Orchid losers and winners after fire in West Australian urban bushland: A response continuum deeply integrated with other traits

Mark C. Brundrett
Biological Sciences, the University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Western Australia
Email: mark.brundrett@uwa.edu.au

Abstract (398 words)

Context: The Southwest Australia Floristic Region (SWAFR) is a global hotspot for plant taxonomic and functional diversity. This region has many orchids with highly specialised associations with pollinators and mycorrhizal fungi that also face increasing threats from habitat loss, grazing, weeds, fire and climate change.

Aims: To identify short and long-term fire outcomes for 17 orchids with diverse ecological strategies in an isolated urban banksia and eucalypt woodland, and to develop fire response monitoring methods and criteria for management of species.

Methods: A 72-year fire record was overlain on 982 orchid locations with 7-11 years of baseline data and 4.5 km of transects to determine fire history effects on orchid abundance and diversity. Key traits such as plant size, flowering, pollination, tuber depth, clonality and population dynamics were also measured.

Key results: Fire history was very complex with 58 large overlapping major fires over 5 decades, averaging 8.7% of the 63-ha area annually. Correlating fire history with orchid occurrences revealed species usually lost to fire (5 spp.), or with substantial fire impacts (6). Others benefited from fire (6), including strongly enhanced flowering (3), but even the latter could be killed by unseasonal autumn fires. Pollination varied from moderate decreases to substantial increases post-fire, including three orchids producing seed primarily post-fire. Overall, impacts of fire greatly out way benefits, as most orchids preferred long-unburnt areas, and five species were confined to them. Paradoxically, *Pyrorchis nigricans* requires fire to flower, but was most productive in long-unburnt areas and primarily reproduced clonally.

Conclusions: Fire history maps revealed a spectrum of outcomes from catastrophic to beneficial for orchid species summarised by fire response indexes (FRI) and fire age safe thresholds (FAST) lasting decades. This response continuum was highly correlated with trait such as tuber depth, seed vs clonal reproduction, dispersion and lifespan. Fire was deeply integrated into the biology and ecology of SWAFR orchids which are adapted for long fire intervals which maximise their diversity and abundance.

Implications: Research in an urban nature reserve provided essential tools for sustainable management of orchids that are also relevant to rare species. These tools include fire history maps, FRI and FAST. Many SWAFR orchids were most productive in long unburnt areas or intolerant to fire, and even fire tolerant orchids can be harmed by autumn fires. Thus, fire must be carefully managed in their habitats, which are most productive two or more decades after fire.

Key words: fire ecology, orchids, pollination, fire history, urban landscapes, sustainable management, Southwest Australian Floristic Region, fire age safe threshold, fire response index

Introduction

The Southwest Floristic Region of Western Australia (SWAFR) is a global diversity hotspot with exceptional plant species richness and endemism (Myers et al. 2000, Hopper & Gioia 2004). Plant diversity in this region is linked to long-term climate stability, complex landscapes and extremely infertile soils (Lambers et al. 2011, Groom & Lamont 2015). Plants in this region have evolved exceptionally complex traits, especially for fire, pollination, and nutrition, with 90% having one or more fire survival adaptations (Brundrett 2021). This makes the region a living laboratory for studying fire trait evolution and its ecological consequences. Despite their scarcity in the arid interior, the SWAFR has an exceptional diversity of terrestrial orchids (450 taxa, https://florabase.dbca.wa.gov.au). Orchids in this region face substantial threats such as fire, weeds, grazing, excessive visitors to fragile habitats, and increasing impacts of drying and warming climate (Duncan et al. 2005, Brundrett 2014, Martín-Forés et al. 2022, Doherty et al. 2024). They also lack long-term persistent seed banks, which are key fire recovery factor in many SWAFR plants (70% of the flora - Brundrett 2021). Biological factors that influence orchid population sustainability include very specific pollinators attracted by to visual (44%) or sexual (38%) deception (Brundrett et al. 2024) and extreme nutritional dependencies on mycorrhizal fungi, since they have very few roots or lack them entirely (Ramsay et al. 1986). However, orchid biology also provides advantages such as wind dispersed seeds and there is a continuum from weedy to very rare species in the SWAFR (Table 1).

Habitats where orchids grow in south Australia are experiencing increasing fire frequency, severity, and substantial reduction in unburnt areas (Bradshaw et al. 2018, Doherty et al. 2024). They also face growing risks from drought, diseases and exotic animals (Hobbs & Atkins 1990, Groom & Lamont 2015, Wraith & Pickering 2019, Brundrett 2021, Gallagher et al. 2022). Existing information about fire and orchids in Australia includes examples of strongly negative to positive associations with fire depending on the orchid species and fire intensity. Adams (2018) found substantially reduced orchid abundance and diversity (14 out 33 original species) of orchids after fuel reduction fires in Victoria with only partial recovery of diversity after 10 years. Reiter and Pollard 2013 found *Caleana disjuncta* was severely impacted by a bushfire. Jasinge et al. (2018) reported that spring or summer fires were less damaging than autumn to winter fires for a *Pterostylis* species. Increased abundance or flowering of orchids after fires an also occur. Duncan (2012) summarised the impacts of catastrophic 2009 fires in Victoria on orchids. These belong to four main categories (a) fire killed species that were epiphytes or had shallow tubers, (b) fire sensitive species with substantial reductions in populations post-fire, (c) fire neutral species, (d) species where fire stimulated flowering and (e) fire dependant species that only flowered after fire. Cargill (2005) found the abundance of most orchids substantially increased with time since fire in WA forests. Australian terrestrial orchids include species that are pioneer, or secondary colonisers of fully disturbed habitats, or only occur in undisturbed habitats (Collins & Brundrett 2015). Some orchids benefit from intermediate levels of disturbance but are intolerant of substantial weed cover (Martín-Forés et al. 2022).

Fire regulates reproduction of SWAFR orchids, with 10 orchids that flower exclusively post-fire, 263 with flowering strongly promoted by fire, but 166 out of 450 taxa were considered fire sensitive (Brundrett 2021, Brundrett et al. 2024). Coates and Duncan (2009) reported reductions in the proportion of flowering plants of *Caledonia orientalis* with time since fire due to increased shrub competition, but rainfall was also an important determinant of flowering effort. However, Brown and York (2016) found the effect of fire on orchid pollination was less important than other factors. Fires potentially also have impacts on specific pollinating insects and mycorrhizal fungi required by orchids, but Marquart (2018) found limited consequences for orchid pollinators in eucalypt woodlands of South Australia, while Phillips et al. (2024) found specific wasp pollinators of mycorrhizal fungi of *Caladenia tessellata* were still present after summer bushfires in southeast Australia. There is currently insufficient data to fully understand impacts or benefits of fire on Australia orchids and how they vary with habitat types and orchid species.

This study occurred in an isolated urban remnant of banksia woodland, threatened plant communities, where it is especially important to monitor threats to biodiversity (Government of Western Australia 2000, Commonwealth of Australia 2016, Ritchie et al. 2021, Fowler et al. 2023). Banksia woodlands in the Swan Coastal Plain bioregion also have an exceptional diversity of indigenous terrestrial orchids, including 149 recorded species (Brundrett & George in prep.). The principal objective of this study was to investigate Indirect and direct impacts of altered fire frequency and severity on orchids in an isolated urban banksia woodland habitat on the Swan Coastal Plain within the Perth Metropolitan Region. Specific objectives were to:

i. Produce fire history maps to summarise spatial and chronological variations in fire impacts in a frequently burnt urban nature reserve as tools for ecological research.
ii. Compare recently burnt and long unburnt areas to measure direct effects on orchid mortality, growth, flower production and seed production relative to plant density.
iii. Use fire history to measure indirect long-term effects on orchid distribution and productivity.
iv. Develop robust fire response and tolerance indexes and determine safe fire age thresholds for species as tools for orchid ecology and conservation.
v. Use these criteria along with ecological and biological characteristics to assign orchids to fire response categories.

This research is part of a comprehensive study of all orchids present in an urban nature reserve dominated by banksia and eucalypt trees in Perth, Western Australia (Brundrett 2019). The present study focuses on 17 relatively common orchid species with years of preexisting demographic and reproductive data (Fig. 1, Table 1). Related ongoing projects are investigating impacts of climate extremes on orchid demographics and variations in their means pf reproduction and spread.

Methods

1. Study site and species

This study occurred in Warwick Bushland a vegetated area of 63 hectares in the City of Joondalup in Perth, Western Australia (Fig. 2A). This is a Bush Forever Site protected due its size, biodiversity and vegetation condition (Government of Western Australia 2000). There are 215 native flora species, including 34 orchids of which 11 are locally rare in Perth (https://friendsofwarwickbushland.com accessed 18-4-2024). Vegetation is dominated by *Banksia* species with a scattered overstory of eucalypts. Trees include *Banksia attenuata*, *B. menziesii* and *Eucalyptus marginata*, along with scattered *Allocasuarina fraseriana* and *E. gomphocephala*. It is in the Karrakatta – Central and South Vegetation Complex within the Spearwood Dune system, which is around 40,000 years old and has pale yellow/grey sands (https://catalogue.data.wa.gov.au/dataset/perth-plant-communities-reference-sites/resource/10bedb8e-9db3-484d-9eca-2044c965cb9a).

Baseline data was provided by 6 to 11 years of monitoring orchid groups at Warwick Bushland (Brundrett 2019) totalling ~30,000 plant, 20,000 spike, 140,000 flowers and 40,000 capsule records (Table S1). The fire study focussed primarily on 17 species which had the most observations (Fig. 1). Fire comparisons were limited for species absent from recently burnt areas or that rarely flower without fire (*Pyrorchis nigricans* and *Leptoceras menziesii*). Pre-existing orchid information is summarised in Table 1.

2. Fire history

Warwick Bushland is an exceptional study site due to its very complex fire history and substantial areas of excellent condition vegetation. Data presented in Figures 2 and 3 extends a 1952-2005 fire map made primarily by tracing fire scars from contact prints of aerial photographs housed in the former WA Department of Land Administration (Clarke & Brundrett 2005). For more recent fires, fire scars visible on digital imagery were digitised into polygons using Google Earth Pro (accessed 26-4-2024) or Nearmap imagery (https://www.nearmap.com/au/en – accessed 25-4-2024) and combined into layers using QGIS. Only one image was available per year prior to 2002 (Google Earth Pro) or 2007 (Nearmap), when imagery become more frequent. Additional information about the dates and sizes of fires was from observations and photographs taken since 1997, direct mapping of recent fires and maps provided by

land managers (the City of Joondalup). Small fires impacting areas <10 m wide are omitted from maps but were common on some years (arson occurred in spates). Mapped fires were primarily visible due to tree canopy loss so their polygons may be a bit smaller than actual fire boundaries.

The age of fires is defined here as the year that a fire scar where major damage is visible on imagery, so these fires sometimes occurred late in the previous year. Unless otherwise stated, recent fires occurred in late spring, summer, or early autumn (November - April) so had very severe impacts, resulting in complete loss of leaves and branches from understory plants and trees across most of the burn areas. Several fuel-reduction burns (FRB) in autumn or winter were also documented (Fig. 2A). These areas were excluded from analyses because they were less intense and more patchy than major fires and deliberately avoided areas with high concentrations of orchids (June 2019).

