	mining	Fire	yes - both	12	Grant 2003
Temperate forests	Spain	NA	Fire	yes - reference	13	Ruiz Benito et al., 2012
Temperate forests	Western Australia, Australia	mining	Fire	yes - reference	14	Smith et al., 2000
Temperate forests	Western Australia, Australia	mining	Fire	yes - reference	15	Smith et al., 2004
Woodlands	Australia Capital Territory, Australia	agriculture	Fire	yes - control	16	Pickup et al., 2013
Woodlands	New South Wales, Australia	mining	Fire	yes - reference	17	Ross et al., 2004
Grasslands and woodlands	Tennessee, USA	mixed - agriculture and logging	Fire	yes - control	18	Vander Yacht et al., 2017
Floodplain	Queensland, Australia	agriculture	Cyclone	yes - reference	19	Bruce et al., 2008
Tropical forest	Queensland, Australia	agriculture	Cyclone	yes - reference	20	Kanowski et al., 2008

Temperate forests	Alabama, USA	mixed - agriculture and logging	Tornado	yes - control	21	Kleinman & Hart 2017
Woodlands	Ohio, USA	NA	Tornado	yes - control	22	Abella et al., 2018

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Chapter 3 supporting information

Figure S3.1: Smoke tent trail; woody material was combusted in a metal barrel (90 L) and the resulting smoke funnelled into three 1 × 4 metre tents using two 3.5 m and one 2.5 m long metal pipes.

Table S3.1: Common dormancy responses for families found in the restoration chronosequence.

Family	Number of species	Smoke responsive	Heat responsive	No dormancy	Other
Aizoaceae	1	✓			
Anarthriaceae	1	✓			
Apiaceae	2	✓			
Araliaceae	1	✓			
Asparagaceae	7	✓			
Asteraceae	13	✓			
Campanulaceae	3	✓			
Caryophyllaceae	1	✓			
Casuarinaceae	1			✓	
Centrolepidaceae	1	✓			✓
Colchicaceae	1				
Crassulaceae	2	✓			
Cyperaceae	3	✓			
Dasypogonaceae	1	✓			
Dilleniaceae	4	✓			
Droseraceae	2	✓			
Ericaceae	6	✓			
Fabaceae	12		✓		
Geraniaceae	1		✓		

Goodeniaceae	3	✓		
Haemodoraceae	6	✓		
Haloragaceae	1	✓		
Hemerocallidaceae	2	✓		
Iridaceae	3	✓		
Lauraceae	1		✓	
Loganiaceae	1	✓		
Molluginaceae	1	✓		
Myrtaceae	14	✓		✓
Orchidaceae	2			✓
Phyllanthaceae	1	✓		
Poaceae	9	✓		
Polygalaceae	1	✓		
Portulacaceae	3	✓		
Primulaceae	1	✓		
Proteaceae	6	✓		✓
Restionaceae	3	✓		
Rubiaceae	1	✓		
Rutaceae	2	✓		
Stylidiaceae	9	✓		

Data sourced from Sweedman & Merritt (2006); Offord & Meagher (2009), Baskin & Baskin (2014) & Stevens et al., (2016)

Table S3.2: Database source and information acquired for trait data.

Author	Reference	Traits sourced
Veber et al., 2019	Unpublished database	Fire response type
Florabase	Western Australian Herbarium (1998–). *Florabase—the Western Australian Flora.* Perth, Western Australia: Department of Biodiversity, Conservation and Attractions. https://florabase.dpaw.wa.gov.au/ (Accessed 2019–)	Origin

Table S3.3: Species, their trait group, and treatment types they were present in.

Species code	Species	Trait group	Smoked SSB	Control SSB	Aboveground vegetation
acachueg	*Acacia huegelii*	Obligate seeder		✓	✓
acacpulc	*Acacia pulchella*	Obligate seeder		✓	✓
acacsten?	*Acacia stenoptera?*	Resprouter	✓		
adencygn	*Adenanthos cygnorum*	Obligate seeder	✓	✓	✓

airacary	*Aira caryophyllea*	Invasive annual	✓	✓	✓
alexnite	*Alexgeorgia nitens*	Resprouter	✓		✓
allohumi	*Allocasuarina humilis*	Resprouter	✓		✓
andehete	*Andersonia heterophylla*	Obligate seeder	✓		
anighumi	*Anigozanthos humilis*	Resprouter			✓
anigmang	*Anigozanthos manglesii*	Obligate seeder			✓
arnoprei	*Arnocrinum preissii*	Resprouter	✓		✓
astrxero	*Astroloma xerophyllum*	Obligate seeder	✓	✓	✓
austcomp	*Austrostipa compressa*	Native annual	✓	✓	✓
austflav	*Austrostipa flavescens*	Resprouter	✓		✓
avenbarb	*Avena barbata*	Invasive annual	✓	✓	✓
bankatte	*Banksia attenuata*	Resprouter	✓	✓	✓
bankmenz	*Banksia menziesii*	Resprouter	✓	✓	✓
beaueleg	*Beaufortia elegans*	Obligate seeder	✓	✓	✓
bororamo	*Boronia ramosa*	Obligate seeder	✓	✓	✓
bosserio	*Bossiaea eriocarpa*	Obligate seeder	✓	✓	✓
brizmaxi	*Briza maxima*	Invasive annual	✓	✓	✓
burccong	*Burchardia congesta*	Resprouter	✓	✓	✓
calabrev	*Calandrinia brevipedata*	Native annual	✓		
calacorr	*Calandrinia corrigioloides*	Native annual	✓	✓	✓
calaflav	*Caladenia flava*	Resprouter	✓	✓	✓
calagran	*Caladrinia granulifera*	Native annual	✓	✓	
calyangu	*Calytrix angulata*	Resprouter	✓	✓	✓
calyflav	*Calytrix flavescens*	Obligate seeder			✓
calyfras	*Calytrix fraseri*	Obligate seeder	✓	✓	✓
carpedul	*Carpobrotus edulis*	Invasive perennial (obligate seeder)	✓	✓	✓
cassytha	*Cassytha sp.*	Obligate seeder	✓		✓
centglab	*Centrolepis glabra*	Native annual	✓	✓	✓
comecaly?	*Comesperma calymega*	Obligate seeder		✓	
conoacul	*Conostylis aculeata*	Resprouter			✓
conoanig	*Haemodoraceae sp*	Resprouter	✓	✓	✓
conojunc	*Conostylis juncea*	Resprouter			✓
conostoe	*Conospermum stoechadis*	Resprouter		✓	✓
crascolo	*Crassula colorata*	Native annual	✓	✓	✓
crasexse	*Crassula exserta*	Native annual	✓	✓	
cronking	*Croninia kingiana*	Obligate seeder	✓	✓	✓
dampline	*Dampiera linearis*	Resprouter	✓		✓
dasybrom	*Dasypogon bromeliifolius*	Resprouter	✓		
davinudi?	*Daviesia nudiflora*	Obligate seeder			✓
davitrif	*Daviesia triflora*	Resprouter			✓
desmflex	*Desmocladus flexuosus*	Resprouter	✓		✓
droseryt	*Drosera erythrorhiza*	Resprouter	✓	✓	✓
drosmenz	*Drosera menziesii*	Resprouter		✓	✓
ehrhcaly	*Ehrharta calycina*	Invasive perennial (resprouter)	✓		✓
ehrhlong	*Ehrharta longiflora*	Invasive annual	✓	✓	✓
erempauc	*Eremaea pauciflora*	Resprouter	✓	✓	✓

erigeronsp	*Erigeron sp.*	Invasive annual	✓		
eucatotd	*Eucalyptus todtiana*	Resprouter			✓
gastcapi	*Gastrolobium capitatum*	Resprouter	✓	✓	✓
gladcary	*Gladiolus caryophyllaceus*	Invasive perennial (resprouter)	✓	✓	✓
gnaphaliumsp	*Gnaphalium sp.*	Invasive annual	✓		
gomptome	*Gompholobium tomentosum*	Obligate seeder	✓	✓	✓
gonopith	*Gonocarpus pithyoides*	Resprouter	✓	✓	✓
haemspic	*Haemodorum spicatum*	Resprouter		✓	✓
hensturb	*Hensmania turbinata*	Resprouter			✓
hibbaure	*Hibbertia aurea*	Resprouter	✓		✓
hibbheug	*Hibbertia huegelii*	Resprouter	✓	✓	✓
hibbhype	*Hibbertia hypericoides*	Resprouter	✓		✓
hibbsubv	*Hibbertia subvaginata*	Obligate seeder	✓	✓	✓
homahoma	*Homalosciadium homalocarpum*	Native annual	✓	✓	✓
hovepung	*Hovea pungens*	Obligate seeder			✓
hyalcotu	*Hyalosperma cotula*	Native annual	✓		✓
hypoglab	*Hypochaeris glabra*	Invasive annual	✓	✓	✓
hyporadi	*Hypochaeris radicata*	Invasive annual	✓	✓	✓
isolmarg	*Isolepis marginata*	Native annual	✓	✓	✓
jackflor	*Jacksonia floribunda*	Resprouter	✓		✓
jackfurc	*Jacksonia furcellata*	Resprouter	✓	✓	✓
kunzglab	*Kunzea glabrescens*	Obligate seeder	✓	✓	✓
laxmramo	*Laxmannia ramosa*	Obligate seeder	✓		
laxmsqua	*Laxmannia squarrosa*	Obligate seeder	✓		✓
lechflor	*Lechenaultia floribunda*	Resprouter	✓	✓	✓
lepidosperma	*Lepidosperma sp.*	Resprouter			✓
lepiprei	*Lepidobolus preissianus*	Resprouter	✓		
leuccono	*Leucopogon conostephioides*	Obligate seeder	✓	✓	✓
leucpoly	*Leucopogon polymorphus*	Resprouter	✓	✓	✓
levestip	*Levenhookia stipitata*	Native annual	✓	✓	✓
lobetenu	*Lobelia tenuior*	Native annual	✓	✓	
lomacaes	*Lomandra caespitosa*	Resprouter			✓
lomasuav	*Lomandra suaveolens*	Resprouter	✓		
lygibarb	*Lyginia barbata*	Resprouter	✓	✓	✓
lysiarve	*Lysimachia arvensis*	Invasive annual	✓	✓	
lysicili	*Lysinema ciliatum*	Obligate seeder			✓
macaapet	*Macarthuria apetala*	Obligate seeder			✓
melaseri	*Melaleuca seriata*	Resprouter	✓	✓	✓
melasyst	*Melaleuca systena*	Resprouter			✓
melatric	*Melaleuca trichophylla*	Resprouter			✓
milltenu	*Millotia tenuifolia*	Native annual	✓	✓	✓
opervagi	*Opercularia vaginata*	Resprouter			✓
pateocci	*Patersonia occidentalis*	Resprouter	✓	✓	✓
pelacapi	*Pelargonium capitatum*	Invasive perennial (obligate seeder)	✓	✓	✓

pentairo	*Pentameris airoides*	Invasive annual	✓	✓	✓
petrdubi	*Petrorhagia dubia*	Invasive annual			✓
petrline	*Petrophile linearis*	Resprouter			✓
philspic	*Philotheca spicata*	Resprouter			✓
phylpara	*Phyllangium paradoxum*	Native annual	✓	✓	✓
podoangu	*Podotheca angustifolia*	Native annual		✓	✓
podochry	*Podotheca chrysantha*	Native annual	✓	✓	✓
podognap	*Podotheca gnaphalioides*	Native annual	✓	✓	✓
poramoor	*Poranthera moorokatta*	Native annual	✓	✓	
pterostylis	*Pterostylis sp.*	Obligate seeder			✓
pultenaea	*Pultenaea sp.*	Obligate seeder	✓	✓	
quinurvi	*Quinetia urvillei*	Native annual	✓	✓	✓
regeliasp	*Regelia sp.*	Resprouter	✓		
regiinop	*Regelia inops*	Resprouter			✓
romurose	*Romulea rosea*	Invasive perennial (resprouter)	✓	✓	✓
scaecane	*Scaevola canescens*	Resprouter			✓
schocurv	*Schoenus curvifolius*	Resprouter			✓
schoinvo	*Scholtzia involucrata*	Resprouter	✓	✓	✓
silohumi	*Siloxerus humifusus*	Native annual	✓	✓	
soncoler	*Sonchus oleraceus*	Invasive annual	✓		✓
sowelaxi	*Sowerbaea laxiflora*	Resprouter	✓		
stirlati	*Stirlingia latifolia*	Resprouter	✓	✓	✓
styladpr	*Stylidium adpressum*	Resprouter	✓		
stylbrun	*Stylidium brunonianum*	Resprouter	✓	✓	✓
stylcalc	*Stylidium calacartum*	Obligate seeder		✓	
stylcross	*Stylidium crossocephalum*	Obligate seeder			✓
styldiur	*Stylidium diuroides*	Obligate seeder			✓
stylneur	*Stylidium neurophyllum*	Resprouter	✓		✓
stylrepe	*Stylidium repens*	Obligate seeder	✓	✓	✓
stylrigi	*Stylidium rigidulum*	Obligate seeder	✓	✓	✓
thysarbu	*Thysanotus arbuscula*	Resprouter	✓		
thysaren	*Thysanotus arenarius*	Resprouter	✓		✓
tracpilo	*Trachymene pilosa*	Native annual	✓	✓	✓
ursianth	*Ursinia anthemoides*	Invasive annual	✓	✓	✓
vertnite	*Verticordia nitens*	Obligate seeder	✓	✓	✓
vulpmyur	*Vulpia myuros*	Invasive annual	✓	✓	✓
wahlcape	*Wahlenbergia capensis*	Invasive annual	✓	✓	✓
wahlprei	*Wahlenbergia preissii*	Native annual	✓	✓	✓
xantheug	*Xanthosia huegelii*	Obligate seeder	✓		✓

Table S3.4: Species with canopy stored seeds or requiring heat removed for Figure S3.7.