3. Survey methods

Long term monitoring of orchids in the study area began in 2015 and increased from 2018 onwards (Brundrett 2019). Additional observations occurred after a very large fire in 2022 that consumed 1/3 of the study area (18 ha) and included orchid groups with 3 to 7 years of demographics and pollination data (Table S1). Additional data collected in 2022 fire included 200 post-fire and 335 unburnt groups, containing ~3000 flowering plants each (Table 2). Monitoring continued for 3 years post-fire to confirm orchids lost to fire, as some may have been grazed or dormant. Orchids missing for three continuous years are very unlikely to be alive (Tremblay et al. 2009, Hutchings 2010, Brundrett 2016). Additional data was provided from a cool winter fuel reduction fire in June 2019 (1.3 ha), as well as two small hot fires in 2023 (0.3 ha) and 2024 (0.1 ha). Observations designated here as “post-fire” occurred within a year of the fire. Long unburnt areas had over 22 years since a major fire (post 1999).

In 2024 orchids were recorded along 30 transects (10 m wide) to increase uniformity of coverage relative to fire age (Table S2). This ensured that spatial data included the full range of habitat conditions, from weedy disturbed areas to almost pristine. There were more transects in unburnt areas (17) than areas burnt in 2022 (13) but their total was very similar length (2.3 vs. 2.4 km). The average length required to count sufficient orchids was longer in burnt areas due to their greater patchiness.

Occurrence records were for individual plants and groups - defined as aggregations of plants separated from other plants of the same species by several times their diameter. Groups include plants derived from seed and/or clonal spread. Groups of some orchids are primarily of clonal origin, but many seeding orchids were also aggregated. Most groups were under 10 m wide, except for *Thelymitra macrophylla*, *P. nigricans* and *Leporella fimbria* which had colonies up to 30 m across. Study locations were marked using GPS waypoints (3-10 m accuracy) and reference photos made with a mobile phone using the SW Maps Android phone app. They were visited multiple times per year to count flowering plants, non-flowering plants, flowers per spike and capsules (all orchids had a single spike per flowering plant). Fire impacts on plant height were measured in 2022. Seedlings of orchids were also recorded.

4. Measurement of responses and traits

Data comparing orchids immediately after a major fire or in long unburnt areas is summarised in Table 2. This is a subset of data in Table S1 with most comparisons occurring after the major fire in 2022 and from two smaller fires in 2023 and 2024. Data from the same orchid groups extending 3 or more years before and after fires were used to measure impacts on plants, flowers and seeds. Representative groups of common orchids and the majority of locally present individuals of less common species were included in sampling (Tables S1, S3). Seed production was the proportion of capsules per flower resulting from insect-pollen transfer or self-pollination that reach full maturity, which may be less than the pollination rate due to seed abortion and grazing (three species self-pollinate). *Ex situ* seed baiting (Brundrett et al. 2003) was used to confirm a high degree of seed viability for all species studied (MCB unpublished data).

Traits measured for ecological comparisons included seed production, seed viability, seedlings, group sizes, clonality, aggregation and dispersion, as well as tuber size, depth and abundance (Table 4). Plants were designated as clonal if they normally produced more than one tuber per plant per year. Their daughter plants are unconnected and may include different genets, so were counted as individuals. Separate indexes were calculated for clonality, aggregation and dispersion, recolonisation potential and lifespan from demographic data (Tables S1-S4), as explained in Table 4. Results present here are part of an ongoing study investigating the lifespans, turnover and propagation of these orchid species.

5. Data analysis

Measurements of height, flowering, flower production and average pollination rates in recently burnt and long unburnt areas were compared graphically with 95% confidence intervals after the 2022 fire (Table 2). Impacts of fire on pollination density dependence were determined by graphing pollination outcomes against the total number of flowers in groups (Brundrett 2019).

Orchid productivity was compared to local fire history using the "Join attributes by location" data analysis tool in QGIS (3.34., Prizren) to intersect orchid group locations or data from transects with all fire history polygons. This produced new point layers with all fires intersecting each location or transect. A data matrix was used to calculate the time since fire and the number of fires for each location. The age of areas without any fires was set the first year where fire data was available (1952), but may have been much older. To summarise fire history for the entire site area, the same QGIS tool was used to join grids over the area to fire history polygons (Fig. 2BC). Results for 25 m and 40 m grids were similar (Fig. 3C), so only the 25 m grid (1024 points) was used. Orchid locations and grid points located near fire polygon borders were manually corrected where required.

Fire response criteria and related traits measured for each orchid are explained in Table 4. These are summarised in common numeric scales using detailed data provided in Tables S2-4. Fire response data from this study was compared with existing ecological information (Table 1), and newly measured biological properties as explained in Table 4. These data were converted to uniform response scales (-3, -2, -1, 0 1, 2, 3) extending from catastrophic impacts to very major benefits, for each factor and combined to produce an overall Fire Response Index (FRI, Table 5). Separate indices for important ecological traits (scale 0-10) were also calculated (Tables S1-4). These represent the capacity of orchids to spread locally or distally by clonal or seed propagation, the degree of aggregation of plants, increases or declines in orchid abundance and estimated lifespans, as well as tuber depth and size (Table S5). Typical population increases or decreases for orchid groups were determined using 3-5 years of occurrence data. These were divided by total groups monitored consistently over time to estimate turnover of orchid plants (Table S4). Correlations between fire responses and traits were calculated and P values shown on graphs. Overall fire outcomes for orchid species were summarised as thresholds for safe fire thresholds (FAST) and optimum fire ages, as explained in Table 4.

Results and Discussion

1. Fire history

Major fires are mapped in Figure 2 and summarised in Figure 3. Typically, fires were of high or very high intensity (Fig. 4A, B) resulting from arson in summer or autumn and their sizes ranged from <100 m^2 to 18 ha of the 63-ha total area (Fig. 3A). The entire area has been burnt multiple times since 1972, excluding a small narrow zone that was cleared for a utility corridor. Fires were generally smaller after 1995, with only the main 2022 fire exceeding 10 ha (Fig. 3A). This likely resulted from increased accessibility to fire vehicles due to improved tracks and new fire gates, but local firefighting resources and protocols have also changed, including use of water bombing aircraft in recent fires (Fig. 4B). Except for two relatively small fires managed for fuel reduction, all fires were caused by arson. Fire areas included some less impacted areas due to patchiness or fire suppression by firefighters especially near edges. Lower intensity fuel reduction burns (FRB) occurred in April 2016 (0.7 ha) and June 2019 (1.7 ha).

These autumn or winter burns were managed to limit tree canopy damage but severe understory scorching still occurred over most of these areas (Fig. 4C).

After 1972 there was an average of 1.1 severe fires annually after 1972 with an average of 5.6 ha bunt (Fig. 3A). These 58 fires covered a cumulative total of 289 ha (4.6 x the vegetated reserve area of 63 ha). There was a major fire on 30 out of the 52 years (post 1972) - often more than one, and a maximum of seven per year (Fig. 3B). In some years there were also numerous small fires (< 100 m^2) that are not included in maps, so the total number of fires is much greater. Larger areas were burnt in fires before 2005, when it was common for entire compartments bounded by tracks to be burnt. Less is known about these earlier fires, but all were severe enough to cause extensive cause canopy clearly visible in aerial photos. Images were available from 1952 onwards, but fires only commenced after surrounding areas were developed for housing in the 1970s. In general, the size of fires has decreased over time, but their frequency has increased (Fig. 3A, B).

Fire history was summarised using a grid to resolve many overlapping polygons from different years. This 25 m virtual point grid allowed the average fire frequency and time since fire by area to be visualised (Figs. 2B, C, 3C, D). Fire frequency by area had a normal distribution with an average of five fires (Fig. 3C), with the largest areas 1-5 years (35%) or 26-30 years post-fire (26%). This bimodal distribution resulted in similar areas of recently or long unburnt habitats (Fig. 3D).

2. Direct impacts on orchid survival

Figure 5AB shows the distributions of orchids in Warwick Bushland relative to recent fire history and indicates where orchids were lost, primarily in 2022 (Fig. 5C). These loses are significant because the overall balance between recruitment and death is positive for most orchids of the study area, which are spreading despite relatively low rates of seed production (Brundrett 2019, Table S4). Grazing by rabbits was more severe after fire, but was only substantial for *L. fimbria*, and grazing rates were similar in unburnt areas (see below).

Leporella fimbria and *P. nigricans* are normally highly resilient to fire, but an unseasonal hot fire in late autumn killed many plants in one area (May 2018). These had emerging shoots just below the soil surface and had yet to initiate new tubers. Plants with partly scorched leaves (Fig. 4D) were found on the margin of the group, which has not recolonised the area substantially after seven years. *Pterostylis orbiculata* (banded greenhood) were less productive in burnt areas but were still common (see below). This orchid also forms shoots in autumn (Fig. 4G) so is also vulnerable to autumn and winter fires, as is the case for *T. macrophylla* and *P. nigricans* (Table 4, Fig 4E).

Thelymitra macrophylla (blue sun orchid) has rapidly increased in abundance and become more widespread in the study area since three groups of 42 were found in 2009 (Brundrett 2019). This orchid includes self-pollinating forms and hybridises with *T. graminea* at the study site. Six *T. macrophylla* groups were lost to fire in 2022 and still missing after 3 years (Fig. 5C). One *T. macrophylla* group with 44 flowering plants pre-fire, was much smaller after a fire in 2019 and absent after a second severe fire in the same area in 2022 (Fig. 6). Three groups of *T. macrophylla* survived a smaller fire in 2023 (Fig. 5C), but two of these were absent in 2024 and one additional plant was found. Overall, only 11% of plants of this species survived in fire areas and all of these were close to edges where fire intensity is likely to be reduced by edge effects and firefighting activities. None of the 31 monitored groups in unburnt areas were lost, some expanded substantially, and new grups were found each year (Fig. 6, Table S1). The smaller blue sun orchid *T. graminea* did not survive fire (43 plants in 2 areas lost). Both blue sun orchids are also vulnerable to autumn fires, as explained above.

A group of over 350 *T. macrophylla* plants were impacted by a fuel reduction burn in June 2019 (Fig. 6). This burn was managed to ovoid most areas with abundant orchids and limit damage to tree canopies, but the ground level intensity was very high due to the highly flammable leaves of *Xanthorrhoea priesii* (Fig. 4C). This winter fire resulted in substantial damage to growing *T. macrophylla* leaves, but spikes

continued to develop (Fig. 4F). However, fire impacts to this group are ongoing after five years with declining numbers of stunted flowering plants, while adjacent unburnt groups expanded (Fig. 6).

Some orchids were consistently absent from recently burnt areas but common elsewhere. These include *Disa bracteata* and *Microtis media* which prefer relatively open areas near tracks and reserve boundaries. The weedy South African Orchid (*D. bracteata*) was an especially good indicator of recent fires, with some groups bisected by fire boundaries. This species was also lost to fire at another site 35 km away (Brundrett & Longman 2016). *Pterostylis ectypha* (a small snail orchid) is also fire intolerant. These three disturbance tolerant orchids have relatively shallow tubers, are relatively short-lived and reproduce by seed (Table 5). They produce abundant seed (*D. bracteata* and *M. media* self-pollinate) so are expected to efficiently recolonise burnt areas once conditions become suitable. *Caladenia latifolia* (close relative of *C. flava*) is also a disturbance opportunist but survived well after a fire in 2023.

3. Orchid reproduction post-fire relative to long unburnt areas

Leporella fimbria (the Hare Orchid) occurs across southern Australia. Its small green and brown flowers (Fig. 2a) use a pheromone to attract flying male bull ants (*Myrmecia* spp.) which pollinate them (see https://www.youtube.com/watch?v=D1FTrJaEFhE&t=89s). Most plants (89%) of this long-lived, highly clonal species remain sterile, and its flowering can be severely impacted by autumn drought (Brundrett 2019). Flowering and seed set were moderately higher (11 %) in burnt areas, especially in large patches (Figs. 7, 8). Fire was less important than seasonal variations on rainfall. This orchid has a strong density effect on pollination with a greater reduction in pollination of large groups after fire (Fig. 9A). Overall, increased seed production post-fire results from greater flower production rather than increased rates of pollination, so *Myrmecia* ants were active in severely burnt areas. Grazing resulted in loss of a few spikes each year (average 6.2% - 2016-2023) but was lower in burnt areas (4% vs. 9% of spikes).

Pheladenia deformis (blue beard orchid) is a close relative of *Caladenia, Ericksonella* and *Cyanicula* that also occurs in eastern Australia. It is a relatively solitary winter-flowering orchid but often occurs within 5-20 m of other plants, perhaps due to seed dispersal or habitat preferences. Many new plants were discovered after the large 2022 fire with another geophyte not previously found in banksia woodland (*Wurmbea dioica*). *Pheladenia deformis* leaves were not substantially larger post-fire, but numbers of plants increased and there were 1.6x more flowers per group (Fig. 7C). Pollination was also substantially increased (19x) after fire (Table 2, Fig. 8), but outcomes of each year and fire differed, due to climate or other factors (Fig 10A). Pollination was very rare in unburnt areas except in 2021. The 2022 fire produced 54% of all capsules formed over 3 years (Fig. 10A) and a very small fire produced ½ of the 2023 capsules (Fig. 4I). Plant density had little effect on pollination, probably due to relatively small group sizes (Fig. 9B).

The bluebeard orchid is very small, so easily overlooked if not flowering. Most plants that flowered in 2022 were rediscovered as leaves only in 2023, by carefully checking the same locations aided by use of habitat photos and markers. This orchid slowly increased flowering capacity each year after fire but takes a decade to fully recover (Fig. 10B). Transitions between flowering and sterile or dormant plants also substantially increased the second year after fire relative to long unburnt areas (Fig. 10C). Reproductive costs often reduce the likelihood of subsequent flowering by small orchids (Shefferson et al. 2020).

Pterostylis orbiculata (banded greenhood) belongs to a complex of seven similar species that flower in winter (*Pterostylis sanguinea* in previous studies). These orchids were substantially smaller after fire with fewer flowers and seeds (Figs. 7, 8). Reproductive success was reduced across all areas after fire with a stronger density affect suggesting there also were fewer pollinators (Fig. 9C). This is not surprising since this is a fungus gnat associated with humid condition and litter accumulation.

Caladenia flava (cowslip orchid) flowers in late winter and early spring. Plants had shorter spikes with similar numbers of flowers per spike after fire (Fig. 7AB), but more spikes formed per group (Figs. 7C,

9D). Pollination frequency was similar after fire (Fig. 8), so increased seed production resulted from greater flowering, especially in large groups (Figure 9D). It may have been easier for insects to find flowers of this orchid due to reduced cover after fire, despite the need for co-flowering plants to support pollinators of this visually deceptive orchid. Flower production was much lower the second year after fire, but also in unburnt areas, so fire promotion of flowering may last for two years but were also determined by climatic factors (Fig. S1).

Diuris magnifica (pansy orchid) is one of many very similar donkey orchid species in the *D. corymbosa* group. Pollination of this species and its close relatives by visual deception is by native bees that primarily visit Fabaceae flowers (Scaccabarozzi et al. 2020). Orchid plants were substantially smaller after fire (Fig. 7A), but pollination was marginally increased (Fig. 8). Overall, this species had a neutral response to fire. However, Figure 9E shows a strong density effect on pollination in burnt areas, but not in unburnt areas, implying pollinators were less abundant after fire. This makes sense since Fabaceae plants that support its pollinators gradually recover by resprouting or germinating after fire.

Blue Sun Orchid (*T. macrophylla*) pollination fluctuated annually and was generally better in years with lower rainfall, presumably due to effects of warmer temperatures on pollinators (Brundret 2019). These primarily are native bees (Edens-Meier et al. 2013). As explained above, comparisons were limited by very low fire survival rates, but a few plants (8 spikes, 76 flowers) survived a 0.32 ha fire in 2023. These plants were shorter and had fewer flowers than those in unburnt areas (average 9.5 vs. 15.5). Pollination was impacted by plant density in unburnt areas (Fig. 9F).

Pyrorchis nigricans (red beak orchid) occurs across southern Australia and flowers in late winter. This very long-lived clonal species flowers almost exclusively after fires. It forms groups up to 30 m wide (average 3.4 m) primarily by clonal division (no seedlings were found). Reproduction is by multiple tubers on droppers and large colonies would be hundreds or thousands of years old. Mass flowering of *P. nigricans* occurred after fires in 2019, when 14% of 128 spikes had capsules and in 2022 when thousands flowered, and 8%, of 2133 spikes formed capsules (Table 2). The higher rates of pollination of *P. nigricans* in 2019 than 2022 may be due to higher plant density in surveyed areas. There was a strong density effect on pollination in 2022, when 2/3 of capsules formed on the edge of groups (i.e. <20% of flowers formed 66% of seed). Single unburnt flowering plants were observed in 2020 and 2023 only (total of 8 flowers and 5 pods). Thus, flowering of this species is thousands of times greater post-fire. Some unburnt plants flowered in 2022 (34 plants 5-10 m from the fire edge). This confirms the flowering stimulus is air-borne and not heat. It is likely to be ethylene gas (Dixon & Barrett 2003).

Pyrorchis nigricans is relatively effective at attracting pollinators compared to other visually deceptive orchids in the same habitat and has comparatively large capsules (570 mm^3), with up to 109 capsules in a group and an average of 14 (Table 1). A halictid bee has been observed visiting flowers in eastern Australia (Kuiter 2024). Its flowers have no visible nectar or discernible scent so have an unknown type of attraction mechanism. *Leptoceras menziesii* (rabbit orchid) also flowers primarily after fire but sporadic flowering occurs at other times. In 2022 a group of 145 plants produced 54 spikes with 68 flowers that formed 44 capsules (65%), while in 2008 there were only 10 flowers on 6 spikes, with 30% seed set at a different location. This orchid also lacks nectar but has relatively high pollination rates.

Excluding three self-pollination species, orchid seed production overall was similar post-fire or in long unburnt areas but was dominated by different species (Table 2). For 10 species that survived fire, seed production was largely unaffected (2 sp.), reduced (3 sp.), substantially increased (3 sp.), or induced by fire (2 sp.). Fire effects on pollination could not be assessed for seven species due to absence or scarcity in burnt areas. There were no major benefits of fire on reproduction for most orchids, which have adequate seed set to support local spread and population increases without fire (Brundrett 2019). However, there were major benefits for *P. deformis,* which produced much more seed after fire, and possibly also for *P. nigricans* and *L. menziesii* (Table 2).

4. Indirect fire effects
The fire in 2022 provided substantial recently burnt areas for comparisons with long unburnt areas. Analysis of about 1000 orchid locations and 4.5 km of transects relative to fire history produced robust information for most species (Table 3, Figs. 11). The transects included a wide range of vegetation conditions and had limited overlap with location records. Fire effects on orchids were analysed relative to time since fire (Fig. 12), since productivity was less well correlated with total numbers of fires or recent fires (Figs. S2, S3). This would presumably be due to recovery of ecosystem functions (Enright et al. 2011, Brundrett 2021) and orchid recolonisation over time.

Four species were small, relatively short-lived and rapidly spreading were extremely fire intolerant (*T. graminea*, *M. media, D. bracteata* and *P. ectypha*). These orchids prefer relatively open habitats and tolerate intermediate levels of disturbance and can grow with some weeds. They should be able to rapidly colonise burnt areas by seed dispersal, provided substantial refugia exist nearby. However, their minimum fire ages for recolonisation was 15 years and peak abundance occurred several decades later (Table 3). In jarrah forest, a close relative of *P. ectypha* was most abundant several decades after fire (Cargill 2015) and started to appear 5 years post mining (Collins & Brundrett 2015).

The fire intolerant sun orchids *T. macrophylla* and *T. graminea* were rare or absent after fire (Fig. 11) and significantly increased in abundance after several decades (Fig. 12G). Three other sun orchids had some degree of fire tolerance (*T. fuscolutea*), or lacked direct evidence of fire impacts (*T. benthamiana* and *T. crinita*). However, *T. fuscolutea* had a strong preference for growth in long unburnt areas (Fig. S2F), as also seems to be the case for *T. benthamiana*. *Thelymitra crinita* was most abundant several decades after fire in the jarrah forest (Cargill 2015) and was absent from restored minesites but common in unmined forests nearby (Collins & Brundrett 2015). Seedlings of *T. benthamiana, T. crinita* and *T. macrophylla* were only found in older fire age areas with accumulated leaf litter and shade (Table 3).

Two orchids survived and flowered well after fire but were most productive in long unburnt areas. *Pterostylis orbiculata* had a significant preference for long unburnt areas (Figs. 11B, 12C) and relatively shady areas under trees, where seedlings were found 3 years after fire (Fig. 4M). There also was evidence of increasing productivity with time since fire for *D. magnifica*, (Fig. 12E).

Some orchids lacked a clear relationship with time since fire. *Caladenia flava* had fire promoted flowering but its abundance may have increased after fire (Fig. 12D). The enamel orchid (*E. brunonis*) also had similar abundance in burnt and unburnt areas (Fig. 11). *Caladenia arenicola* was found more often after fire (Fig. 11B) and had a flat response to time since fire (Fig. S2D). Bluebeard orchid (*P. deformis*) also had a relatively flat fire age response (Fig 12A). It was the only orchid in this study likely to have substantially benefited from fires, due to fire-enhanced seed production, reproduction primarily from seed, relatively short lifespan and shade intolerance.

In theory, the pyrogenic orchids *P. nigricans* and *L. menziesii* benefitted the most from fire-promoted mass flowering. However, both were highly clonal and rarely recruited from seed, so these benefits cannot be measured in practical timeframes. Furthermore, *P. nigricans* was most abundant in long unburnt areas where it increased over time until some groups had thousands of leaves (Figs. 11, 12F). Gargill (2015) also categorised*, P. nigricans* as an intermediate fire age species in jarrah forest. *Leptoceras menziesii* was also more abundant in long unburnt areas (Fig. 11). *Leporella fimbria* also flowered substantially more after fire and its abundance poorly correlated with fire age (Fig 12A), but its distribution had a significant bias towards long unburnt areas (Fig. 11). Resolving fire age trends for this species is difficult because of inherently large variations in group sizes (3 - 492).