Family	Species	Canopy stored seed	Heat responsive
Casuarinaceae	*Allocasuarina humilis*	✓	
Fabaceae	*Acacia huegelii*		✓

Fabaceae	*Acacia pulchella*		✓
Fabaceae	*Acacia stenoptera?*		✓
Fabaceae	*Bossiaea eriocarpa*		✓
Fabaceae	*Daviesia nudiflora*		✓
Fabaceae	*Daviesia triflora*		✓
Fabaceae	*Gastrolobium capitatum*		✓
Fabaceae	*Gompholobium tomentosum*		✓
Fabaceae	*Hovea pungens*		✓
Fabaceae	*Jacksonia furcellata*		✓
Fabaceae	*Jacksonia floribunda*		✓
Fabaceae	*Pultenaea sp.*		✓
Geraniaceae	*Pelargonium capitatum*		✓
Lauraceae	*Cassytha sp.*		✓
Myrtaceae	*Beaufortia elegans*	✓	
Myrtaceae	*Eremaea pauciflora*	✓	
Myrtaceae	*Eucalyptus todtiana*	✓	
Myrtaceae	*Kunzea glabrescens*	✓	
Myrtaceae	*Melaleuca seriata*	✓	
Myrtaceae	*Melaleuca systena*	✓	
Myrtaceae	*Melaleuca trichophylla*	✓	
Myrtaceae	*Regelia inops*	✓	
Myrtaceae	*Regelia sp.*	✓	
Proteaceae	*Banksia attenuata*	✓	
Proteaceae	*Banksia menziesii*	✓	
Proteaceae	*Petrophile linearis*	✓	

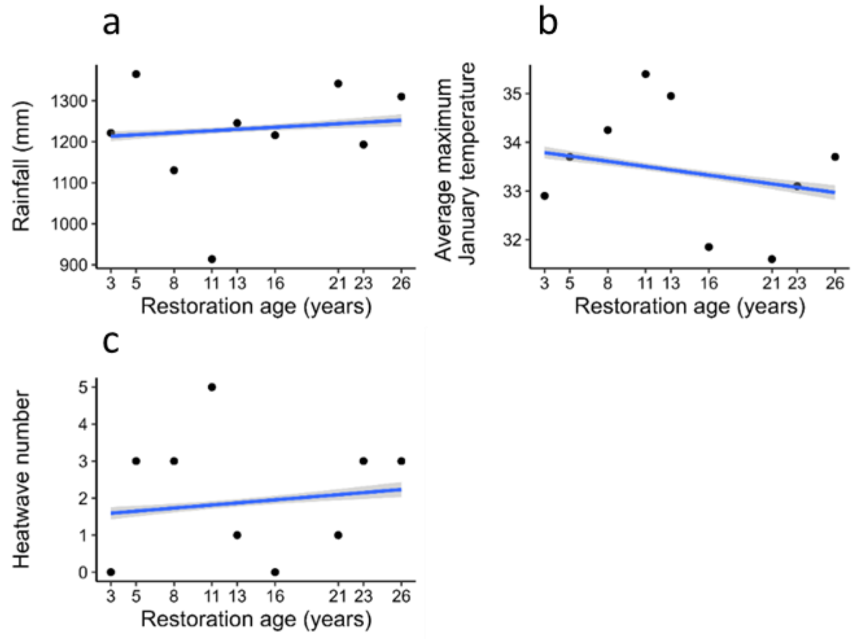

Figure S3.2: Relationships between restoration age and a) rainfall (mm), b) average maximum January temperature (°C) and c) number of heatwaves for the first two years since the initiation of restoration fitted with a linear smoother. See Table 3.1 for more details on predictors. n = 9.

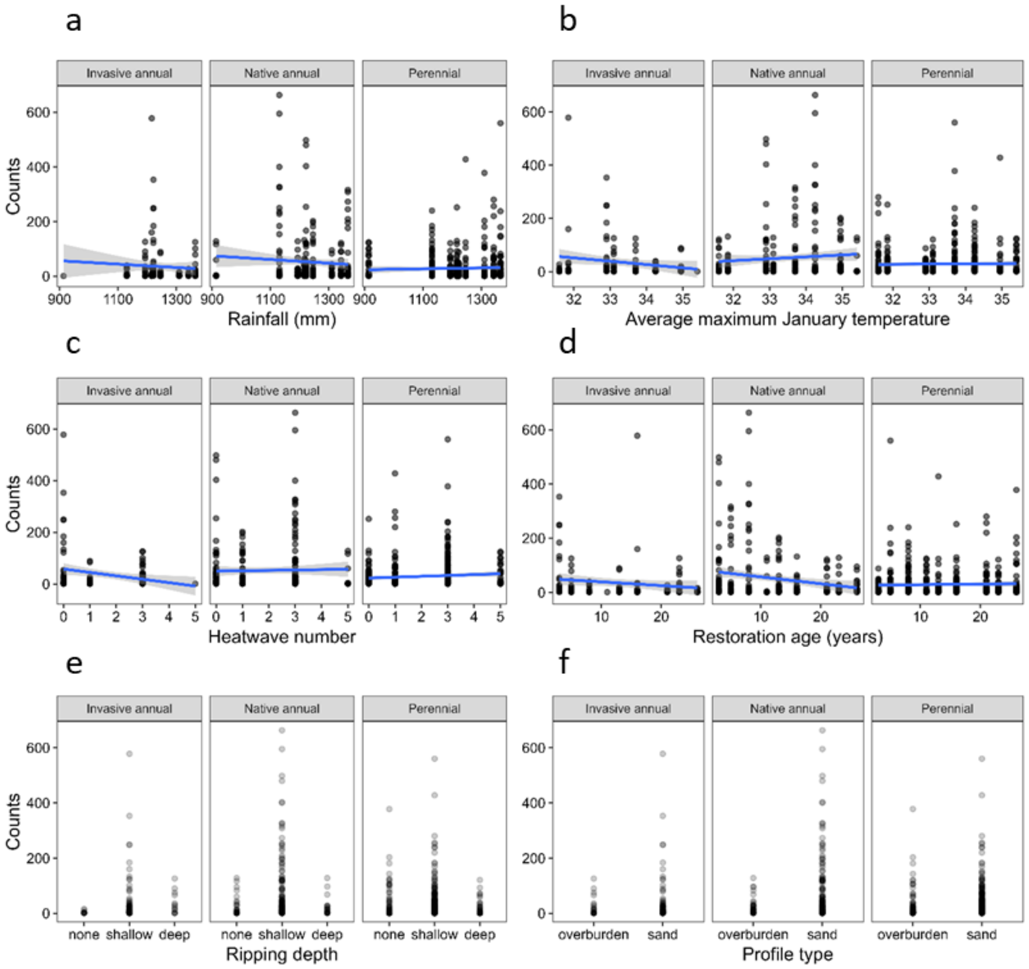

Figure S3.3: Relationships of smoked SSB counts for plant trait groups with model predictors of a) rainfall (mm), b) average maximum January temperature (°C), c) heatwave number, d) restoration age, e) ripping depth and f) profile type. a-d are fitted with a linear smoother. See Table 3.1 for further explanation of predictors.

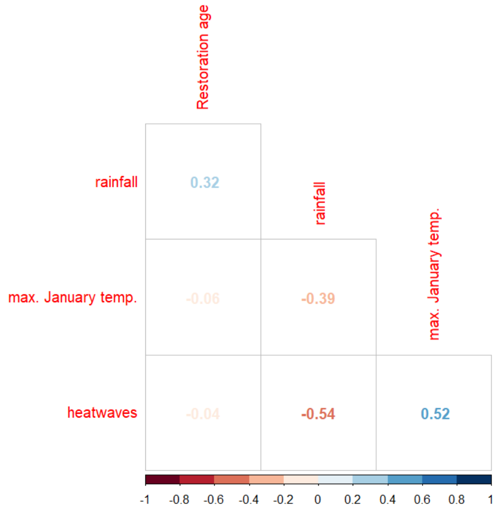

Figure S3.4: Correlation matrix of continuous climate data (see Table 3.1 for further explanation of predictors).

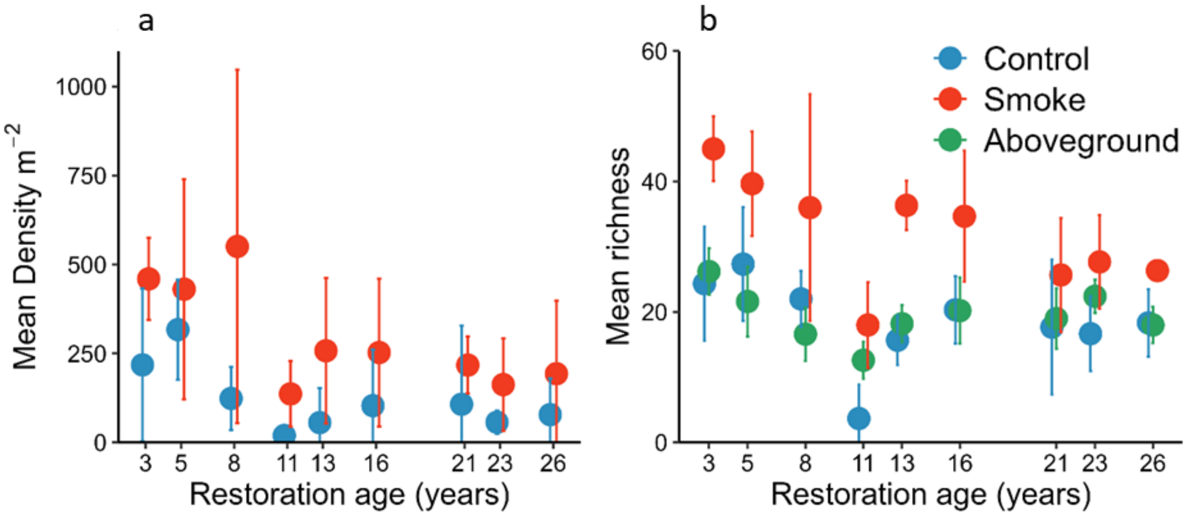

Figure S3.5: Means and 95% confidence intervals for a) germinant densities m^{-2} for smoked and control SSB, and b) mean richness for aboveground vegetation and SSB (smoked and control). SSB n=3, aboveground vegetation n=5.

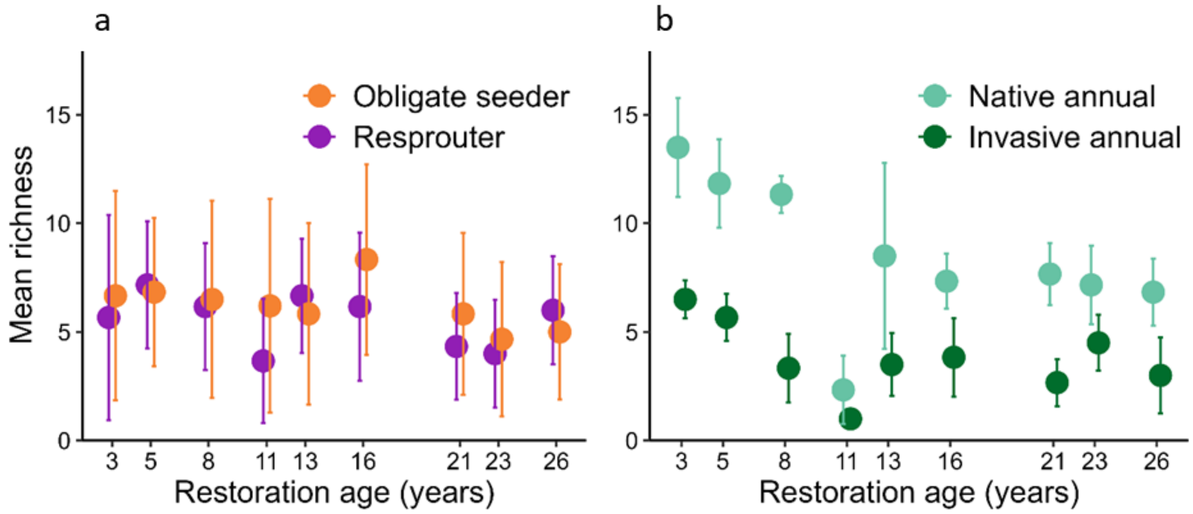

Figure S3.6: Means and 95% confidence intervals for total SSB germinants (control and smoked SSB) for a) annuals and b) perennials across the 23-year restoration chronosequence. N=6.

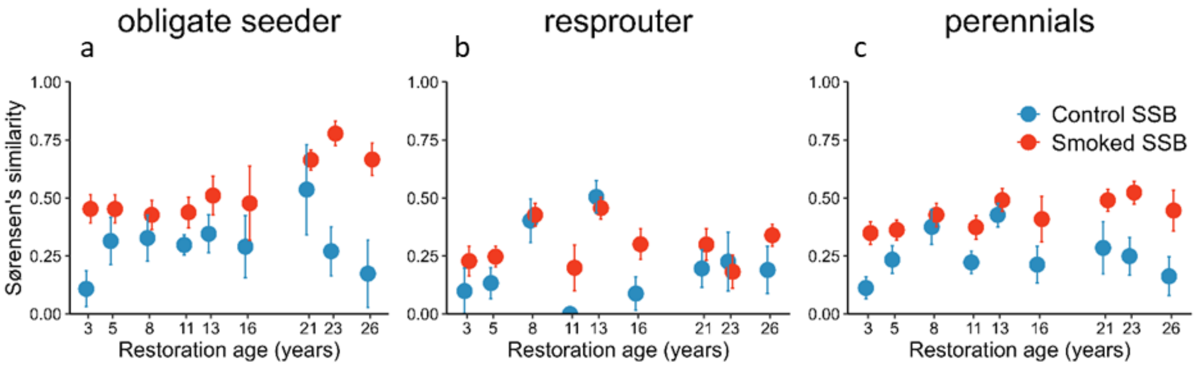

Figure S3.7: Mean Sørensen’s similarity and 95% CI of species presence/absence comparing smoked or control SSB to aboveground vegetation for a) native perennial obligate seeders, b) native perennial obligate seeders and c) entire native perennials community excluding species that store their seeds in the canopy or require heat to stimulate germination (i.e., those that are unlikely to be stimulated by smoke; see Table S3.4 for list of species). n = max. 15; three smoked plots compared to each of five aboveground plots.