5. Comparing fire responses and traits for orchids
While overall fire effects on orchid diversity and abundance were dramatic, there were substantial differences in fire responses between orchid species that need to be summarised in a consistent manner. The approach taken here was to test the validity of exiting fire tolerance scales by using

consistently applied criteria. These criteria were based on 10 measured fire response indexes and 12 ecological traits measured for each species (Table 4). These indexes used common numeric scales so could be combined into a comprehensive overall fire response index (FRI) for each orchid (Tables 5A, 6). The FRI, which extended from -18 to 18, was used to assign orchids to tolerance categories (Table 5). These categories were fire opportunists (13 to 18), major benefits (7 to 12), minor benefits (1 to 6), minor harm (0 to -6), major harm (-7 to -12), fire intolerant (-13 to -18). Orchids identified as fire intolerant (Table 6) were normally lost to fire and increase in abundance several decades later as habitat quality improves, as illustrated by *T. macrophylla* (Fig. 12E). Overall, there were more orchids that are harmed by fire than benefit from it (Figure 13).

Indexes provided in Table 5B represent fire responses as well as key biological and ecological traits of orchids, which are based on data in Tables S1 to S5. This revealed that orchid fire responses were highly correlated with biological traits such as flowering and seed production, clonality, tuber depth, aggregation and lifespan (Table 7, Fig. 14). One exception was tuber size which was only related to the overall size of orchids. Thus, fire traits are deeply integrated into orchid ecology. Traits that regulate dispersal and local persistence and are highly correlated with fire susceptibility. Flower and seed production are inversely correlated with clonality, aggregation and lifespan indexes. The strongest relationship is an inverse correlation between lifespan and colonisation indexes (Fig. S5A, correlation coefficient = 0.95). Orchids which reproduce by seed are very effective at local dispersal, as would be expected. Indexes for aggregation and dispersion are also inversely correlated (Fig. S5B, correlation coefficient = 0.65). The dispersion index compares results from monitoring specific orchids (chosen to maximise orchid diversity), and counting orchids on transects (representing overall diversity patterns). This index summarises the uniformity of orchid distribution (Table 5B), and was also correlated with the overall fire response index (Table 7).

Due to shared habitat preferences, there were positive correlations for orchids that often co-occur due to shared habitat preferences (e.g. *C. flava, T. macrophylla* and *L. fimbria*). Very common orchids such as *T. macrophylla* and *P. nigricans* had strong positive correlations with total orchid density and diversity (Table 7B). In contrast, the abundance of *P. deformis* was inversely correlated with most other orchid species (and total orchid density and diversity) due to disparate habitat preferences (Table 7B).

6. Determining fire age safe thresholds

Quantifying fire impacts by intersecting orchid locations with fire maps allowed a Fire Age Safe Threshold (FAST) to be estimated by comparing orchid abundance with fire history (Figs. 12, S2). Fast is highly correlated with the overall fire index (FRI), which is dominated by short term fire responses (Fig. 14H). Peak fire ages for orchid species, where diversity and abundance are maximised, could be as important than FAST ages, but could not be estimated because there were limited areas with fire ages over 40 years, a time when orchid abundance and diversify may still be increasing (Fig. 15). Comparing orchid abundance and distributions to fire history revealed that most orchid species had preferences for long unburnt areas, including those that benefit from fire due to increased seed production (Figs. 11, 12). It also confirmed the rarity or absence of fire intolerant orchids in recently burnt areas and that overall orchid diversity and abundance were strongly correlated with fire age (Fig. 15).

Some orchids may lack FAST periods due to similar abundance in recently burnt and long unburnt areas (Figs. 11, 12). Thus, the designation of fire tolerance for orchids with intermediate FRI categories may vary with circumstances. These included *E. brunonis, C. flava, P. deformis,* and *P. orbiculata*. *Caladenia arenicola* was the only orchid more common after fire, but this may be due to its need for relatively open areas. Even low FAST age orchids may require long unburnt areas for seedling establishment, since 86% seedling nurseries were found there. Thus, there are very few if any orchids that are fully fire positive or neutral when relationships between fire habitat age and productivity or germination are considered.

7. Orchid fire ecology

A large fire in 2022 that covered one third of the study site allowed 17 orchids belonging to 10 genera to be monitored in post-fire and long unburnt areas with similar sampling intensity. This revealed substantial fire impacts on orchid distribution pattens due to variations in their fire tolerance (Box 1), but there were some contradictions. For example, *P. nigricans* an orchid with obligate fire induced flowering was most productive in long unburnt areas where the largest colonies were found, some with thousands of leaves. The fire response categories used here (Fig. 13, Box 1) are similar to those used by others (e.g. Jones 1988, Duncan 2012, Adams 2018). However, orchids belonged to a continuum from obligate fire flowering to fully fire intolerant species, so it was difficult to assign some species to specific categories (see Fig. 16). This highlights the importance of determining safe fire age thresholds (FAST) based on fire history analysis, determine post-fire times required for maximum orchid diversity and abundance and designate orchids which are susceptible to unseasonal fires (Box 1).

Text Box 1. Orchid fire response summary

a) Short-term comparisons of recently burnt and long unburnt areas revealed clear winners and losers after fire (Table 6, Fig. 15). Three orchids had very large short-term fire benefits such as strongly promoted flowering, while five others had less major or minor benefits. In contrast, six species experienced minor or major harm from fire due to reduced productivity and five orchids rarely survived in or were entirely absent from recently burnt areas.
b) Three orchids had pyrogenic (fire-induced) flowering (Lamont & Downes 2011, Bower 2019, Brundrett 2021). Two of these were very long-lived clonal species that rarely reproduced by seed, so fire benefits may be minimal, especially for *P. nigricans* which was far more abundant in long unburnt areas. The third species (*P. deformis)* formed most of its seed after fire, is relatively short lived and propagates primarily by seed. This orchid may function as a fire opportunist but was equally common in long unburnt areas (Fig. 11).
c) Orchid with substantial declines or loss of some orchid populations followed fires include two sun orchids *T. macrophylla* (89% fire mortality) and *T. graminea* (100% mortality). Three other fire intolerant species were small and relatively short-lived and can rapidly spread due to abundant seed production (*M. media, D. bracteata* and *P. ectypha*), but required several decades to recolonise burnt areas (Table 3).
d) At least 5 orchid species that were otherwise highly resilient to fire could be lost to unseasonal fires, especially in autumn (Table 5A), which also occurs for some eastern Australian orchids (Jasinge et al. 2018, Tomsen et al. 2024).
e) Overall, eight species were relatively common in recently burnt areas, while nine species were found much more often (4 sp.) or only (5 sp.) in long unburnt areas (Figs. 11, 14). The total FRI score is biased to the negative (-3.8) since more species had negative fire effects even if they normally survive and flower more after fire (Table 5).

In this study, there were clear trends in increasing orchid diversity and abundance with time since fire, presumably due to gradual recovery of suitable habitat conditions. Thus, fire age was more important than the total number of fires impacting an area, since fire impacts diminished over time. This study demonstrates the importance of long-term orchid monitoring to provide data from orchids before and after fire. There are very few other scientific studies that have attempted to correlate the productivity of orchids with time since a wildfire (Duncan 2012).

The ecology and biology of terrestrial orchids in an ancient biodiversity hotspot is highly correlated with fire responses. These relationships were revealed using trait indexes, many of which are correlated with each other (Table 7A). In particular, fire history responses were correlated with orchid colonisation, aggregation, clonality, dispersion and lifespan indexes, as well as tuber depth (Table 7A). Fire tolerant or intolerant species had divergent index profiles for these traits, which are also central to other aspects of orchid ecology. Fire tolerant orchids were more likely to be widely dispersed, have long lifespans, reproduce clonally and have relatively deep tubers. In contrast, fire intolerant orchids tended to have greater flower and seed production, reproduced primarily by seed and spread more rapidly (after

sufficient time post-fire). They also had more localised distributions, shallower tubers and shorter lifespans and were more likely to be associated with shade and leaf litter. Overall, fire tolerance traits were most important for relatively long-lived clonal species. In contrast, orchids with relatively short lifespans did not benefit from fire or were harmed by it. However, the latter have less need for fire resilience because they are more mobile in habitats due to recruitment from seed, provided dispersal from areas of sufficient fire age is possible.

The impact of fire intensity on the relative success of fire tolerant and fire sensitive orchids requires further investigation. Fire intolerant orchids sometime survived in fire areas, presumably due to fire patchiness and intensity differences that were not revealed by fire mapping. For example, *Thelymitra macrophylla* survived a winter fuel reduction fire after substantial leaf scorching, but usually failed to survive intensive summer fires when dormant. This may be associated with its relatively shallow tubers or a preference for leaf litter and soils high in organic matter (see below). Long-term effects on habitat quality may explain why population viability had not recovered after five years. *Leporella, Pyrorchis,* some *Pterostylis* and some *Thelymitra* species initiate shoot growth in mid-autumn resulting in tuber depletion and vulnerable new shoots. These shoots are held just below the soil surface until there is sufficient rain, so can be killed by fires at these times (see Fig. 4G). These orchids will not become resilient to fire until tubers are replaced (usually over winter).

FAST times of intolerant orchid species are determined by separate interacting processes that regulate their fire responses. These include (i) fire-induced mortality, (ii) reduced fecundity (flowering, pollination and seed production), (iii) recruitment failure (dispersal and germination), (iv) soil incompatibility (loss of symbiotic fungi, fertility or structure) and (v) altered habitat conditions (loss of shade, increased weed cover, etc.). These factors work in concert, but their relative importance and the time required for recovery of each are unknown. In contrast, fire tolerant orchids are less impacted by these factors, especially mortality, while their fecundity and recruitment may increase or decrease.

Orchid fire traits were highly consistent within species here, but could vary across the ranges of widespread or variable species. For example, *P. nigricans*, which has an Australia wide distribution, flowers more often without fire in habitats where fire is less frequent (Brundrett 2014). Other widespread species with potentially complex fire ecology include *P. orbiculata, D. magnifica* and *T. macrophylla*, which are indistinct taxa in species complexes (Brundrett 2014). Their placement on the fire response spectrum may also vary across regions, as occurs for other SWAFR plants (Brundrett 2021).

In this study, fire dramatically modified habitat suitability for orchids due to increased light from canopy loss, removing superficial organic matter and promoting major environmental weeds, especially veldt grass (*Ehrharta calycina*). Most orchid species were substantially less common in relatively poor condition vegetation with many weeds, but persisted in these areas. Increasing weed abundance is likely to be a major factor limiting the productivity of relatively fire-resilient orchids. Interactions between fire history, vegetation condition and the diversity and cover of native plants or weeds requires further study.

The ability to recolonise or spread within areas by wind dispersed seed is very important for orchids after fire. Many SWAFR orchids have highly specific relationships with insect pollinators and mycorrhizal fungi, so orchid habitats must also be suitable for their fungal and insect symbionts. These relationships also tend to be more one-sided (exploitative) than other SWAFR plants (Brundrett 2021). Most SWAFR orchids use deceptive pollination syndromes to exploit insects (Brundrett et al. 2024). These insects include native bees, that require flowering peas to support them near visually deceptive orchids such as *C. flava* and *D. magnifica*, and the wasps, ants or fungus gnats required by sexually deceptive orchids such as *C. arenicola, L. fimbria* and *Pterostylis* species (Scaccabarozzi et al. 2018, 2020, Kuiter 2024). Pollination is also affected by pollinator decline in isolated urban habitats where these insects must compete with abundant feral honeybees, which rarely transfer pollinia (Scaccabarozzi et al. 2024).

Orchids are parasites of fungi, at least for part of their life cycles, while the majority of other SWAFR plants have mutualistic mycorrhizal associations (Brundrett 2021). Seed baiting trials have shown that orchid fungi are associated with coarse soil organic matter (Brundrett et al. 2003), and micro-habitats suitable for their germination are very patchy in soils (Batty et al. 2001). Thus, orchid habitats are defined by soil organic matter, leaf litter, shade and food sources for their mycorrhizal fungi, all of which are impacted by fire. This would explain why most orchid seedlings were found in long unburnt areas. The only exception was *P. orbiculata,* where seedlings emerged three years after a fire where litter accumulated under eucalypt trees. A study of a restored bauxite mine in the jarrah forest found that fungi germinating orchid seeds were detected more frequently in forest than in restored areas, where they were strongly associated with litter accumulation in rip lines (Collins et al. 2007). Unfortunately, not much is known about the fire ecology of orchid pollinators or fungi, especially if they can survive intense fires or how they recolonise habitats from refugia.

The FAST status of orchids is likely to be regulated by both orchid and site-specific factors, but only the former was measured here. For example, the time required for fire intolerant orchids to recover post-fire is limited by seed dispersal from surrounding unburnt areas, so they may may fail to recolonise small, isolated patches of suitable habitat. New orchid species occasionally arrive from distant sites into urban remnants such as Warwick Bushland where five new species were discovered recently, but often failed to persist. These "vagrant" species include *Caladenia falcata*, a species which is common in the West Australian wheatbelt further east, and temporarily appeared at five separate locations.

It is likely that FAST concept also applies to many other plants and organisms – specially fungi and small animals involved in recycling organic materials which are consumed by fire. Thus, research to establish FAST data for these species should be a very high priority in ecosystems where fire impacts are increasing. The relative impacts of fuel reduction fires relative to very hot summer fires on of FAST times is another critical knowledge gap. Further research is also required to measure short- and long-term impacts of unseasonal fires which impact orchids when they are most vulnerable.

Fire responses reported here resulted from research in one banksia-jarrah woodland site in an urban setting with an exceptionally high fire frequency. However, fire tolerance rankings presented here agree with results of studies of the same or closely rated species in other SWAFR habitats (Table 6). These include comprehensive fire age data from 9 of the same species in the jarrah forest (Cargill 2005) and successional trends for recolonisation of jarrah forest post mining which included 14 of the same species (Collins & Brundrett 2015). Adams (2018) found similar relationships between fire age and orchid diversity in eastern Australia. Orchids with traits likely to make them fire intolerant include 37% of SWAFR species (Brundrett 2021). Taken together there is strong evidence to support fire tolerance indexes (e.g. FAST and FRI) as a keystones of Australian orchid ecology.

8. Management implications

Sustainable management of orchid populations and habitats requires a thorough understanding of life history traits regulating their persistence and dispersal in ecosystems, and how they interact with fire history and climate extremes. Key trait data for orchids includes their lifespans, turnover, seed production, dispersal efficiency and the relative importance of clonal or seed reproduction, but is lacking for most Australian species. Maintaining local populations of orchids also requires an understanding of the dynamic processes and resources they require to grow and the organisms that mediate these processes, especially symbiotic fungi and pollinating insects. Orchids with a limited capacity to spread require large nature reserves or good connectivity between natural areas to persist. Short lived orchids with weed-like life history traits require conditions that favour seed production and seedling establishment, and may benefit from intermediate levels of disturbance such as grazing, or fire (Coates et al. 2006, Hutchings 2010). In contrast, very long-lived clonal species should be resilient in the short term, but this makes it harder to detect impacts of adverse factors such as fires on their sustainability. Thus, both short and long-lived orchids require FAST and FRI data for effective management.

It may be possible to effectively manage orchid habitats where fire ages are unknown by estimating the fire tolerance of orchid species using FRI traits listed in Table 4B, or using FAST values from closely related species (there was some fire trait consistency for genera or subgenera here). However, none of these alternative approaches have been validated. Strong relationships between fire history and orchid diversity may also allow fire intolerant orchid abundance to be used to estimate fire age in ecosystems, but this also requires investigation.

Results of this study suggest that mixed fire ages in landscapes are essential to maintain orchid diversity, with long unburnt areas the most important overall. Correlations between fire age and orchid diversity have also been measured in SWAFR forests (Cargill 2005). Fuel reduction fires in autumn, winter, or spring are especially damaging for orchids, since they initiate shoot growth in autumn or winter and form tubers for summer survival several months later (Brundrett 2014, Thomsen et al. 2024). Spring fires are also potentially very damaging because most orchids are flowering or forming seed at that time. Unfortunately, both autumn and spring fuel reduction fires are common in SWAFR orchid habitats (Bradshaw et al. 2018). Thus, orchids have evolved mechanisms to withstand or avoid occasional hot summer fires but can be very susceptible to fires at other times of the year. They also tend to be intolerant of frequent fires with an optimal fire age for orchid diversity of about 30 years in banksia woodland. Thus, even common orchids, which are a key resource of sustainable ecotourism in Western Australia, may be declining in many habitats. Other major fire-induced changes to orchid habitats in banksia woodland included substantially increased weed cover and canopy reduction, as well as understory shading due to pyrogenic seed germination and resprouting of native plants and weeds. It may be possible to promote recovery of burnt orchid habitats by augmenting soils with organic materials, providing artificial shade, etc., but this would still require many years to be effective.

In Australian ecosystems where orchids grow, designating Fire Age Safe Thresholds (FAST) is essential for their sustainable management, and critically important for habitats of rare species. Thus, it is essential to use precautionary approaches by excluding core habitat areas of rare orchids from managed fires. The Wheatbelt Orchid Rescue project developed protocols for mapping core habitat areas for rare orchids (see Brundrett 2016), but this only included 5 of the 44 threatened SWAFR orchids and there are another 72 “priority flora” species that may be threated but require further study (ttps://florabase.dbca.wa.gov.au, 28-10-24).

Fire drastically impacts orchid habitats, and this also applies to fires managed to reduce fuel in natural ecosystems, because these “fuels” include litter and organic matter required by orchid symbiotic fungi. Cumulative impacts from the increased frequency of managed fires in WA (Bradshaw et al. 2018) are of particular concern since they occur at proscribed intervals which are much shorter than the FAST times for many orchid species. Thus, setting maximum burn areas and frequencies for managed fires and monitoring their biodiversity impacts is required to ensure orchid diversity is maintained. Alternatively, habitat management could aim to maintain a mosaic of fire ages, with fuel reduction fires used to protect long unburnt vegetation in core habitat areas for orchids and other fire intolerant organisms. This would provide refugia where seed is produced for recolonisation of other areas and nurseries for the recruitment of fire intolerant species. These approaches are especially important for habitats of rare orchids, but would also protect focal points for tourism and local biodiversity hotspots such as exposed granite, sheoak or wandoo woodlands, damplands, organic soils, shady areas under large habitat trees, rotten logs, damplands, etc.

Text Box 2. Orchid Fire Management Implications

1. Orchids have diverse fire responses which require separate analysis of direct and indirect effects on their survival and productivity, as well as knowledge of fire history to be understood.
2. Ecological and biological trait indexes (FRI) and safe fire age thresholds (FAST) provide valuable tools for habitat management for orchids, and provide a framework for understanding their local distribution, turnover and abundance.
3. When fire response data is lacking a precautionary approach is required, so fire age thresholds should be set to values longer than typical FAST values for similar species or peak fire ages resulting in maximum orchid diversity and abundance in similar habitats.
4. Fire ages of 2 to 3 decades are likely to be optimal for most orchids and even longer times may be required for some species. There was no evidence that any orchid species was more productive with shorter fire intervals, even when they tolerate them.
5. Some of the most beautiful and iconic SWAFR orchid species are fire intolerant so require long unburnt areas (Fig. 17).
6. Arson is the main cause of fire in urban Perth and results in major damage to local ecosystems, but lacks effective management (e.g. surveillance when conditions are dangerous, not locating schools in bushland).
7. Severe droughts and groundwater decline magnify fire impacts in banksia woodland but lack sufficient recognition or effective management.
8. Effective weed management in banksia woodland substantially reduces impacts on vegetation due to fire. Post-fire control of grazing by rabbits or other animals is also often required, but rarely happens.
9. Some orchids are relatively short-lived dynamic species with efficient spread by wind-dispersed seed while others are much more static, forming large clonal groups hundreds or thousands of years old. Orchids in both these categories vary in fire tolerance, but impacts of fire are much more concerning for the latter.
10. Orchid seedling recruitment primarily occurred in long unburnt areas with substantial litter accumulation and relatively few weeds. Landscapes should be managed to protect such areas as refugia for intolerant species and nurseries for orchid seedlings.
11. Understanding ecological impacts from fuel reduction activities requires adequate data on impacts to biodiversity. Evidence that benefits out way their costs is required, especially in areas were fire frequency is already unsustainably high due to arson and climate change.
12. Orchids have a major role in attracting visitors to SWAFR natural areas, but changes to fire management may be required to ensure this continues. These iconic species should be used more often to promote the importance of healthy and diverse ecosystems, especially within urban areas (e.g. friendsofwarwickbushland.com/walk-trails/jarrah-trail).
13. Nature reserve management should aim to maximise diversity of orchids, as well as other flora and fauna, to conserve rare or locally rare species and support sustainable ecotourism.
14. Measuring orchid diversity is a relatively easy and effective way to monitor fire impacts on ecosystem health, and can utilise existing or new data obtained by volunteers. Studies in urban areas can also provide essential knowledge for conserving rare orchids in less accessible areas.
15. Effective management of rare species requires enforceable fire management goals and protocols and effective monitoring that triggers appropriate remedial actions. An alarming case study is provided by the critically endangered Queen of Sheba orchid (*Thelymitra variegata*) which has had catastrophic population losses, with <25 left in the wild. Its largest population has declined considerably following a fuel reduction fire (MCB 2023 unpublished report).

9. Conclusions

This study presents a comprehensive analysis of orchid fire ecology in an urban nature reserve with a very complex 72-year fire history. Comparing orchid distributions and flowering data with fire maps revealed they belong to a continuum from very fire tolerant to fully intolerant species. However, some species that require fire for seed production were most productive in long unburnt areas. This paradox

likely resulted because evolution of orchid fire traits was driven by very infrequent intense fires in the SWAFR, following Gondwanan origins of plant fire traits in the Cretaceous (Lamont & He 2012). Consequently, orchid habitats require substantial areas with a fire age greater than 20 years to maintain sustainable populations, at least in banksia woodland. This study includes representatives of the four most important genera of Australian terrestrial orchids, so some conclusions can be extrapolated to habitats where orchid fire responses are unknown. Research in an urban reserve provided essential tools for management of rare species elsewhere, but further research is required to understand orchid fire ecology in Australia and globally.