Table S3.5: Models summary of richness following smoke treatment for different trait types. Bolding of *P* values indicates significance at <0.05 level.

Trait group	*Predictor*	*Estimate*	*SE*	*Z value*	*P*
Native perennial	**Intercept**	**2.214**	**0.107**	**20.644**	**<0.001**
	Fire response [obligate seeder]	**0.197**	**0.094**	**2.097**	**0.036**
	Restoration age	**-0.013**	**0.006**	**-2.104**	**0.035**
	Marginal R^2	0.152			
Native annual	**Intercept**	**2.687**	**0.121**	**22.133**	**<0.001**
	Restoration age	**-0.036**	**0.009**	**-4.185**	**<0.001**
	Marginal R^2	0.435			
Invasive annual	**Intercept**	**1.746**	**0.186**	**9.393**	**<0.001**
	Restoration age	**-0.025**	**0.127**	**-1.966**	**0.049**
	Marginal R^2	0.148			

Table S3.6: Model summary of similarity for native perennial species. Bolding of *P values* indicates significance at <0.05 level.

Trait group	*Predictor*	*Estimate*	*SE*	*Z value*	*P*
Native perennial	**Intercept**	**0.241**	**0.023**	**10.618**	**<0.001**
	Restoration age	<0.001	0.001	0.426	0.670
	Comparison [smoked SSB]	**0.093**	**0.032**	**2.911**	**0.003**
	Age × comparison [smoked SSB]	**0.004**	**0.002**	**2.056**	**0.040**
	Marginal R^2	<1			

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Offord, C. A. & Meagher, P. F. (2009) *Plant Germplasm Conservation in Australia: Strategies and Guidelines for Developing, Managing and Utilising Ex Situ Collections, full rev. edn.,* Canberra, Australia: Australian Network for Plant Conservation. Available at: https://www.anpc.asn.au/wp-content/uploads/2021/02/Plant-Germplasm-Conservation-InAustralia-online.pdf (Accessed: 16 March 2021).

Stevens, J. C., Rokich, D. P., Newton, V. J., Barrett, R. L. and Dixon, K. W. (2016) *Banksia Woodlands - A Restoration Guide for the Swan Coastal Plain.* Nedlands, Western Australia, Australia: University of Western Australia Press.

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Chapter 4 supporting information

Table S4.1: Sample size of each species per response and restoration age.

				Restoration age (years)									
Response	Resprouter type	Species	n	4	6	9	12	14	17	22	24	27	# ages
Resprout & survival	Root sucker	*Damperia linearis*	49	6	0	0	17	0	0	19	7	0	4
		Gonocarpus pithyoides	55	0	0	6	0	0	0	5	27	17	4
		Lechenaultia floribunda	139	25	47	43	0	0	0	5	0	19	5
	Rhizomes	*Conostylis aculeata*	84	12	0	6	8	30	12	2	14	0	7
		Conostylis juncea	25	21	0	1	0	0	0	1	2	0	4
		Patersonia occidentalis	46	2	0	0	7	2	23	7	5	0	6
	Lignotuber	*Scholtzia involucrata*	233	44	15	17	34	24	43	16	22	18	9
		Stirlingia latifolia	100	8	26	19	0	14	6	16	6	5	8
	Root crown	*Gastrolobium capitatum*	51	0	0	0	16	1	12	5	15	2	6
Vigour	Root sucker	*Damperia linearis*	25	0	0	0	11	0	0	12	2	0	3
		Gonocarpus pithyoides	25	0	0	0	0	0	0	3	15	7	3
		Lechenaultia. floribunda	63	10	21	16	0	0	0	1	0	15	5
	Rhizomes	*Conostylis aculeata*	64	7	0	6	6	29	10	2	4	0	7
		Conostylis juncea	7	5	0	1	0	0	0	1	0	0	3
		Patersonia occidentalis	42	0	0	0	7	2	23	6	4	0	5
	Lignotuber	*Scholtzia involucrata*	89	12	5	2	16	12	11	7	16	8	9
		Stirlingia latifolia	77	5	18	13	0	13	2	16	6	4	8
	Root crown	*Gastrolobium capitatum*	2	0	0	0	0	1	0	0	1	0	2

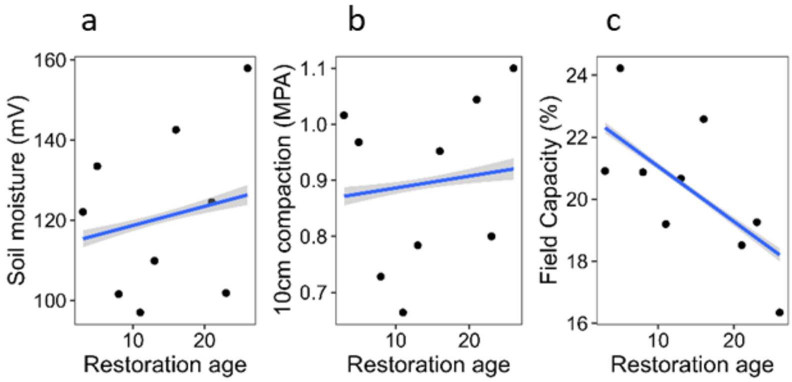

Figure S4.1: Relationships between restoration age and soil parameters (Table 4.1).

Supplementary text S4.1: Relationships between roots and above-ground plant size.

To determine relationships between aboveground plant size and root biomass, we harvested root biomass for 5–7 plants of each species that were destructively harvested before the experimental burning treatment. We separated root and above-ground parts and placed the material in drying ovens at 80°C until constant weight was achieved. All plant size variables were log-transformed to reduce the spread of the data. We found log-transformed pre-fire canopy volume to be most strongly correlated with root biomass for all species (r = 0.66–0.94; mean = 0.79; Table S4.3; Figure S4.3), the high r values suggesting this variable was a good predictor of root biomass. Therefore, we used log-transformed pre-fire canopy volume as our measure of pre-fire plant size in all analyses. Restoration age (as an indication of maximum plant age) was also recorded as resprouting success of individual plants may develop with time.

Table S4.2: Pre-fire and biomass plant size measurements. Plant canopy volume was determined using height and width measurements, estimate of resprout organ size was determined by calculating a rectangle from the two width measurements.

Measurement	Details
Plant height	Height of plant to tallest live part (cm)
Plant width	Perpendicular width of plants (cm)

Estimate of resprout organ size	x2 measurements of area with alive stems arising from ground (cm; Figure S4.2)

Figure S4.2: Diagram showing measurements used to calculate an estimate of lignotuber size. Two perpendicular measurements of the area of alive stems arising from the ground were collected.

Table S4.3: Correlation coefficients (r) between root biomass and log-transformed measures of pre-fire size of harvested samples.

Resprouter type	Species	Height (log)	Canopy volume (log)	Approximate resprout organ size (log)
Root sucker	*D. linearis*	0.31	0.66	0.94
	G. pithyoides	0.89	0.93	0.86
	L. floribunda	0.76	0.79	0.94
Rhizomes	*C. aculeata*	0.95	0.82	0.82
	C. juncea	-0.41	0.71	0.85
	P. occidentalis	0.84	0.94	-0.62
Lignotuber	*S. involucrata*	0.50	0.74	0.66
	S. latifolia	0.95	0.84	0.39
Root crown	*G. capitatum*	0.69	0.73	0.92
	Correlation mean	0.60	0.79	0.64

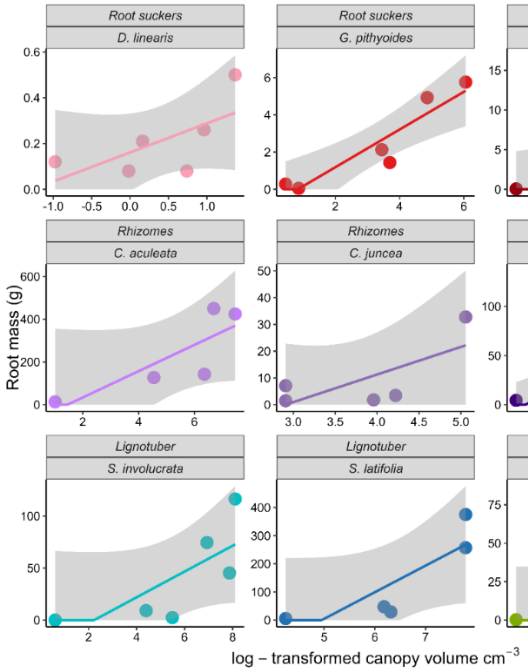

Figure S4.3: Relationships between log-transformed pre-fire canopy volume (cm^{-3}) and root biomass (g) per species. Data is fitted with a loess smoother with 95% CI. Axes scales differ between species. N per species = 5–7.

Supplementary text S4.2: Sampling of soil conditions

Soil compaction (25 replicates per age) was measured using an Eijkelkamp Penetrologger 6.08. We analyzed 10 cm compaction as all individuals had roots to this depth and a 10 cm layer of topsoil was deposited across all sites. Soil moisture (50 replicates per age) was measured at a depth of 6 cm using an ICT MP406 moisture probe. Both measurements were conducted in early November 2021 (late spring) when soils had largely dried. We expected little variation in field capacity as soil profiles were established in the same way per age (Table 4.1). Therefore, we collected soils (five replicates per age) to 6 cm in the profile to match the depth of the moisture probe. Soils were wet until saturation occurred, drained for 24 hours and oven dried at 80°C until constant weight was achieved.

Table S4.4: GLM summaries the effects of resprouter type on each response for all species except *G. capitatum* combined. Bolding of values indicates significance at *P*<0.05.

Response	Predictor	*Estimate*	*SE*	*z value*	*P*
Resprout	**Intercept**	**0.574**	**0.114**	**5.027**	**<0.001**
	Resprout type [rhizome]	**2.478**	**0.403**	**6.144**	**<0.001**
	Resprout type [root sucker]	**0.413**	**0.184**	**2.244**	**0.025**
	R^2	0.074			
Survival	Intercept	-0.006	0.110	-0.055	0.956
	Resprout type [rhizome]	**0.996**	**0.211**	**4.711**	**<0.001**
	Resprout type [root sucker]	-0.134	0.169	-0.794	0.427
	R^2	0.041			
Vigour	**Intercept**	**45.178**	**2.396**	**18.852**	**<0.001**
	Resprout type [rhizome]	**-19.819**	**3.766**	**-5.263**	**<0.001**
	Resprout type [root sucker]	**-34.151**	**3.766**	**-9.069**	**<0.001**
	R^2	0.180			

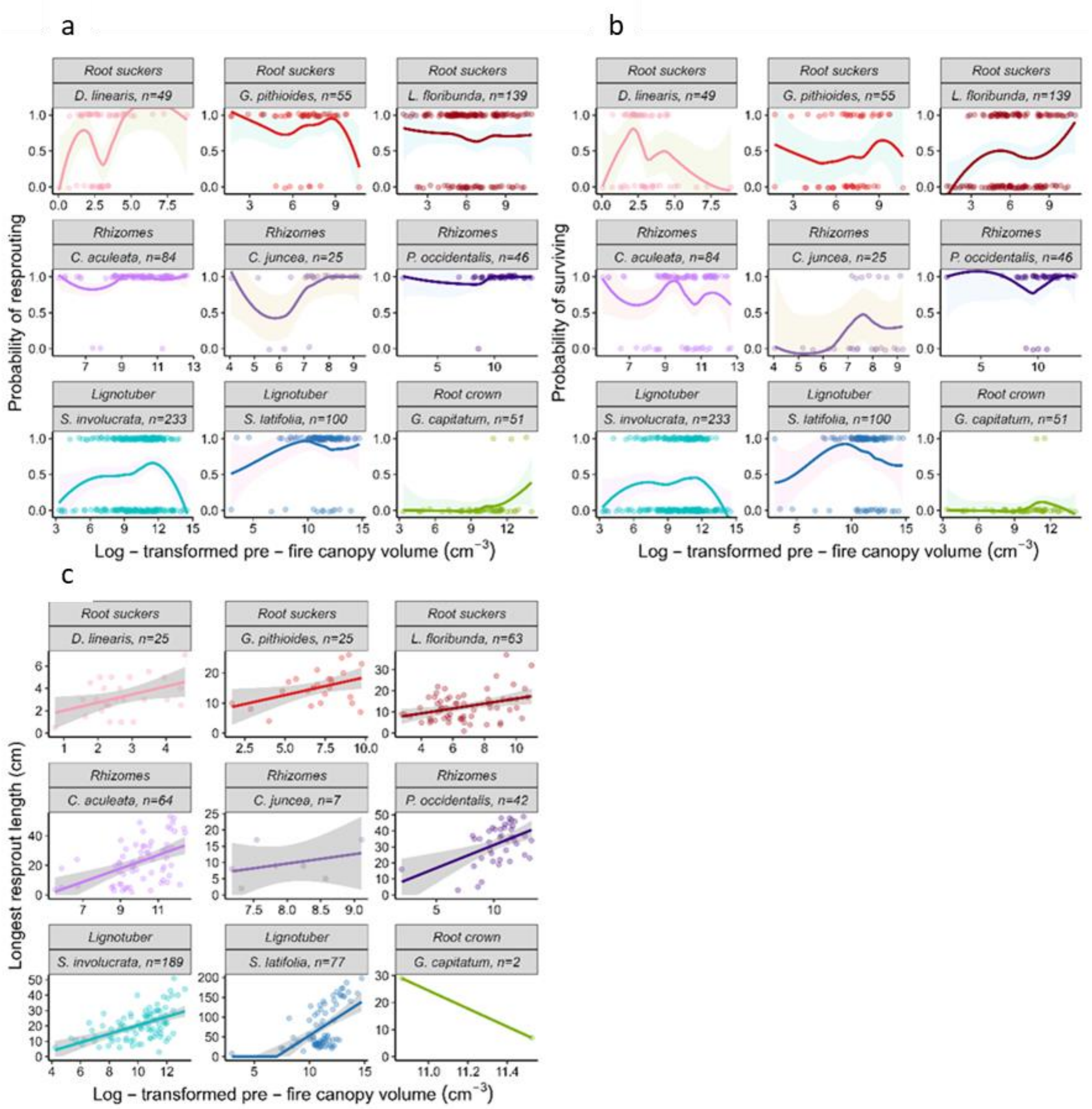

Figure S4.4: Species relationships between log-transformed pre-fire plant size (cm^{-3}) and the probability of a) resprouting, b) survival and c) vigour. Data has 95% CI and is fitted with a loess smoother for a) and b) and a linear smoother for c). Axes differ between species.