Results of this study suggest that orchid diversity can be threatened by current fire regimes in Western Australia due to increasing frequencies of managed fires, arson and climate driven extreme fire events (Bradshaw et al. 2018, Bergstrom et al. 2021, Udy et al. 2024). Managing orchids during this crisis requires an understanding of relationships between time since fire and orchid population sizes, as well as their mechanisms for recolonisation of burnt areas. Even though pyrogenic flowering can lead to amazing orchid displays in the SWAFR, the harm caused by fire to orchids is substantially greater than its benefits overall. The intensity, frequency and timing of fires is also important, and unseasonal fires have major impacts on some species. Orchid fire ecology is closely linked to other key aspects of their ecology and biology, such as tuber depth, clonality, dispersion and disturbance tolerance. These traits reveal an ecological spectrum which allows orchids to be classified into distinct fire risk categories summarised as fire tolerance indices (e.g. FRI and FAST). These indexes should also help predict elevated risks in the future from changing fire regimes due to climate change and human activities. Quantification of orchid life history traits (as standardised indexes) also revealed a complex network of interactions which is the key to understanding Australian orchid ecology.

The SWAFR has wider orchid functional diversity than most other regions, including more species with complex fire response traits. These responses are deeply integrated into their biology and ecology, as is typical of SWAFR plants (Brundrett 2021). While, some orchids are remarkably resilient to fire, others are highly vulnerable, so fire must be carefully managed in their habitats. This requires protection of long unburnt areas as refugia for intolerant orchid species and nurseries for their seedlings. Knowledge about fire tolerance and other key aspects of orchid ecology is often lacking, but tools provided here can be used to fill these knowledge gaps.

Acknowledgements
Special thanks to Karen Clarke for patience, joining me on many walks through the study site to discover local biodiversity. I am also very grateful to many others for help locating orchids, especially Tim Hodgkins and other Friends of Warwick Bushland, as well as City of Joondalup staff.

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Tables

Table 1. Orchid species in this study with key biological and ecological characteristics from pre-existing data.

Table 2. Direct effects of fire on flowering, seed set and survival of 17 orchid species.

Table 3. Indirect effects of fire on abundance of 17 orchid species with numbers of plants and groups counted (FAST is fire age safe threshold).

Table 4. List of traits linked to fire responses used in Table 5 with explanations and data sources.

Table 5A. Orchid fire responses on a unified scale: rare or absent (-3), greatly decreased / major impacts (-2), decreased / minor impacts (-1), neutral / negligible impacts (0), increased / minor benefits (1), greatly increased / major benefits (2), fire opportunist (3). Fire responses are based on data in Tables 1-3, as explained in Table 4.

Table 5B. Orchid fire trait indexes (B) with a common scale (0-10) based on Tables S1-S5 as explained in Table 4.

Table 6. Summary of reproductive and ecological traits and fire tolerance categories for orchids in the study (RAB - rare or absent after fire, FPF - fire promoted flowering).

Table 7A. Correlation matrix for fire response indexes or traits for all orchid species.

Table 7B. Species correlation matrix comparing relative abundance of common species.

Table S2. Summary of data from 30 transects used or comparisons of 17 orchid species abundance and distribution patterns in recently burnt (2.2 km total) or long unburnt (2.3 km) areas.

Table S3. Fire history data for groups of 17 orchids used to calculate fire response indexes.

Table S4. Data and calculations and data for clonality, tuber size, lifespans, etc. for Table 5.

Table S5. The size, type and number of tubers formed annually for 17 orchid species.

Figures

Figure 1. Orchid species included in study arranged by flowering sequence from autumn to early summer. **A** *Leporella fimbria.* **B** *Pheladenia deformis*. **C** *Pterostylis orbiculata*, **D** *Pyrorchis nigricans*, **E** *Caladenia flava*, **F** *Pterostylis ectypha*, **G** *Leptoceras menziesii*, **H** *Diuris magnifica*, **I** *Elythranthera emarginata*, **J** *Caladenia Arenicola*, **K** *Thelymitra crinita*, **L** *Thelymitra macrophylla*, **M** *Thelymitra graminea*, **N** *Thelymitra benthamiana*, **O** *Disa bracteata*, **P** *Microtis media*, **Q** *Thelymitra fuscolutea*.

Figure 2. A. History of major fires in Warwick Bushland between 1973 and 2023 with colour shading by decade from the most recent in red to oldest in blue. **B**. Map summarising the total number of fires in each areas using a 25 m grid. **C**. Map of time since the most recent fire using a25 m grid. **D**. Location or Warwick Bushland in the Perth Metropolitan region of Western Australia and in Australia (inset). Map imagery is by Google

Figure 3. Fire history data for Warwick Bushland summarising data in Figure 2. Annual fire totals (**A**) and fire frequency (**B**) by year, or fire frequency (**C**) and fire age (**D**) by area.

Figure 4. An intense summer arson fire in 2022 (**A**) with water bomber (**B**). Winter fuel reduction burn (**C**). Leaf damage to orchids by unseasonal fire in late autumn for *Leporella fimbria* (**D**) and *Pyrorchis nigricans* (**E**). **F.** Scorching of *Thelymitra macrophylla* by a winter fuel reduction burn. **G**. *Pterostylis orbiculata* shoots are initiated several months before emerging. **H**. *Caladenia flava* seed capsules after fire. **I**. *Pheladenia deformis* seed formed after fire. Seedlings of *Diuris magnifica* (**J**), *Thelymitra* sp. (**K**) and *Disa bracteata* on wood in a long unburnt area (**L**). **M**. *Pterostylis orbiculata* seedings three years post-fire.

Figure 5. The distribution and survival of ~1000 monitored groups of 17 orchids relative to fire age (**A**) and recent fire frequency (**B**). **C.** The distribution of sun orchids (*Thelymitra* spp.) relative to recent fires. Locations where sun

orchids were killed or survived fires in 2022 or 2023 are indicated by circles (Tm = *Thelymitra macrophylla*, Tg = *T. graminea*). **D**. Transects used to measure orchid abundance and diversity relative to fire history.

Figure 6. Changes over time in abundance of flowering *Thelymitra macrophylla* groups showing impacts of multiple very hot summer fires (F1, F2) and a cooler winter fuel reduction burn (FR) relative to unburnt groups of similar age nearby.

Figure 7. Fire effects on plant growth (**A**) and flower production per plant (**B**) or group (**C**) for common orchid species comparing long unburnt and post-fire areas after the major fire in 2022.

Figure 8. Effects of fire on overall pollination rates of eight common orchid species summarised per flower (**A**), plant (**B**) or group (**C**).

Figure 9 A-F. Effects of plant density and fire on pollination outcomes for six orchid species that were sufficiently common in both long unburnt and post-fire areas after a major fire in 2022 (see labels).

Figure 10. Detailed analysis of (**A**) fire impacts on pollination of *Pheladenia deformis* (bluebeard orchid), changes to flowering capacity over time after fire (**B**) and transitions between vegetative, flowering and absent or dormant plants (**C**).

Figure 11. A. The relative abundance of 17 orchids in recently burnt (<3 years) or long unburnt (>20 years) areas on 30 transects (4.5 km x 10 m total). **B**. The proportion of individuals or groups of orchids found in long unburnt areas on these transects. **C**. The relative proportions of all orchid plants or groups (corrected for transect length) and average group sizes in recently burnt or unburnt areas.

Figure 12 A-H. The abundance of eight common orchids relative to time since fire on transects (see labels). Regression equations and correlation probabilities are also provided.

Figure 13. Orchid density (**A**) and diversity (**B**) relative to time since fire on transects corrected for differences in transect length.

Figure 14. Data from monitoring the average fire frequency and fire age where orchids occur. Data are from Table S4 and species name codes are provided in Table 1. The average fire history for the entire site is shown for comparison (red dot).

Figure 15. Overall fire tolerance rankings for 17 orchid species using combined index data from Table 5.

Figure 16. Correlations between tuber depth or size (**A, B**) or key ecological trait indices (**C-F**) with the overall fire response index for 17 orchid species (index definitions are in Table 4, data are from Table 5).

Figure. 17. The blue sun orchid (*Thelymitra macrophylla*) requires areas without fire for 15 to 30 or more years to thrive. This orchid attracts many visitors to Warwick Bushland, and is a focus of education activities (friendsofwarwickbushland.com/walk-trails/jt020).

Figure S1. *Caladenia flava* flowering trends over two years. Graphs **A-D** compare four measures of plant productivity in burnt or unburnt areas on subsequent years.

Figure S2. The productivity of groups of eight common orchids relative to time since fire measured by the number of flowering plants (**A-I**). The frequency distribution of fires by area is shown for comparison (**J**).

Figure S3. Relationships between frequency of all fires and flowering productivity of eight locally common orchids (**A-I**). The frequency distribution of fires by area is shown for comparison (**J**).

Figure S4. The productivity of groups of nine common orchids (**A-I**) relative to the frequency of recent fires (2000-2023). The frequency distribution of fires by area is shown for comparison (**J**).

Figure S5. Additional trait correlation graphs (index definitions are in Table 4, data are from Table 5). **A.** Estimated lifespan and colonisation capacity. **B**. Aggregation and dispersion.

Table 1. Orchid species in this study with key biological and ecological characteristics from pre-existing data.

Orchid	Common Name	Label	Pollination syndrome	Flowering time (order)	Post-fire flowering	Flowers per spike	Capsules per flower	Organic matter in soil	Litter cover	Shade tolerance	Local abundance
Caladenia arenicola	Carousel spider	Ca	SD	Sep-Oct (10)	neutral	1.4	0.16	Low or medium	low	low	Scattered, stable
Caladenia flava	Cowslip	Cf	VD	Aug-Oct (5)	increased	2.0	0.17	High or medium	medium	medium	Common most areas
Disa bracteata	South African orchid	Db	SP	Oct-Nov (160	none	26.3	0.57	high	low	low	Fairly common in some areas
Diuris magnifica	Pansy	Dm	VD	Aug-Oct (8)	neutral	3.6	0.05	various	medium	low	Very common most areas
Elythranthera brunonis	Enamel	Eb	VD	Sep-Oct (9)	neutral	1.8	0.15	High or medium	medium	medium	Scattered
Leporella fimbria	Hare	Lf	VD	Apr-Jun (1)	increased	1.7	0.34	low or medium	low	high	Common, scattered
Leptoceras menziesii	Rabbit	Lm	SD	Aug-Sep (7)	obligate	1.3	0.60	High or medium	medium	medium	Uncommon
Microtis media	Mignonette	Mm	SP	Oct-Nov (17)	none	35.8	0.88	High or medium	low	low	Scattered, weedy
Pheladenia deformis	Bluebeard	Bb (Pd)	VD	Jun-Aug (2)	increased	1.0	0.11	Low	low	low	Common, scattered
Pterostylis ectypha	Short-eared snail	Pe	SD	Aug-Sep (6)	none	4.0	0.40	High	high	high	Scattered
Pterostylis orbiculata	Banded Greenhood	Po	SD	Aug-Sep (3)	neutral	1.0	0.42	High	high	high	Very common
Pyrorchis nigricans	Red Beak	Pn	VD	Aug-Sep (4)	obligate	3.5	0.08	high or low	high	medium	Very common
Thelymitra benthamiana	Leaopard	Tb	SP	Aug-Sep (14)	no data	13.5	0.03	High or medium	medium	low	Localised, increasing
Thelymitra crinita	Blue lady	Tc	VD	Aug-Sep (11)	no data	3.9	0.14	high or medium	medium	medium	Localised, increasing
Thelymitra fuscolutea	Chestnut sun	Tf	VD	Aug-Sep (18)	no data	2.4	0.88	high	medium	low	Localised, stable
Thelymitra graminea	Small Blue Sun	Tg	VD	Aug-Sep (13)	none	6.7	0.08	high	high	medium	Localised, increasing
Thelymitra macrophylla	Blue Sun	Tm	VD	Aug-Sep (12)	rare	6.6	0.06	high	high	medium	Common and increasing
Main data sources			Brundrett et al 2024	Brundrett 2019	Brundrett 2021	Brundrett 2019	Brundrett 2019	Brundrett 2014	Brundrett 2014	Brundrett 2014	Brundrett 2019

Pollination Syndromes: SD = sexual deception, VD = visual deception, SP = self-pollination

Table 2. Direct effects of fire on flowering, seed set and survival of 17 orchid species.