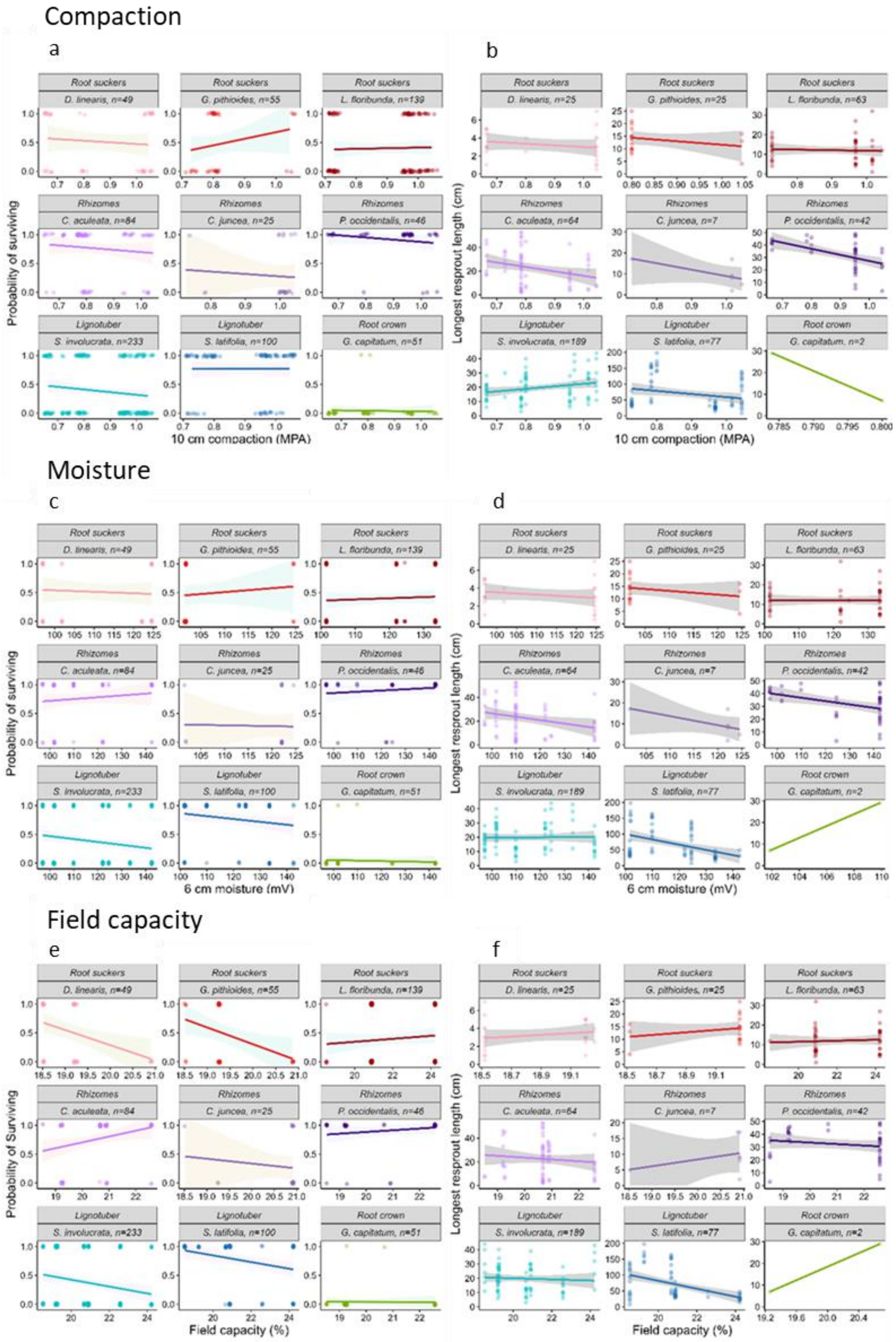

Figure S4.5: Species relationships of survival and vigour against soil (a&b) 10 cm compaction (MPA), (c&d) 6 cm moisture (mV) and (e&f) field capacity (%). Data has 95% CI and is fitted with a linear smoother. Axes differ between species.

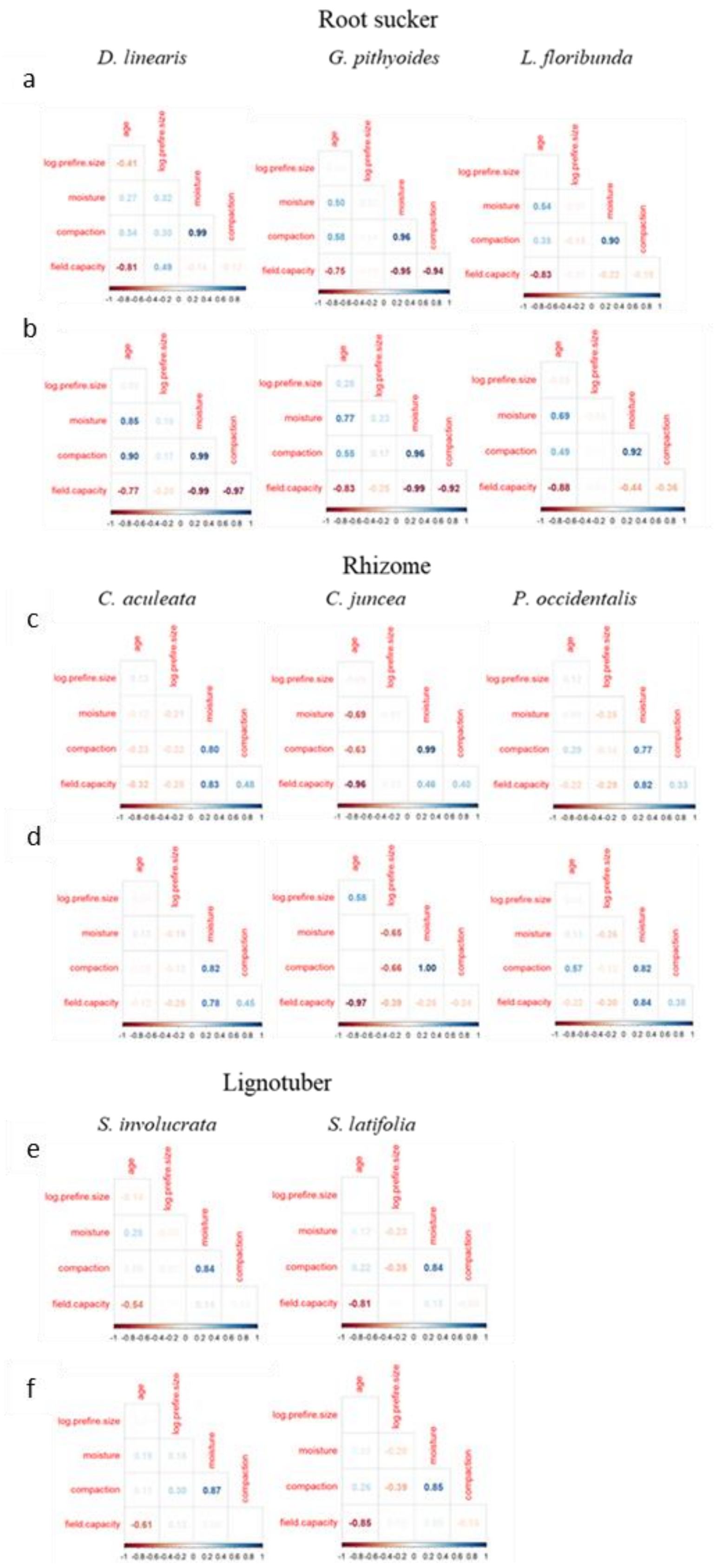

Figure S4.6: Pearson's correlation coefficients between predictors for root sucker, rhizomes and lignotuber species survival (a, c & e) and vigour (b, d & f).

Table S4.5: GAM summaries of the effect of smoothed (s) log-transformed plant size (cm^{-3}) on species probability of resprouting. Bolding of values indicates significance at $p<0.05$. A negative R^2 indicates the model is not explaining the variability of the dependent variable more effectively than a horizontal with an R^2 of 0, demonstrating poor model performance.

Resprouter type	Species	Predictor				
Root sucker	*D. linearis*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**1.032**	**0.465**	**2.221**	**0.026**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1.691	3.434	0.187	
		Adjusted R^2	0.068			
	G. pithyoides	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**1.774**	**0.384**	**4.624**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1	0.065	0.799	
		Adjusted R^2	-0.018			
	L. floribunda	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**0.873**	**0.186**	**4.687**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1	0.237	0.627	
		Adjusted R^2	-0.006			
Rhizome	*C. aculeata*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**3.502**	**0.688**	**5.093**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1	1.534	0.215	
		Adjusted R^2	0.003			
Lignotuber	*S. involucrata*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	0.143	0.133	1.072	0.284
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1.819	6.399	0.058	
		Adjusted R^2	0.022			
	S. latifolia	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**2.028**	**0.316**	**6.42**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1.262	2.213	0.318	
		Adjusted R^2	0.018			

Table S4.6: Root sucker species top generalised additive models (GAMs) for probability of survival, and generalised linear models (GLMs) for vigour with ΔAICc < 5 from full subsets analysis. Additive effects between variables is denoted by (+), (s) refers to smoothing of a predictor. Single predictor models, null models, AIC corrected for small sample size (AICc), difference from lowest reported AICc (ΔAICc), AICc model weights (ωAICc), variance explained (R^2) and estimated degrees of freedom (edf) are reported for model comparison. Size refers to pre-fire size, compaction measures were collected in November 2021.

Response	Species	Model	AICc	ΔAICc	ωAICc	R^2	Log-likelihood	edf
Survival	*D. linearis*	field capacity + compaction	61.992	0	0.684	0.171	-27.729	3
		field capacity	63.961	1.969	0.256	0.119	-29.850	2
		s(size)	67.571	5.579	0.042	0.080	-30.568	2.79
		Intercept only (null)	69.993	8.001	0.013	0	-33.954	1
		compaction	71.695	9.703	0.005	-0.011	-33.717	2
	G. pithyoides	Intercept only (null)	77.866	0	0.425	0	-37.900	1
		field capacity	79.772	1.906	0.164	-0.015	-37.771	2
		s(size)	79.935	2.068	0.151	-0.006	-37.458	2.2
		compaction	79.942	2.076	0.151	-0.017	-37.856	2
		s(size) + field capacity	81.845	3.979	0.058	-0.024	-37.461	3.1
		s(size) + compaction	82.114	4.247	0.051	-0.025	-37.459	3.17
	L. floribunda	s(size) + compaction	187.624	0	0.388	0.060	-90.723	3
		s(size) + field capacity + compaction	188.275	0.651	0.28	0.063	-89.988	4
		s(size) + field capacity	190.192	2.568	0.108	0.037	-92.006	3
		s(size)	190.849	3.225	0.077	0.025	-93.380	2
		field capacity + compaction	191.948	4.324	0.045	0.026	-92.885	3
		compaction	191.951	4.327	0.045	0.019	-96.932	2
		field capacity	192.350	4.726	0.037	0.0163	-94.131	2
		Intercept only (null)	193.507	5.882	0.02	0	-95.739	1
Vigour	*D. linearis*	size	96.403	0	0.287	0.153	-44.630	2
		size + field capacity	96.418	0.015	0.285	0.210	-43.209	3
		size + compaction	96.476	0.073	0.277	0.208	-43.238	3
		Intercept only (null)	99.016	2.613	0.078	0	-47.235	1
		compaction	100.438	4.035	0.038	0.004	-46.647	2
		field capacity	100.561	4.158	0.036	0	-46.709	2
	G. pithyoides	size	157.573	0	0.428	0.155	-75.215	2
		size + field capacity	159.168	1.596	0.193	0.160	-74.584	3
		size + compaction	160.099	2.526	0.121	0.128	-75.050	3
		Intercept only (null)	160.254	2.681	0.112	0	-77.854	1
		field capacity	160.473	2.9	0.1	0.051	-76.665	2
		compaction	162.054	4.481	0.046	-0.011	-77.455	2
	L. floribunda	size	418.643	0	0.544	0.110	-206.118	2
		size + field capacity	420.400	1.757	0.226	0.103	-205.855	3
		size + compaction	420.781	2.139	0.187	0.098	-206.046	3
		Intercept only (null)	424.827	6.185	0.025	0	-210.314	1
		field capacity	426.726	8.083	0.01	-0.011	-210.160	2
		compaction	426.954	8.312	0.009	-0.015	-210.274	2

Table S4.7: Rhizome species top generalised additive models (GAMs) for probability of survival, and generalised linear models (GLMs) for vigour with ΔAICc < 5 from full subsets analysis. Additive effects between variables is denoted by (+), (s) refers to smoothing of a predictor. Single predictor models, null models, AIC corrected for small sample size (AICc), difference from lowest reported AICc (ΔAICc), AICc model weights (ωAICc), variance explained (R^2) and estimated degrees of freedom (edf) are reported for model comparison. Size refers to pre-fire size, compaction measures were collected in November 2021.

Response	Species	Model	AICc	ΔAICc	ωAICc	R^2	Log-likelihood	edf
Survival	*C. aculeata*	field capacity	90.452	0	0.541	0.073	-43.152	2
		s(size) + field capacity	91.683	1.232	0.292	0.073	-42.692	3
		Intercept only (null)	94.260	3.808	0.081	0	-46.105	1
		compaction	95.507	5.055	0.043	-0.002	-45.679	2
		s(size)	96.294	5.842	0.029	-0.011	-46.073	2
	C. juncea	Intercept only (null)	31.822	0	0.373	0	-14.824	1
		s(size)	32.869	1.047	0.221	0.038	-12.977	2.71
		field capacity	33.874	2.052	0.134	-0.028	-14.664	2
		compaction	34.062	2.24	0.122	-0.037	-14.758	2
		s(size) + compaction	34.901	3.079	0.08	0.023	-12.539	3.76
		s(size) + field capacity	35.117	3.295	0.072	0.024	-12.655	3.75
Vigour	*C. aculeata*	size + compaction	509.537	0	0.704	0.270	-250.043	3
		size	511.828	2.292	0.224	0.229	-252.714	2
		size + field capacity	514.092	4.556	0.072	0.216	-252.707	3
		compaction	523.914	14.378	0.001	0.068	-258.757	2
		Intercept only (null)	527.256	17.719	0	0	-261.530	1
		field capacity	528.711	19.174	0	-0.004	-261.156	2
	P. occidentalis	size + compaction	309.390	0	0.988	0.422	-150.155	3
		compaction	318.791	9.4	0.009	0.253	-156.080	2
		size	321.043	11.652	0.003	0.212	-157.206	2
		Intercept only (null)	329.739	20.349	0	0	-162.716	1
		field capacity	330.769	21.379	0	0.006	-162.069	2

Table S4.8: Lignotuber species top generalised additive models (GAMs) for probability of survival, and generalised linear models (GLMs) for vigour with ΔAICc < 5 from full subsets analysis. Additive effects between variables is denoted by (+), (s) refers to smoothing of a predictor. Single predictor models, null models, AIC corrected for small sample size (AICc), difference from lowest reported AICc (ΔAICc), AICc model weights (ωAICc), variance explained (R^2) and estimated degrees of freedom (edf) are reported for model comparison. Size refers to pre-fire size, compaction measures were collected in November 2021.

Response	Species	Model	AICc	ΔAICc	ωAICc	R^2	Log-likelihood	edf
Survival	*S. involucrata*	s(size) + field capacity + compaction	304.727	0	0.431	0.045	-147.253	4.86
		s(size) + field capacity	306.436	1.71	0.183	0.033	-149.168	3.81
		field capacity	307.243	2.517	0.061	0.025	-151.596	2
		field capacity + compaction	307.304	2.578	0.119	0.030	-150.600	3
		s(size) + compaction	307.928	3.202	0.087	0.027	-149.892	3.88
		s(size)	309.899	5.172	0.032	0.014	-151.922	2.84
		compaction	311.782	7.056	0.013	0.005	-153.865	2
		Intercept only (null)	311.918	7.191	0.012	0	-154.950	1
	S. latifolia	s(size) + field capacity	101.509	0	0.827	0.110	-46.557	3.89
		field capacity	105.759	4.250	0.099	0.046	-50.818	2
		s(size)	108.760	7.251	0.022	0.038	-51.288	2.83
		Intercept only (null)	109.896	8.387	0.012	0	-53.928	1
		compaction	111.974	10.465	0.004	-0.010	-53.925	2
Vigour	*S. involucrata*	field capacity + size	632.220	0	0.963	0.332	-311.872	3
		size	638.724	6.504	0.037	0.272	-329.149	2
		compaction	658.567	26.347	0	0.090	-316.221	2
		field capacity	664.580	32.360	0	0.027	-330.853	2
		Intercept only (null)	665.846	33.626	0	0	-326.142	1
	S. latifolia	field capacity + size	742.133	0	1	0.707	-366.789	3
		field capacity	802.676	60.543	0	0.346	-398.174	2
		size	806.380	64.245	0	0.314	-400.025	2
		Intercept only (null)	834.266	92.133	0	0	-415.052	1
		compaction	836.023	93.891	0	-0.008	-414.874	2

Table S4.9: GAM summaries of the effect of smoothed (s) log-transformed plant size (cm^{-3}) on species probability of surviving the first summer. Bolding of values indicates significance at *P*<0.05. Top-ranked model (those in Table 4.3) is predicted for *L. floribunda, S. involucrata* & *S. latifolia*, other species are modelled against size only. A negative R^2 indicates the model is not explaining the variability of the dependent variable more effectively than a horizontal with an R^2 of 0, demonstrating poor model performance.

Resprouter type	Species	Predictor				
Root sucker	*D. linearis*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	-0.133	0.345	-0.384	0.701
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1.795	2.616	0.223	
		Adjusted R^2	0.080			
	G. pithyoides	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	-0.184	0.272	-0.675	0.5
		Smooth terms	*edf*	*Chi.sq*	*P*	

		s(log(size))	1.198	0.283	0.643	
		Adjusted R^2	-0.006			
	L. floribunda	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	-0.293	0.183	-1.601	0.109
		Compaction	**0.427**	**0.190**	**2.249**	**0.025**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	**1**	**6.006**	**0.014**	
		Adjusted R^2	**0.060**			
Rhizome	*C. aculeata*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**1.164**	**0.256**	**4.54**	**<0.001**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1	0.066	0.798	
		Adjusted R^2	-0.011			
	C. juncea	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	-1.599	0.928	-1.723	0.085
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1.711	1.28	0.52	
		Adjusted R^2	0.038			
Lignotuber	*S. involucrata*	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**-0.528**	**0.141**	**-3.709**	**<0.001**
		Field capacity	**-0.347**	**0.151**	**-2.295**	**0.022**
		Compaction	-0.255	0.137	-1.866	0.062
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	1.856	5.497	0.072	
		Adjusted R^2	0.045			
	S. latifolia	*Linear terms*	*Estimate*	*SE*	*z value*	*P*
		Intercept	**1.640**	**0.321**	**5.103**	**<0.001**
		Field capacity	**-0.724**	**0.258**	**-2.805**	**0.005**
		Smooth terms	*edf*	*Chi.sq*	*P*	
		s(log(size))	**1.892**	**7.852**	**0.026**	
		Adjusted R^2	0.110			

Table S4.10: GLM summaries of the top model driving resprouting vigour for all species. Bolding of values indicates significance at $P<0.05$.

Resprout type	Species	Predictor	*Estimate*	*SE*	*t value*	*P*
Root sucker	*D. linearis*	Intercept	1.302	0.900	1.447	0.161
		log(size)	**0.718**	**0.311**	**2.309**	**0.030**
	G. pithyoides	Intercept	6.683	3.720	1.796	0.086
		log(size)	**1.192**	**0.513**	**2.325**	**0.029**
	L. floribunda	Intercept	4.704	2.778	1.694	0.095
		log(size)	**1.160**	**0.393**	**2.948**	**0.005**
Rhizome	*C. aculeata*	**Intercept**	**-22.158**	**10.074**	**-2.200**	**0.032**
		log(size)	**4.263**	**1.001**	**4.258**	**<0.001**
		Compaction	**-4.244**	**1.998**	**-2.125**	**0.038**

	P. occidentalis	Intercept	5.877	7.576	0.776	0.443
		log(size)	**2.554**	**0.716**	**3.565**	**<0.001**
		Compaction	**-6.249**	**1.584**	**-3.945**	**<0.001**
Lignotuber	*S. involucrata*	**Intercept**	**-9.770**	**4.770**	**-2.048**	**0.044**
		log(size)	**2.960**	**0.463**	**6.387**	**<0.001**
		Field capacity	**-2.819**	**0.949**	**-2.971**	**0.004**
	S. latifolia	**Intercept**	**-132.244**	**22.052**	**-5.997**	**<0.001**
		log(size)	**18.949**	**1.963**	**9.655**	**<0.001**
		Field capacity	**-30.232**	**3.002**	**-10.072**	**<0.001**

Chapter 5 supporting information

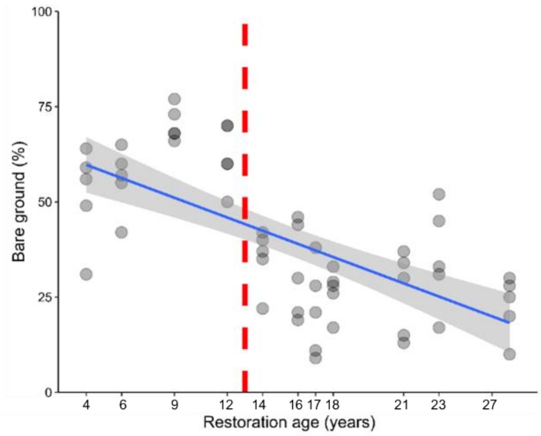

Figure S5.1: Pre-fire bare ground cover (%) against restoration age. Ages younger than the red line did not have fire attempted.

Table S5.1: Reference Banksia woodlands site information and distances from Hanson. Post-fire data was measured one year following fire, with time since previous fire recorded in the table. Age groups reflect groups pooled for analysis of resilience within ages.

Measurement type	Age (years)	Number of sites	Number of plots	Distance from Hanson (km)
Pre-fire	4	Two	15	1.3–4.5
	9-24	Six	42	3.2–8.5
	49	One	7	8.5
Post-fire	10	One	5	4.5
	22	One	7	6

Supplementary text S5.1: Data structure for responses to fire analyses

For regeneration responses (~5 months post-fire), we determined post-fire annual and perennial seedling densities by species, grouped by plot and restoration age. Annuals were separated by their origin (native vs invasive) as invasive species can influence restoration success, while native perennial seedlings were separated according to the smoke-responsive status of their seedbank (likely vs unlikely smoke-responsive; 73 and 27% of perennial species in restored sites respectively; Figure 5.1). This allowed us to quantify the unlikely smoke-responsive component of Banksia woodlands (dominated by heat-responsive and species with no seed dormancy) separately which was unable to be quantified in Chapter 3. Within perennial seedlings' smoke-responsive status, we further separated species based on their fire-response type (obligate seeder vs resprouter) as the development of these attributes may differ due to plant longevity and resource allocation (Enright et al., 2014; Pausas & Keeley 2014).

The resprouting response at ~5 months post-fire was calculated using the proportion of post-fire established resprouts (those that had resprouted by ~5 months post-fire) compared to pre-fire established plants that were capable of resprouting (resprouter fire-response type) and was grouped by species and clonality type. Separating species into clonal (49% of resprouting species) and non-clonal (51%) species allowed us to assess if drivers of resprouting differ as suggested by Chapter 4. Common resprouter organ types for clonal species included rhizomes and root suckers, while non-clonal species typically had epicormic buds or lignotubers (Clarke et al., 2013).

Table S5.2: Databases used for plant trait data.

Trait	Source
Fire response type (resprouter vs obligate seeder), growth category & seed storage mode	Veber et al., (2019; unpublished data)
Origin & longevity	Western Australian Herbarium (1998–)
Smoke-responsive status	Sweedman & Merritt (2006); Offord & Meagher (2009); Baskin & Baskin (2014); Stevens et al., (2016)
Clonal type (as per Clarke et al., 2013)	Wilson et al., (2010); Pausas et al., (2018); Veber et al., (2019; unpublished data)
Seed mass	Falster et al., (2021); Lewandrowski & Turner, unpublished data
Specific leaf area	Falster et al., (2021)
Microbial associations	Tsakalos et al., (2020)

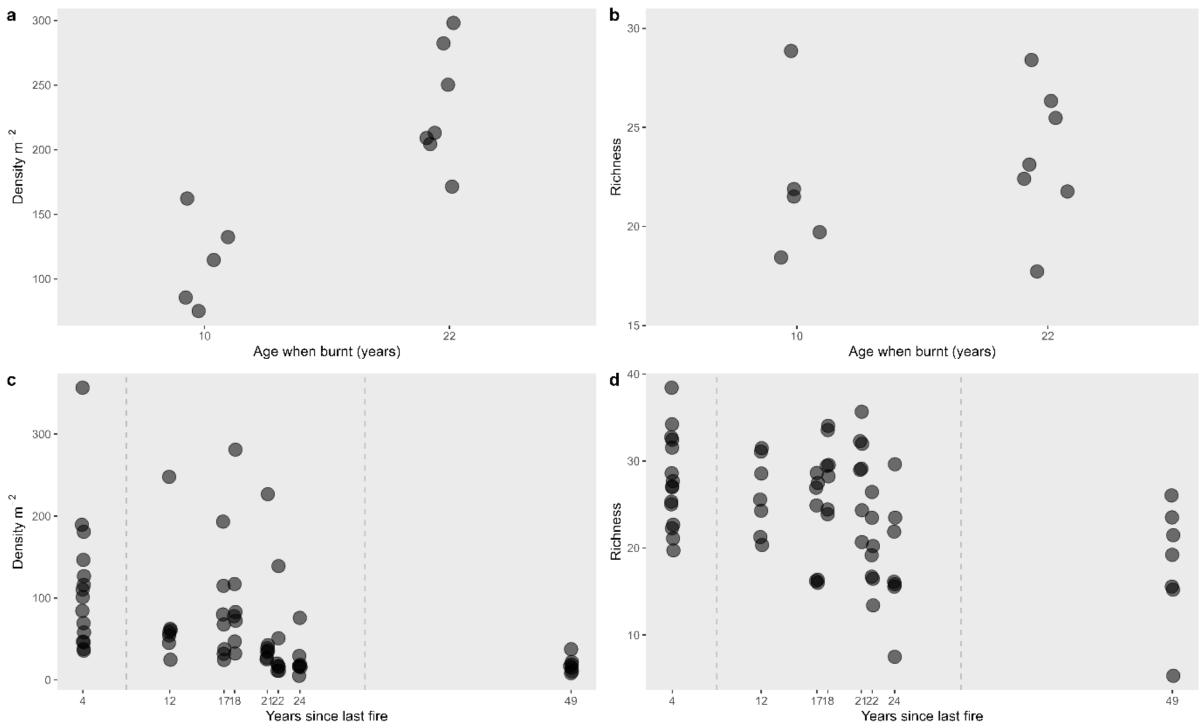

Figure S5.2: Post-fire (a.b) and pre-fire (c,d) reference sites densities and richness against years since last disturbance. The dotted lines on c & d indicate where different aged sites have been split for analysis.