Orchid	Main data year	Other fire data	Pre-fire data (years)	Monitored plants each year	Flowering plants (groups) unburnt	Flowering plants (groups) post-fire	Total spikes 2022	Total flowers 2022	Total capsules 2022	Capsules per flower unburnt	Capsules per flower post-fire	Plants (groups) lost to fire	Notes
Caladenia arenicola	2022	2023	8	8-87	91 (41)	12 (8)	76	108	25	26%	10%	none	Good seed post-fire
Caladenia flava	2022		4	12-68	61 (17)	144 (23)	187	395	80	27%	19%	none	Fire promoted flowering
Disa bracteata	2022		5	13-134	134 (60	0 (0)	134	3338	1935	58%	0%	2 (12)	One plant found after fire
Diuris magnifica	2022	2023	6	127-670	428 (43)	91 (7)	519	1882	104	5%	8%	few	Minor fire effects
Elythranthera brunonis	2022		7	5-63	33 (6)	9 (2)	42	75	11	18%	0%	none	Equally common post fire
Leporella fimbria	2022	2018	11	64-245	197 (14)	201 (11)	398	685	301	38%	50%	none	Only flowering plants counted, fire promoted flowering
Leptoceras menziesii	2022	2008	NA	145	1 (2)	54 (2)	54	68	44	0%	65%	none	Near obligate fire flowering (also responded to soil disturbance)
Microtis media	2022		4	7-148	193 (4)	0 (0)	193	6870	6184	90%	0%	all	Fire intolerant self-pollinating orchid
Pheladenia deformis	2022	2000, 2021, 2023	4	39-46	366 (126)	308 (78)	627	627	77	2%	16%	none	Fire promoted flowering
Pterostylis orbiculata	2022		3	67-284	224 (37)	151 (24)	395	1537	843	60%	44%	few	Stunted after fire
Pyrorchis nigricans	2022	2019	NA	128-2133	1 (1)	2133 (41)	2133	7367	592	3%	8%	none	Near obligate fire flowering
Thelymitra fuscolutea	2022	2023	5	28-335	323		178	1220	16	1%	0%	none	Plants found post-fire are close to burn edges
Thelymitra graminea	2022		2	33-149	149 (12)	0 (0)	148	842	74	9%	0%	43 (2)	fire intolerant
Thelymitra macrophylla	2023	2019, 2022	11	124-698	1094	8 (5)	1102	17017	631	5%	11%	62 (8)	Plants found post-fire close to burn edges
Total					**2971 (670)**	**3111 (201)**	**6186**	**42031**	**10917**	**24%**	**16%**	**115 (12)**	

Table 3. Indirect effects of fire on abundance of 17 orchid species with numbers of plants and groups counted (FAST is fire age safe threshold).

	Monitoring fire age (years)			Transect fire age (years)			FAST	Seedlings observed		Number of plants (groups)	
Orchid	**Minimum**	**Peak**	**Maximum**	**Minimum**	**Peak**	**Maximum**	**years**	**Long unburnt**	**Recent fire**	**Transects**	**Monitoring**
Caladenia arenicola	0	30	40	2	30	30	15	7		28 (15)	415 (44)
Caladenia flava	0	35	40	0	15	40	8	2		3454 (709)	1299 (42)
Disa bracteata	5	30	40	15	30	40	23	24		109 (45)	578 (23)
Diuris magnifica	0	30	40	0	30	40	15	9		1167 (304)	4043 (41)
Elythranthera brunonis	1	5, 25	40	2	15	40	9			53 (19)	355 (44)
Leporella fimbria	0	5, 35	40	0	30	40	15			11144 (24)	5146 (42)
Leptoceras menziesii	0	10	30	2	30	30	10			957 (3)	163 (16)
Microtis media	5	30	40	16	25	>70	20	5		151 (2)	663 (21)
Pheladenia deformis	0	5, 30	>70	0	20	40	10		2	53 (46)	1053 (395)
Pterostylis ectypha	5	30	>70	16	40	>70	20	5		102 (22)	903 (16)
Pterostylis orbiculata	0	25	>70	0	40	40	10	36	125	1191 (245)	2204 (69)
Pyrorchis nigricans	0	20	30	0	40	40	25			11653 (99)	2263 (62)
Thelymitra benthamiana	15	25	40	16	30	40	20	90		127 (6)	653 (12)
Thelymitra crinita	15	25	40				20	36		14 (3)	43 (12)
Thelymitra fuscolutea	1*	30	40	0	40	38	20			37 (11)	1363 (49)
Thelymitra graminea	20	30	>70				25			10 (1)	359 (15)
Thelymitra macrophylla	1*	20	>70	3*	30	>70	20	32		737 (115)	6104 (42)
Notes or totals	*fire edge	Fig. S2			Fig. 12			246	125	31007 (1676)	27607 (945)

Table 4. List of traits linked to fire responses used in Table 5 with explanations and data sources.

	Trait or response category	Data sources and methods	Data sources
A	**Fire responses**		
1	Post-fire mortality	Counts of plants and groups absent for three years after fire	Figs. 5c, 6
2	Abundance relative to time since fire	Group sizes and locations joined with map of all fires	Figs. 11-13
3	Abundance relative to fire frequency or recent fires	Group sizes joined with map of all fires or recent fires (post 1999)	Figs. S3, S4
4	Susceptibility to unseasonal fires	Counts of orchids lost to fire in late autumn (when shoots are emerging)	Table 2, Fig. 4D, E
5	Post-fire flowering promotion or reduction	Ration of post-fire relative to long unburnt areas on the same year	Fig. 7B, C, Fig. 11
6	Plant size after fire vs long unburnt areas	as above	Fig. 7A
7	Pollination and seed production fire response	as above	Table 1
6	Fire intolerance	Consistent absence from recently burnt areas	Table 3
9	Fire response summary	Sum of all fire traits over 6 intervals from 18 to -18, 0 = neutral	Table 5
10	Fire age safe threshold (FAST)	Median of minimum and peak habitat age post-fire from abundance in monitored areas and transects	Table 3, Figs. 12, S2
B	**Reproduction and ecology**		
11	Pollination syndrome	From observations and references	Brundrett et al 2024
12	Pollination efficacy	Average pollination per flower from 5-10 years data from the same area	Brundrett 2019
13	Average seed production per spike	as above by per spike (flowering plant)	Figs. 8, 9
14	Availability of pollinators	Relationship between plant density and pollination rate from graphs	Fig. 9
15	Seed production capacity	Long-term averages measured in unburnt areas (except for fire-flowering species)	Table 1, Fig. 8
16	Seedling recruitment	Numbers of tiny seedlings or small young plants observed	Table 3, Fig. 4
17	Clonality	Relative abundance of in clonal groups relative to individual plants	Table S3
18	Aggregation	Proportion of plants in groups relative to scattered individuals	Table S3
19	Dispersion	Ratio of relative numbers of orchids found by uniform (transect) sampling to targeted sampling to maximise species included	Table
19	Recolonisation capacity after severe disturbance	Data from a time-course study in a bauxite mine from bare soil	Collins & Brundrett 1995
20	Typical plant lifespan	Proportion of groups or plants lost during long-term monitoring of unburnt areas	Preliminary data
21	Tuber size and number per plant	10 or more plants measured non-destructively	Table S3
22	Tuber crown bud depth in soil	As above	Table S3

Table 5A. Orchid fire responses on a unified scale: rare or absent (-3), greatly decreased / major impacts (-2), decreased / minor impacts (-1), neutral / negligible impacts (0), increased / minor benefits (1), greatly increased / major benefits (2), fire opportunist (3). Fire responses are based on data in Tables 1-3, as explained in Table 4.

Orchid species	Fire mortality	Rare or absent in after fire	Unseasonal fire risk	Flowering capacity post-fire	Plant size post-fire	Availability of pollinators post-fire	Seed production post-fire	Abundance & time since fire	Abundance & fire frequency	Overall fire response
Caladenia arenicola	0			1	1	2	-1	-1	1	**3**
Caladenia flava	0			2	0	2	2	1	0	**7**
Disa bracteata	-3	-3		-3		Selfing	ND	-3	-3	**-15**
Diuris magnifica	0			-1	-2	-1	0	-2	1	**-5**
Elythranthera brunonis	0			1	-1	-1	-1	1	-1	**-2**
Leporella fimbria	0		-3	3	1	0	0	2	2	**5**
Leptoceras menziesii	0			3	3	1	3	2	1	**13**
Microtis media	-3	-3		-3		Selfing	ND	-3	-3	**-15**
Pheladenia deformis	0			2	2	2	2	1	2	**11**
Pterostylis ectypha	-3	-3	-3	-3		ND	ND	-3	-3	**-18**
Pterostylis orbiculata	-1		-3	-1		-1	-1	-1	-1	**-9**
Pyrorchis nigricans	0		-2	3	3	2	3	-1	2	**10**
Thelymitra benthamiana	ND	-3		ND	ND	Selfing	ND	-2	-2	**-7**
Thelymitra crinita	ND	-3		ND	ND		ND	-3	-2	**-8**
Thelymitra fuscolutea	0			1	-1	ND	-1	-2	-1	**-4**
Thelymitra graminea	-3	-3		-3	-3	ND	ND	-3	-3	**-18**
Thelymitra macrophylla	-2	-2	-2	-2	-1	1	-1	-3	0	**-12**
Total or average	**-1.00**	**7**	**5**	**0.00**	**0.18**	**0.70**	**0.45**	**-1.18**	**-0.59**	**-3.76**
Data sources and notes	Table 2	Table S3	see text	ND = no data		Fig. 9	Table 1, Fig. 8	Figs. 11, 13	Fig. 13	-64

Selfing = self-pollinating, ND = no data due to absence from burnt areas

Table 5B. Orchid fire trait indexes (B) using a unified scale (0-10) based on data in Tables S1-S5 as explained in Table 4.