Supplementary text 5.2: Modelling drivers of post-fire responses in restored Banksia woodlands

Using generalized linear mixed models (GLMMs), we sought to determine the effects of various drivers on post-fire regeneration (~5 months post-fire) and survival (~17 months post-fire) of perennial seedlings, annuals (~5 months only) and established resprouts (Figure 5.1). Regardless of smoke-responsive status, perennial seedlings were modelled together, and both clonal and non-clonal established resprouts were also modelled together as there was little difference between the trait types in data exploration and this helped to increase sample sizes.

For all models, restoration age was included as a continuous predictor. The following traits for responses to fire were modelled as fixed effects: fire response type (obligate seeder or resprouter) and smoke-responsive seedbank status (likely smoke responsive or unlikely) for perennial seedlings, origin for annuals (native vs invasive), and clonality for established resprouts (clonal or not; Figure 5.1). For models of post-fire regeneration (~5 months post-fire), perennial and annual seedling models also included the average percent fire coverage of each subplot burnt per plot as a continuous predictor as this was where the seedling response was assessed. For models of established resprouts, fire coverage of each subplot was substituted for fire severity per plot (continuous predictor) as this describes how many plants were burnt which is necessary for resprouting. Fire impact variables were not included in models of ~17 month (survival) responses as we expected soil conditions to be more important for survival than fire impact. Therefore, field capacity per plot was included as a continuous predictor in models for both perennial seedlings and established resprouts proportions of survival. Additionally, average soil compaction per plot at 10 cm was included as a continuous predictor in models for seedlings, and 30 cm compaction (continuous predictor) for resprouts, with the depth of compaction matching expected rooting depths. Interaction terms were added between restoration age and fire response type (perennial seedlings), clonality (established resprouts), and origin (annuals) to assess whether responses along the restoration age chronosequence varied for species in different classes of these variables. Interaction terms were also included between fire impact and plant traits described above to assess if the responses among trait groups varied with the amount of fire.

Models of perennial and annual seedling counts at ~5 months were constructed using a negative binomial distribution with a log-link due to overdispersion observed in the data (McCullagh & Nelder 1989). All proportion data (i.e., established resprouts at ~5 & 17 months, and perennial seedlings survival at ~17 months) were modelled using a beta distribution (Ospina & Ferrari 2010; Geissinger et al., 2022). All models included separate random effects of species and restoration age to account for potential unexplained differences among groups. Continuous predictors were standardized by subtracting the mean of each value and dividing by the standard deviation to reduce estimate biases (Zuur et al., 2009; Schielzeth 2010).

All models of post-fire responses were conducted in the R package *glmmTMB* (Brooks et al., 2017), with the *performance* (Lüdecke et al., 2021), *MuMIN* (Barton 2023) and *rcompanion* (Mangiafico 2023) packages used to assess collinearity of covariates, normality and heterogeneity of model residuals, and model performance. The presented models include all predictors as removing predictors from initial models did not result in a change to Akaike Information Criteria (AIC; Akaike 1973) scores (i.e., all models within 2 AIC; Burnham & Anderson 2004). To prevent overfitting, we removed predictors that had a variance inflation factor (VIF) of >5 (Alauddin & Nghiemb 2010). For count models using a negative binomial distribution, trigamma R^2 was reported due to its highly accurate estimates of the variance in models using a log-link function (Nakagawa et al., 2017), while Cox and Snell's (1989) pseudo-R^2 was estimated for proportional models using a beta distribution as per Geissinger et al., (2022). In some cases, random effect estimates were approximately 0 resulting in no difference between the conditional and marginal R^2 (Schielzeth et al., 2020). *P values* were adjusted using the 'Holm-Bonferroni' adjustment to account for multiple statistical tests (Holm 1973) with the adjusted *p values* reported using the 'p.adjust' function in the *stats* package (R Core Team 2020).

Table S5.3: Traits used in functional redundancy analysis and their reasoning. For categorical traits, the potential factors and number of species (pooled across restored and reference plant communities) are included. Traits with * were not included for calculation of obligate seeders and resprouters functional redundancy. Invasive perennials are not included as they were removed from analysis.

Trait (number of species missing trait value)	Reasoning	Factors	Number of species

Fire response*	Main post-fire response mechanism	Resprouter	89
		Obligate seeders (includes annuals)	88
Longevity*	Relates to growth and regeneration	Perennial	130
		Annual	47
Status*	Relates to growth, dispersal and restoration success	Native	158
		Invasive	19
Growth form	Ability to compete for light, ecosystem structure	Herb	64
		Shrub	56
		Tussock	24
		Grass	16
		Tree	6
		Succulent	6
		Geophyte	3
		Palmoid	2
Smoke-responsive status	Relates to dormancy responses	Likely	138
		Unlikely	39
Seed storage location	Relates to regeneration	Soil	160
		Canopy	15
		None	2
Microbial associations (5)	Nutrient acquisition and soil microbial composition	Arbuscular-Ectomycorrhizal	115
		Root microbial	43
		Ericoid	14
Seed mass (69)	Impact dispersal, persistence, establishment, survival	Numerical	
Specific leaf area (110)	Relates to photosynthesis, growth, water balance	Numerical	

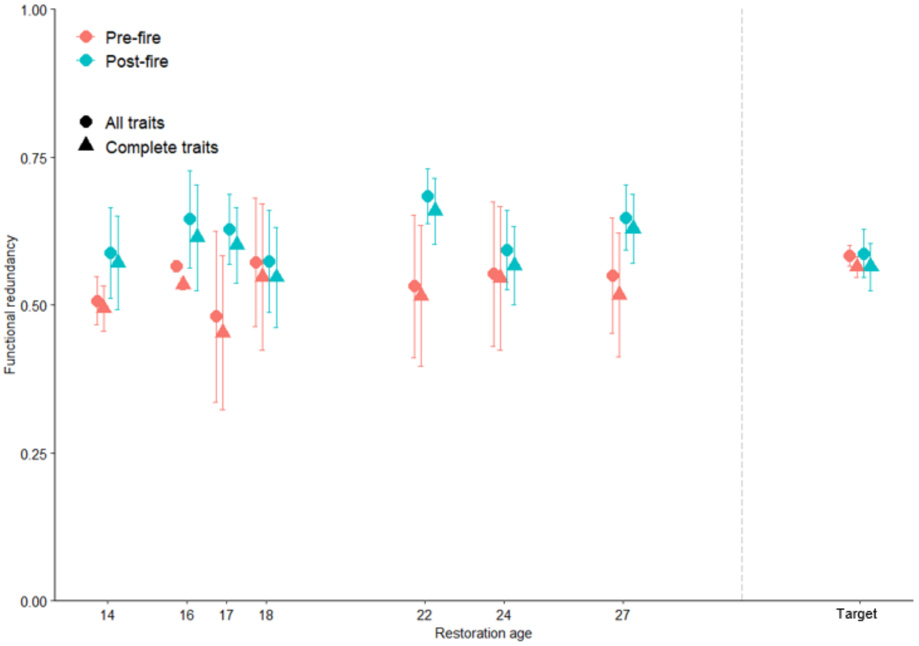

Figure S5.3: Mean and 95%CI of functional redundancy for each restoration age and measurement type (colours) for all traits and complete traits used in calculation. Reference data is to the left of the dashed grey arrow. Complete traits are those with >95% of species with a trait value (i.e., excludes SLA and seed mass).

Table S5.4: List of species found in each data type, and their trait types. For resprouters C=clonal, NC=non-clonal. * in life history type = unlikely smoke responsive.

			Restoration		Reference		
Species			Pre-fire	Post-fire	Pre-fire	Post-fire	Life history type
acachueg	*Acacia huegelii*	Fabaceae	✓		✓		Obligate seeder *
acacpulc	*Acacia pulchella*	Fabaceae	✓	✓	✓		Obligate seeder *
adencygn	*Adenanthos cygnorum*	Proteaceae	✓	✓	✓	✓	Obligate seeder
airacary	*Aira caryophyllea*	Poaceae	✓		✓	✓	Invasive annual
airacupa	*Aira cupaniana*	Poaceae			✓		Invasive annual
alexnite	*Alexgeorgia nitens*	Restionaceae	✓	✓	✓	✓	Resprouter (C)
allohumi	*Allocasuarina humilis*	Casuarinaceae	✓	✓	✓		Resprouter (NC) *
amphturb	*Amphipogon turbinatus*	Poaceae			✓	✓	Resprouter (C)
andehete	*Andersonia heterophylla*	Ericaceae			✓	✓	Obligate seeder
anighumi	*Anigozanthos humilis*	Haemodoraceae	✓	✓	✓		Resprouter (C)
anigmang	*Anigozanthos manglesii*	Haemodoraceae	✓	✓	✓		Obligate seeder

arnoprei	*Arnocrinum preissii*	Hemerocallidaceae	✓		✓	✓	Resprouter (C)
astrpall	*Astroloma pallidum*	Ericaceae			✓		Obligate seeder
astrxero	*Astroloma xerophyllum*	Ericaceae	✓	✓	✓	✓	Obligate seeder
austcomp	*Austrostipa compressa*	Poaceae	✓	✓	✓	✓	Native annual
austflav	*Austrostipa flavescens*	Poaceae	✓	✓			Resprouter (NC)
avenbarb	*Avena barbata*	Poaceae	✓	✓			Invasive annual
bankatte	*Banksia attenuata*	Proteaceae	✓	✓	✓	✓	Resprouter (NC) *
bankilic	*Banksia ilicifolia*	Proteaceae	✓		✓		Resprouter (NC) *
bankmenz	*Banksia menziesii*	Proteaceae	✓	✓	✓	✓	Resprouter (NC) *
beaueleg	*Beaufortia elegans*	Myrtaceae	✓	✓	✓	✓	Obligate seeder
boropurd	*Boronia purdieana*	Rutaceae			✓		Obligate seeder
bororamo	*Boronia ramosa*	Rutaceae	✓	✓	✓		Obligate seeder
bosserio	*Bossiaea eriocarpa*	Fabaceae	✓	✓	✓	✓	Obligate seeder *
brizmaxi	*Briza maxima*	Poaceae	✓	✓	✓	✓	Invasive annual *
burccong	*Burchardia congesta*	Colchicaceae	✓		✓	✓	Resprouter (C) *
calabrev	*Calandrinia brevipedata*	Portulacaceae			✓		Native annual
calacorr	*Calandrinia corrigioloides*	Portulacaceae		✓	✓		Native annual
calaflav	*Caladenia flava*	Orchidaceae			✓	✓	Resprouter (C) *
calagran	*Caladrinia granulifera*	Portulacaceae		✓	✓		Native annual
calalini	*Calandrinia liniflora*	Montiaceae			✓		Native annual
calyangu	*Calytrix angulata*	Myrtaceae	✓		✓		Resprouter (NC)
calyflav	*Calytrix flavescens*	Myrtaceae			✓	✓	Obligate seeder
calyfras	*Calytrix fraseri*	Myrtaceae	✓		✓	✓	Obligate seeder
calysapp	*Calytrix sapphirina*	Myrtaceae				✓	Obligate seeder
calystri	*Calytrix strigosa*	Myrtaceae			✓		Resprouter (NC)
cassytha	*Cassytha sp.*	Lauraceae	✓		✓	✓	Obligate seeder *
carpedul	*Carpobrotus edulis*	Aizoaceae	✓	✓	✓	✓	Invasive perennial
centdrum	*Centrolepis drummondiana*	Centrolepidaceae			✓		Native annual
centglab	*Centrolepis glabra*	Centrolepidaceae		✓	✓	✓	Native annual
conoacul	*Conostylis aculeata*	Haemodoraceae	✓	✓	✓	✓	Resprouter (C)

conoaure	*Conostylis aurea*	Haemodoraceae			✓		Resprouter (C)
conocant	*Conostylis canteriata*	Haemodoraceae			✓		Resprouter (C)
conojunc	*Conostylis juncea*	Haemodoraceae	✓		✓	✓	Resprouter (C)
conopend	*Conostephium pendulum*	Ericaceae			✓		Resprouter (NC)
conoprei	*Conostephium preisii*	Ericaceae			✓		Resprouter (NC)
conoseti	*Conostylis setigera*	Haemodoraceae			✓		Obligate seeder
conostoe	*Conospermum stoechadis*	Proteaceae	✓	✓	✓		Resprouter (NC)
conybona	*Conyza bonariensis*	Asteraceae		✓			Invasive annual
corymicr	*Corynotheca micrantha*	Antheriaceae			✓		Resprouter (C)
crascolo	*Crassula colorata*	Crassulaceae	✓	✓	✓	✓	Native annual
crasexse	*Crassula exserta*	Crassulaceae			✓	✓	Native annual
cronking	*Croninia kingiana*	Ericaceae	✓		✓		Obligate seeder
dampline	*Dampiera linearis*	Goodeniaceae	✓	✓	✓	✓	Resprouter (C)
dasybrom	*Dasypogon bromeliifolius*	Dasypogonaceae	✓	✓	✓	✓	Resprouter (C)
davitrif	*Daviesia triflora*	Fabaceae	✓	✓	✓		Resprouter (NC) *
desmflex	*Desmocladus flexuosus*	Restionaceae	✓	✓	✓	✓	Resprouter (C)
ehrhcaly	*Ehrharta calycina*	Poaceae	✓	✓	✓		Invasive perennial
ehrhlong	*Ehrharta longiflora*	Poaceae	✓	✓			Invasive annual
eremfimb	*Eremaea fimbriata*	Myrtaceae			✓		Resprouter (NC) *
erempauc	*Eremaea pauciflora*	Myrtaceae	✓	✓	✓	✓	Resprouter (NC) *
eucatodt	*Eucalyptus todtiana*	Myrtaceae	✓			✓	Resprouter (NC) *
gastcapi	*Gastrolobium capitatum*	Fabaceae	✓		✓		Resprouter (NC) *
gladcary	*Gladiolus caryophyllaceus*	Iridaceae	✓	✓	✓	✓	Invasive perennial
gomptome	*Gompholobium tomentosum*	Fabaceae	✓	✓	✓	✓	Obligate seeder *
gonopith	*Gonocarpus pithyoides*	Haloragaceae	✓	✓	✓	✓	Resprouter (C)
haemlaxu	*Haemodorum laxum*	Haemodoraceae			✓		Resprouter (C) *
haemsimp	*Haemodorum simplex*	Haemodoraceae			✓		Resprouter (C) *
haemspic	*Haemodorum spicatum*	Haemodoraceae			✓		Resprouter (C) *
helipusi	*Heliophila pusilla*	Brassicaceae			✓		Invasive annual
hensturb	*Hensmania turbinata*	Hemerocallidaceae	✓				Resprouter (C)

hibbaure	*Hibbertia aurea*	Dilleniaceae	✓	✓	✓		Resprouter (NC)
hibbhueg	*Hibbertia huegelii*	Dilleniaceae			✓		Resprouter (NC)
hibbhype	*Hibbertia hypericoides*	Dilleniaceae	✓	✓	✓	✓	Resprouter (NC)
hibbsubv	*Hibbertia subvaginata*	Dilleniaceae	✓	✓	✓	✓	Obligate seeder
homahoma	*Homalosciadium homalocarpum*	Apiaceae		✓	✓	✓	Native annual
hovepung	*Hovea pungens*	Fabaceae	✓		✓		Obligate seeder *
hyalcotu	*Hyalosperma cotula*	Asteraceae	✓	✓	✓		Native annual
hypoangu	*Hypocalymma angustifolium*	Myrtaceae	✓	✓	✓		Resprouter (NC)
hypoglab	*Hypochaeris glabra*	Asteraceae	✓	✓	✓	✓	Invasive annual
hypolrobus	*Hypolaena robusta*	Restionaceae			✓		Resprouter (NC)
hyporobu	*Hypocalymma robustum*	Myrtaceae			✓		Obligate seeder
isolmarg	*Isolepis marginata*	Cyperaceae		✓	✓	✓	Native annual
isotcune	*Isotropis cuneifolia*	Fabaceae			✓	✓	Resprouter (C) *
jackflor	*Jacksonia floribunda*	Fabaceae	✓	✓	✓	✓	Resprouter (NC) *
jackfurc	*Jacksonia furcellata*	Fabaceae	✓	✓	✓	✓	Resprouter (NC) *
kunzglab	*Kunzea glabrescens*	Myrtaceae	✓	✓	✓		Obligate seeder *
lagehueg	*Lagenphora huegelii*	Asteraceae			✓		Native annual
laxmramo	*Laxmannia ramosa*	Asparagaceae		✓	✓	✓	Obligate seeder
laxmsqua	*Laxmannia squarrosa*	Asparagaceae	✓	✓	✓		Obligate seeder
lechflor	*Lechenaultia floribunda*	Goodeniaceae	✓	✓	✓	✓	Resprouter (C)
lepidosperma	*Lepidosperma sp.*	Cyperaceae	✓				Resprouter (C)
lepisqua	*Lepidosperma squamatum*	Cyperaceae			✓		Resprouter (C)
leptempe	*Leptomeria empetriformis*	Santalaceae			✓		Obligate seeder
leuccono	*Leucopogon conostephioides*	Ericaceae	✓		✓	✓	Obligate seeder
leucgrac	*Leucopogon gracillimus*	Ericaceae			✓		Obligate seeder
leucinsu	*Leucopogon insularis*	Ericaceae			✓		Obligate seeder
leucpoly	*Leucopogon polymorphus*	Ericaceae	✓	✓	✓	✓	Resprouter (NC)
leucprop	*Leucopogon propinquus*	Ericaceae	✓		✓		Resprouter (NC)
leucrace	*Leucopogon racemulosus*	Ericaceae			✓		Obligate seeder
levestip	*Levenhookia stipitata*	Stylidiaceae	✓	✓	✓		Native annual

lobetenu	*Lobelia tenuior*	Campanulaceae		✓		✓	Native annual
lomacaes	*Lomandra caespitosa*	Asparagaceae	✓		✓	✓	Resprouter (C)
lomaherm	*Lomandra hermaphrodita*	Asparagaceae			✓	✓	Resprouter (C)
lomamicr	*Lomandra micrantha*	Asparagaceae			✓		Resprouter (C)
lomaprei	*Lomandra preissii*	Asparagaceae			✓		Resprouter (C)
lomasuav	*Lomandra suaveolens*	Asparagaceae			✓	✓	Resprouter (C)
lygibarb	*Lyginia imberbis*	Anarthriaceae	✓	✓	✓	✓	Resprouter (C)
lygiimbe	*Lysimachia arvensis*	Primulaceae			✓	✓	Resprouter (C)
lysicili	*Lysinema ciliatum*	Ericaceae	✓				Obligate seeder
macaaust	*Macarthuria australis*	Molluginaceae			✓		Resprouter (C)
macrfras	*Macrozamia fraseri*	Zamiaceae			✓		Resprouter (NC) *
melaseri	*Melaleuca seriata*	Myrtaceae	✓	✓			Resprouter (NC) *
melasyst	*Melaleuca systena*	Myrtaceae			✓		Resprouter (NC) *
melatric	*Melaleuca trichophylla*	Myrtaceae	✓	✓	✓	✓	Resprouter (NC) *
mesopseu	*Mesomelaena pseudostygia*	Cyperaceae	✓				Resprouter (C)
micrstip	*Microlaena stipoides*	Poaceae			✓		Obligate seeder
milltenu	*Millotia tenuifolia*	Asteraceae		✓	✓		Native annual
neuralop	*Neurachne alopecuroidea*	Poaceae			✓		Resprouter (C)
nuytflor	*Nuytsia floribunda*	Loranthaceae			✓		Resprouter (C) *
opervagi	*Opercularia vaginata*	Rubiaceae	✓		✓		Resprouter (C)
pateocci	*Patersonia occidentalis*	Iridaceae	✓	✓	✓		Resprouter (C)
pelacapi	*Pelargonium capitatum*	Geraniaceae	✓	✓			
pentairo	*Pentameris airoides*	Poaceae		✓		✓	Invasive annual *
perssacc	*Persoonia saccata*	Proteaceae			✓		Resprouter (NC)
petrdubi	*Petrorhagia dubia*	Caryophyllaceae	✓				Invasive annual *
petrline	*Petrophile linearis*	Proteaceae	✓	✓	✓	✓	Resprouter (NC)
philspic	*Philotheca spicata*	Rutaceae	✓		✓	✓	Resprouter (NC)
phlecili	*Phlebocarya ciliata*	Haemodoraceae			✓		Resprouter (C)
phylpara	*Phyllangium paradoxum*	Loganiaceae	✓	✓	✓	✓	Native annual
podoangu	*Podotheca angustifolia*	Asteraceae		✓	✓		Native annual

podochry	*Podotheca chrysantha*	Asteraceae			✓		Native annual
podognap	*Podotheca gnaphalioides*	Asteraceae	✓	✓	✓		Native annual
poramicr	*Poranthera microphylla*	Phyllanthaceae			✓	✓	Native annual
quinurvi	*Quinetia urvillei*	Asteraceae	✓	✓			Native annual
regeinop	*Regelia inops*	Myrtaceae			✓	✓	Resprouter (NC)
rhodchlo	*Rhodanthe chlorocephala*	Asteraceae		✓	✓		Native annual
rhodcitr	*Rhodanthe citrina*	Asteraceae			✓		Native annual
romeacet	*Acetosella vulgaris*	Polygonaceae				✓	Invasive perennial
romurose	*Romulea rosea*	Iridaceae	✓	✓	✓		Invasive perennial
rytiocci	*Rytidosperma occidentale*	Poaceae			✓		Obligate seeder
scaerepe	*Scaevola repens*	Goodeniaceae	✓	✓			Resprouter (NC)
schocurv	*Schoenus curvifolius*	Cyperaceae	✓	✓	✓	✓	Resprouter (C)
schoinvo	*Scholtzia involucrata*	Myrtaceae	✓	✓	✓	✓	Resprouter (NC)
scholaxi	*Scholtzia laxiflora*	Myrtaceae			✓	✓	Resprouter (NC)
schopedi	*Schoenus pedicellatus*	Cyperaceae			✓		Resprouter (C)
soncaspe	*Sonchus asper*	Asteraceae		✓			Invasive annual
soncoler	*Sonchus oleraceus*	Asteraceae	✓	✓	✓	✓	Invasive annual
sowelaxi	*Sowerbaea laxiflora*	Asparagaceae			✓	✓	Resprouter (C)
stacmono	*Stackhousia monogyna*	Celastraceae			✓		Obligate seeder
stirlati	*Stirlingia latifolia*	Proteaceae	✓	✓	✓	✓	Resprouter (NC)
styladpr	*Stylidium adpressum*	Stylidiaceae			✓		Resprouter (C)
stylbrun	*Stylidium brunonianum*	Stylidiaceae	✓	✓	✓	✓	Resprouter (C)
stylcros	*Stylidium crossocephalum*	Stylidiaceae	✓			✓	Obligate seeder
styldiur	*Stylidium diuroides*	Stylidiaceae	✓	✓	✓	✓	Obligate seeder
stylneur	*Stylidium neurophyllum*	Stylidiaceae	✓		✓		Resprouter (C)
stylpili	*Stylidium piliferum*	Stylidiaceae	✓	✓	✓	✓	Obligate seeder
stylrepe	*Stylidium repens*	Stylidiaceae	✓	✓	✓	✓	Obligate seeder
stylrigi	*Stylidium rigidulum*	Stylidiaceae	✓	✓	✓	✓	Obligate seeder
thysarbu	*Thysanotus arbuscula*	Asparagaceae	✓		✓		Resprouter (C)
thysaren	*Thysanotus arenarius*	Asparagaceae	✓				Resprouter (C)

thysmang	*Thysanotus manglesianus*	Asparagaceae		✓	✓		Resprouter (C)
thyspate	*Thysanotus patersonii*	Asparagaceae				✓	Obligate seeder
thysspar	*Thysanotus sparteus*	Asparagaceae			✓		Resprouter (C)
thysthyr	*Thysanotus thyrsoideus*	Asparagaceae			✓		Resprouter (C)
tracpilo	*Trachymene pilosa*	Araliaceae	✓	✓	✓	✓	Native annual
tricelat	*Tricoryne elatior*	Hemerocallidaceae			✓	✓	Resprouter (C)
trictene	*Tricoryne tenella*	Hemerocallidaceae			✓		Resprouter (C)
urospicr	*Urospermum picroides*	Asteraceae		✓			Invasive annual
ursianth	*Ursinia anthemoides*	Asteraceae	✓	✓	✓	✓	Invasive annual *
vertnite	*Verticordia nitens*	Myrtaceae	✓	✓	✓	✓	Obligate seeder
vulpmura	*Vulpia muralis*	Poaceae			✓		Invasive annual *
vulpmyur	*Vulpia myuros*	Poaceae	✓	✓	✓		Invasive annual *
wahlcape	*Wahlenbergia capensis*	Campanulaceae	✓	✓	✓	✓	Invasive annual
wahlgrac	*Wahlenbergia gracilenta*	Campanulaceae			✓		Native annual
wahlprei	*Wahlenbergia preissii*	Campanulaceae	✓	✓	✓	✓	Native annual
waitsuav	*Waitzia suaveolens*	Asteraceae		✓	✓		Native annual
xanthueg	*Xanthosia huegelii*	Apiaceae	✓	✓	✓	✓	Obligate seeder
xantprei	*Xanthorrhoea preissii*	Xanthorrhoeaceae			✓		Resprouter (NC) *

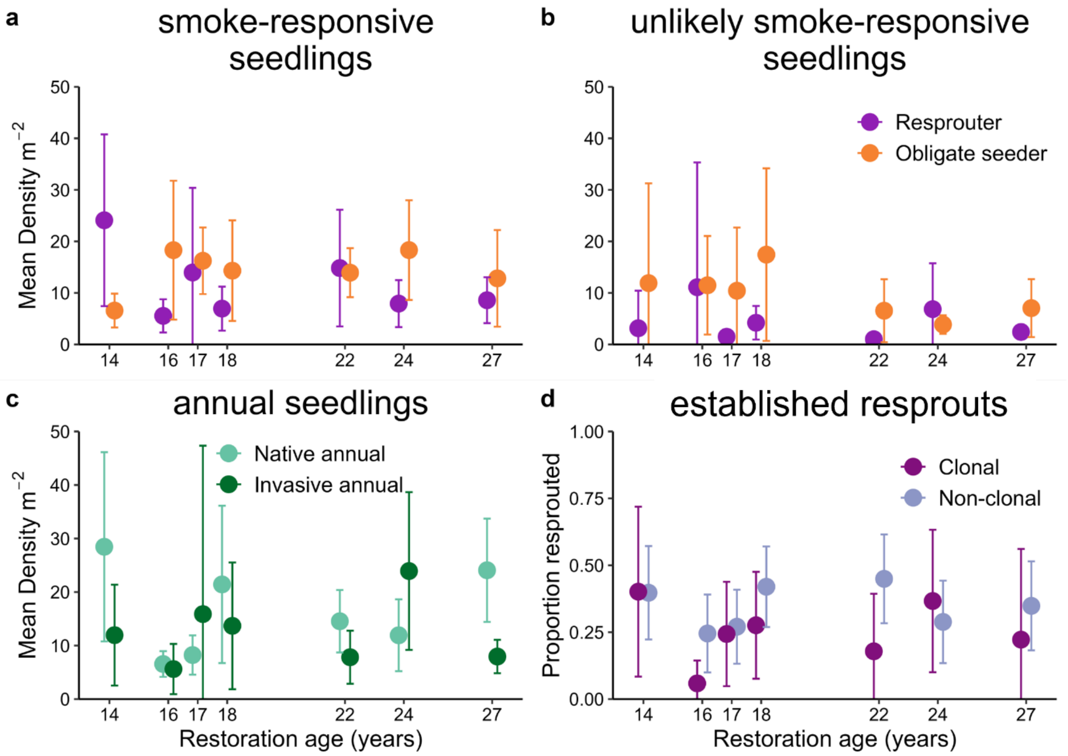

Figure S5.4: Five-month post-fire mean±95% CI of perennial a) smoke-responsive, b) unlikely smoke-responsive seedlings, c) annual seedling density (m^2), and d) proportion of pre-fire individuals that had resprouted across the 13-year restoration chronosequence. Y axes differ, colours in b reflect those in a. n = 2–8 0.7×0.7 m plots per point for a,b & c, n = 9–25 species point for d.

Table S5.5: Effects of potential drivers on seedling and resprouting responses at five months following fire. Bolding of text indicates a significant *P* value at = <0.05 level, × denotes an interaction, τ00 refers to individual random intercept variance explained.

Response	*Predictor*	*Estimate*	*SE*	*Z value*	*P*
Perennial seedlings	**Intercept**	**1.377**	**0.282**	**4.884**	**<0.001**
	Restoration age	-0.098	0.096	-1.028	0.950
	Fire response [obligate seeder]	0.163	0.278	0.586	0.950
	Smoke response [yes]	0.372	0.310	1.200	0.950
	Fire coverage	0.138	0.115	1.195	0.950
	Age × fire response [obligate seeder]	0.283	0.113	2.508	0.088
	Smoke response [yes] × fire coverage	-0.225	0.126	-1.788	0.380
	Random effects				
	$\tau00_{\text{age}}$	<0.001			
	$\tau00_{\text{species}}$	0.770			
	Marginal R^2 / Conditional R^2	0.025 / 0.319			

Annual seedlings	**Intercept**	**2.249**	**0.233**	**9.662**	**<0.001**
	Restoration age	0.149	0.153	0.951	0.951
	Status [invasive]	-0.303	0.331	-0.915	0.951
	Fire coverage	0.047	0.115	0.409	0.951
	Status[invasive] × age	0.243	0.195	1.247	0.097
	Status[invasive] × fire coverage	-0.386	0.187	-2.058	0.323
	Random effects				
	$\tau_{00\ \mathrm{age}}$	0.071			
	$\tau_{00\ \mathrm{species}}$	0.486			
	Marginal R^2 / Conditional R^2	0.021 / 0.217			
Established resprouts	Intercept	-0.097	0.167	-0.581	0.999
	Restoration age	-0.055	0.118	-0.470	0.999
	Fire severity	0.103	0.122	0.848	0.999
	Clonal [yes]	-0.515	0.259	-1.987	0.282
	Age × clonal [yes]	0.077	0.207	0.372	0.999
	Fire severity × clonal [yes]	-0.023	0.190	-0.122	0.999
	Random effects				
	$\tau_{00\ \mathrm{age}}$	<0.001			
	$\tau_{00\ \mathrm{species}}$	0.278			
	Marginal R^2 / Conditional R^2	0.024 / 0.072			

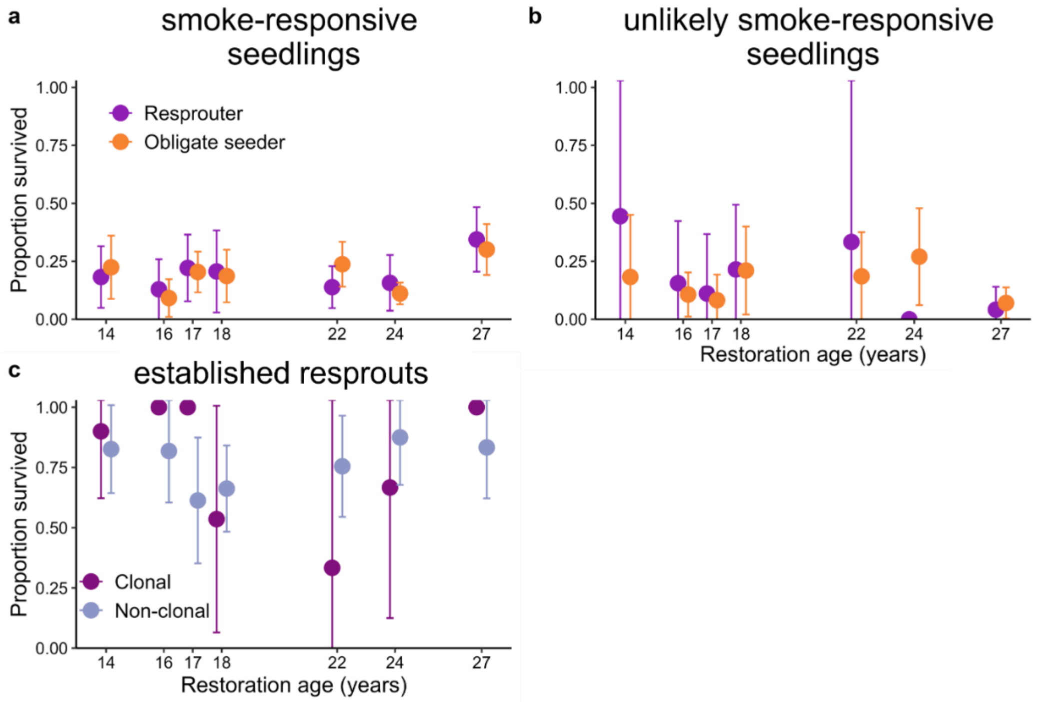

Figure S5.5: ~17-month mean±95% CI of post-fire survival proportions of perennial a) smoke-responsive, b) unlikely smoke-responsive perennial seedlings and c) established resprouts across the 13-year restoration chronosequence. n = 3–42 species per point for a and b, d = 2–19 species per point.

Table S5.6: Effects of potential drivers of survival of perennial seedings and established resprouts. Bolding of text indicates a significant *P* value at = <0.05 level, × denotes an interaction, τ00 refers to individual random intercept variance explained.

Response	*Predictor*	*Estimate*	*SE*	*Z value*	*P*
Perennial seedlings	**Intercept**	**-1.231**	**0.151**	**-8.163**	**<0.001**
	Restoration age	-0.004	0.097	-0.038	0.999
	Fire response [obligate seeder]	0.103	0.127	0.809	0.999
	Smoke response [yes]	0.172	0.142	1.213	0.999
	Compaction (10 cm)	0.083	0.063	1.305	0.999
	Field capacity	0.003	0.059	0.052	0.999
	Age × fire response [obligate seeder]	0.072	0.114	0.635	0.999
	Random effects				
	$\tau_{00\ \mathrm{age}}$	<0.001			
	$\tau_{00\ \mathrm{species}}$	0.029			
	Marginal R^2 / Conditional R^2	0.012 / 0.015			
Established resprouts	**Intercept**	**0.690**	**0.146**	**4.734**	**<0.001**
	Restoration age	0.034	0.149	0.22	0.999
	Clonal [yes]	-0.002	0.277	-0.008	0.999
	Compaction (30 cm)	0.089	0.135	0.657	0.999
	Field capacity	-0.037	0.135	-0.275	0.999
	Age × Clonal [yes]	-0.228	0.280	-0.814	0.999
	Random effects				
	$\tau_{00\ \mathrm{age}}$	<0.001			
	$\tau_{00\ \mathrm{species}}$	<0.001			
	Marginal R^2 / Conditional R^2	0.012 / 0.012			

Table S5.7: Indicator species per age and treatment type. Species with ʺ are those found in either the restored or reference sites, but not both.

Treatment	Age	Trait type	Species
Pre-fire restoration	16	Resprouter	*Gastrolobium capitatum*
	17	Resprouter	*Melaleuca seriata ʺ*
	17	Resprouter	*Lepidosperma sp ʺ*
	24	Resprouter	*Allocasuarina humilis*
	24	Invasive annual	*Aira caryophyllea*
	27	Resprouter	*Hensmania turbinata ʺ*
	27	Resprouter	*Opercularia vaginata*
	27	Invasive annual	*Petrorhagia dubia*
Post-fire restoration	14	Resprouter	*Scholtzia involucrata*
	17	Invasive annual	*Avena barbata*
	18	Resprouter	*Hypocalymma angustifolium*
	18	Native annual	*Centrolepis glabra*
	22	Obligate seeder	*Verticordia nitens*

	22	Native annual	*Levenhookia stipitata*
	22	Native annual	*Phyllagium paradoxum*
	24	Invasive annual	*Pentameris airoides*
	27	Resprouter	*Gonocarpus pithyoides*
	27	Native annual	*Waitzia suaveolens*
	27	Native annual	*Wahlenbergia preissii*
	27	Native annual	*Isolepis marginata*
	27	Native annual	*Austrostipa compressa*
	27	Native annual	*Trachymene pilosa*
	27	Invasive annual	*Hypochaeris glabra*
	27	Invasive annual	*Brixa maxima*
	27	Invasive annual	*Sonchus oleraceus*
Pre-fire reference	4	Resprouter	*Scholtzia laxiflora ″*
	49	Resprouter	*Alexgeorgea nitens*
	49	Resprouter	*Leucopogon propinquus ″*
Post-fire reference	10	Resprouter	*Lomandra suaveolens*
	10	Resprouter	*Banksia menziesii*
	10	Resprouter	*Lyginia barbata*
	22	Resprouter	*Melaleuca trichophylla*
	22	Resprouter	*Lyginia imberbis*
	22	Resprouter	*Eremaea pauciflora*
	22	Resprouter	*Burchardia congesta*
	22	Obligate seeder	*Leucopogon conostephioides*
	22	Obligate seeder	*Stylidium rigidulum*
	22	Obligate seeder	*Calytrix flavescens*
	22	Obligate seeder	*Hibbertia subvaginata*
	22	Obligate seeder	*Stylidium repens*
	22	Obligate seeder	*Laxmannia ramosa*
	22	Obligate seeder	*Xanthosia huegelii*
	22	Obligate seeder	*Thysanotus patersonii″*
	22	Obligate seeder	*Stylidium diuroides*

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Chapter 6 supporting information

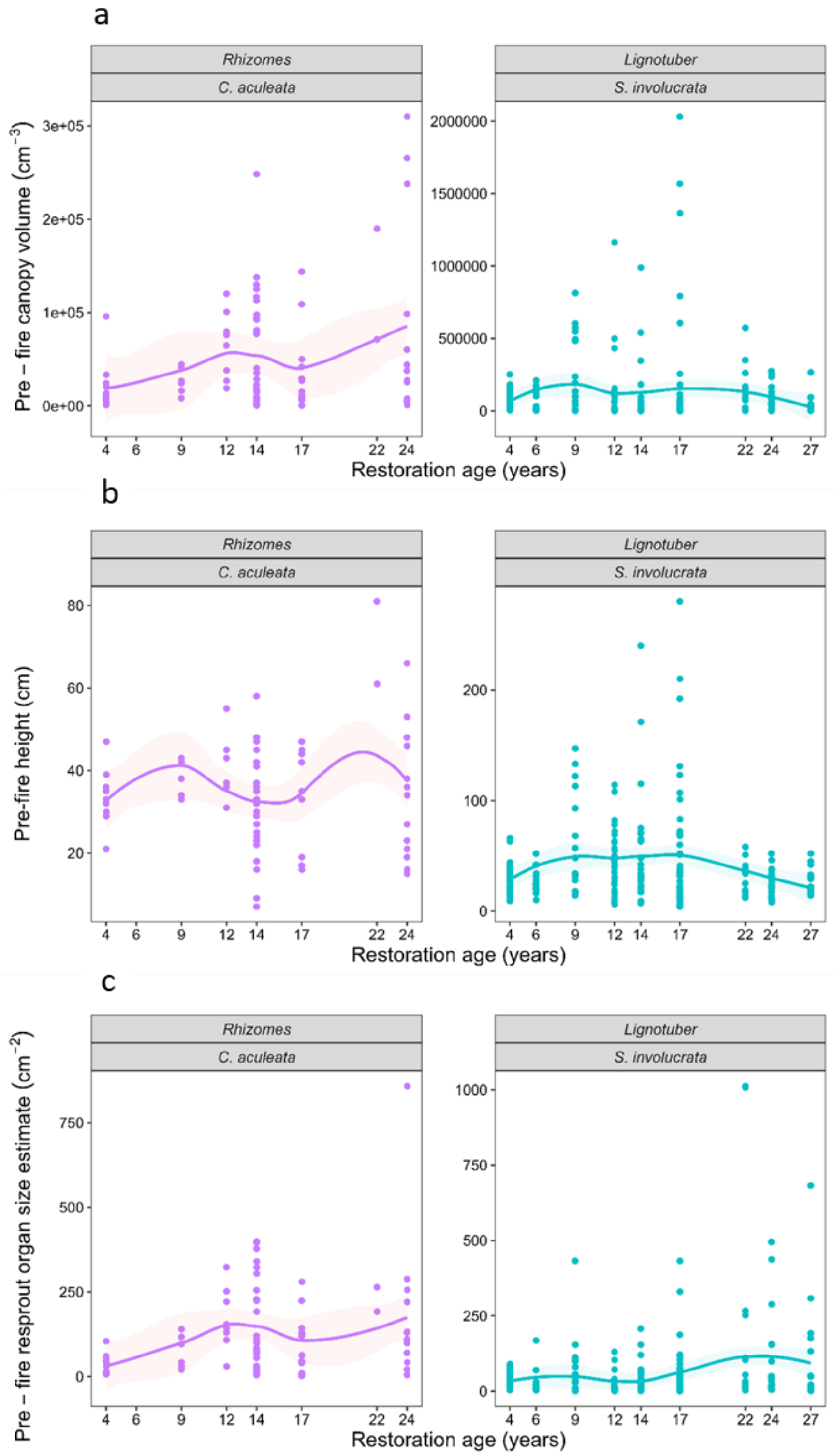

Figure S6.1: Species relationships between restoration age and pre-fire a) canopy volume, b) height and c) resprouting organ size. Data has 95% CI and is fitted with a loess smoother. Species are those surveyed in >75% of restoration ages with age 12 having >8 individuals.