Orchid species	Flower production index	Seed production index	Colonisation index	Clonality index	Aggregation index	Lifespan index	Dispersion index	Tuber radius (mm)	Crown bud depth (mm)
Caladenia arenicola	2	6	7	0	4	5	2	8.0	123
Caladenia flava	1	4	1	9	6	9	8	4.4	124
Disa bracteata	9	10	10	1	2	1	4	9.0	36
Diuris magnifica	3	5	5	9	6	8	6	14.5	48
Elythranthera brunonis	2	4	6	0	3	7	4	4.5	67
Leporella fimbria	1	1	1	10	8	9	8	4.3	28
Leptoceras menziesii	1	2	3	10	7	8	10	5.3	54
Microtis media	10	9	10	0	3	1	5	4.2	29
Pheladenia deformis	1	1	7	4	2	4	2	5.0	84
Pterostylis ectypha	1	3	8	8	8	2	3	2.5	37
Pterostylis orbiculata	3	9	6	9	7	5	7	7.4	63
Pyrorchis nigricans	4	6	1	10	10	10	9	7.3	62
Thelymitra benthamiana	8	6	7	0	3	4	4	7.9	45
Thelymitra crinita	6	6	6	0	3	5	6	10.0	35
Thelymitra fuscolutea	2	9	4	4	3	6	1	6.0	52
Thelymitra graminea	7	7	8	0	4	3	1	6.8	29
Thelymitra macrophylla	3	3	7	5	5	4	3	9.4	44
Total or average	**3.76**	**5.35**	**5.71**	**4.65**	**4.94**	**5.35**	**4.88**	**6.85**	**56.47**
Data sources and notes	Table S1	Table S1	Table S2	Table S4	Table S4	Table S3	Table S4	Table S5	Table S5

Table 6. Summary of reproductive and ecological traits and fire tolerance categories for orchids in the study (RAB - rare or absent after fire, FPF - fire promoted flowering).

Orchid	Lifespan / aggregation	Primary means of reproduction	Seedlings or new plants	Disturbance response	Fire response category	FRI	FAST	Fire traits / responses	Ecological traits and fire responses	Colonisation potential in new habitats
Caladenia arenicola	medium / low	seed	uncommon	weak positive	Minor benefits	**3**	**15**	very deep tubers	highly resilient, very deep tubers	colonised slowly (similar species)
Caladenia flava	long / medium	dropper tubers, seed	not seen	negative	Major benefits	**7**	**8**	FPF (weak)	more seed after fire	colonised slowly
Disa bracteata	short / low	abundant seed readily germinates	common	strong positive	Fire intolerant	**-15**	**23**	RAB	exotic weed. very rare in burnt areas, seed readily germinates	colonised very rapidly
Diuris magnifica	medium / medium	root tubers, seed	uncommon	weak positive	Minor harm	**-5**	**15**	recovery from tuber pieces	highly resilient, very deep tubers	colonised rapidly (similar species)
Elythranthera brunonis	long / low	seed	not seen	negative	Minor harm	**-2**	**9**		temporary decline after fire	failed to return
Leporella fimbria	long / very high	dropper tubers, seed	not seen	negative	Minor benefits	**5**	**15**	FPF (strong)	more seed after fire	failed to return
Leptoceras menziesii	long / very high	dropper tubers, seed	not seen	negative	Fire required	**13**	**10**	FPF (very strong)	very strongly promoted fire flowering	no data
Microtis media	short / low	seed	common	strong positive	Fire intolerant	**-15**	**20**	RAB	weedy indigenous orchid	colonised very rapidly
Pheladenia deformis	medium / low	seed, tubers	uncommon	weak positive	Major benefits	**11**	**10**	FPF (strong)	most seed produced after fire	spreading locally
Pterostylis ectypha	short / high	tubers, seed	uncommon	positive	Fire intolerant	**-18**	**20**	RAB	Not found in any burnt areas	colonised rapidly (similar species)
Pterostylis orbiculata	medium / high	dropper tubers, seed	very common	weak positive	Major harm	**-9**	**10**	stunted post-fire	First seedlings found 3 years after fire	colonised slowly (similar species)
Pyrorchis nigricans	very long / very high	dropper tubers, seed	not seen	negative	Major benefits	**10**	**25**	PFF (obligate)	Near obligate fire flowering	failed to return
Thelymitra benthamiana	short / low	seed	uncommon	negative	Major harm	**-7**	**20**	no data	avoids burnt areas	colonised rapidly
Thelymitra crinita	medium / low	seed	uncommon	negative	Major harm	**-8**	**20**	no data	many seedlings in 2022	colonised very slowly, rare in restored areas
Thelymitra fuscolutea	medium / low	seed	uncommon	negative	Minor harm	**-4**	**20**	limited data	avoids burnt areas	no data
Thelymitra graminea	short / low	seed	uncommon	negative	Fire intolerant	**-18**	**25**	RAB	all groups lost to fire	no data
Thelymitra macrophylla	medium / medium	seed, tubers	common	negative	Fire intolerant	**-12**	**20**	RAB	some groups lost to fire	Colonised slowly
Notes and data sources	Table 5	Table S3, Brundrett 2019, Pate & Dixon 1982	Table 3	local observations	From FRI	From Table 5		FRI = overall fire response index RAB - rare or absent post fire, FPF - fire promoted flowering, FAST = fire age safe threshold		Post-mining data from Grant & Koch 2003, Collins & Brundrett 2015

Table 7A. Correlation matrix for fire response indexes or traits for all orchid species.

	Fire age safe threshold (FAST)	*Overall fire response index (FRI)*	*Flower production index*	*Seed production index*	*Colonisation index*	*Clonality index*	*Aggregation index*	*Lifespan index*	*Dispersion index*	*Tuber radius (mm)*
Fire age safe threshold	1									
Overall fire response	-0.549	1								
Flower production index	0.628	-0.594	1							
Seed production index	0.451	-0.531	0.679	1						
Colonisation index	0.328	-0.741	0.606	0.419	1					
Clonality index	-0.316	0.453	-0.619	-0.416	-0.706	1				
Aggregation index	-0.033	0.291	-0.452	-0.324	-0.636	0.851	1			
Lifespan index	-0.401	0.764	-0.596	-0.415	-0.950	0.631	0.576	1		
Dispersion index	-0.310	0.501	-0.164	-0.221	-0.650	0.663	0.646	0.641	1	
Tuber radius (mm)	0.234	-0.158	0.260	0.270	0.105	-0.081	-0.126	0.062	-0.010	1
Tuber depth (mm)	-0.580	0.574	-0.489	-0.166	-0.306	0.093	0.000	0.355	0.031	-0.103

Table 7B. Species correlation matrix comparing relative abundance of common species.

	Caladenia flava	*Disa bracteata*	*Diuris magnifica*	*Leporella fimbria*	*Pterostylis orbiculata*	*Pyrorchis nigricans*	*Thelymitra macrophylla*	*Pheladenia deformis*	Total plants	Fire age	All orchids	Plants/ m
Caladenia flava	1											
Disa bracteata	0.300	1										
Diuris magnifica	0.135	0.312	1									
Leporella fimbria	-0.090	-0.043	-0.138	1								
Pterostylis orbiculata	0.296	0.203	-0.046	-0.198	1							
Pyrorchis nigricans	0.136	0.065	-0.065	0.273	0.267	1						
Thelymitra macrophylla	0.526	0.211	0.015	0.454	0.123	0.031	1					
Pheladenia deformis	-0.295	-0.185	-0.022	-0.148	-0.115	-0.185	-0.217	1				
Total plants	-0.009	-0.031	-0.027	0.931	-0.102	0.466	0.376	-0.121	1			
Fire age	0.244	0.376	0.311	0.235	0.446	0.534	0.375	0.016	0.397	1		
All orchids	0.494	0.016	0.256	-0.113	0.190	0.176	0.428	0.091	0.037	0.469	1	
Plants/ m	0.110	0.049	-0.072	0.839	0.038	0.736	0.417	-0.236	0.905	0.514	0.084	1
Species / m	0.463	0.249	0.019	0.029	0.345	0.465	0.564	-0.306	-0.008	0.503	0.446	0.335

Figure 1. Common orchids in Warwick Bushland

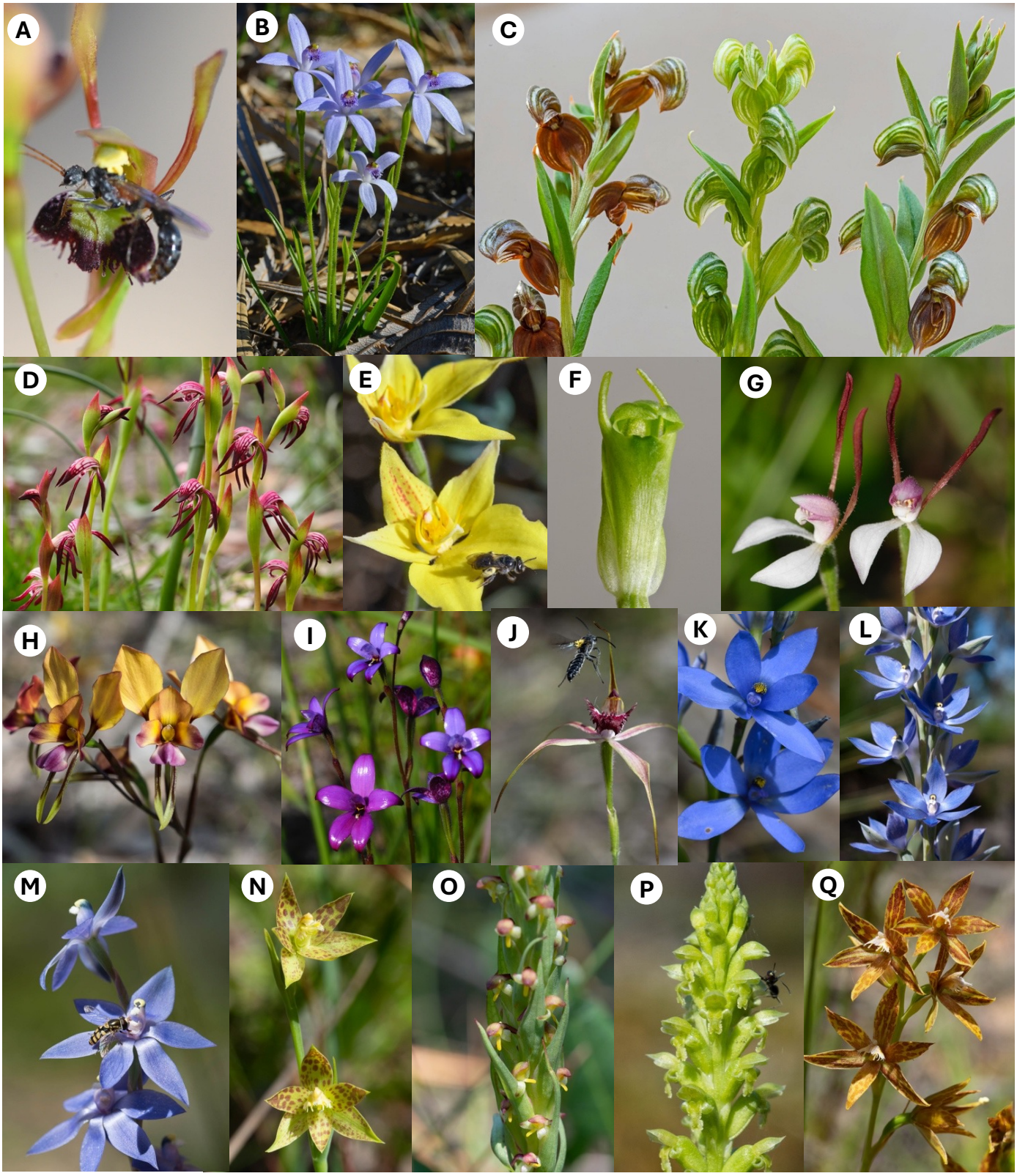
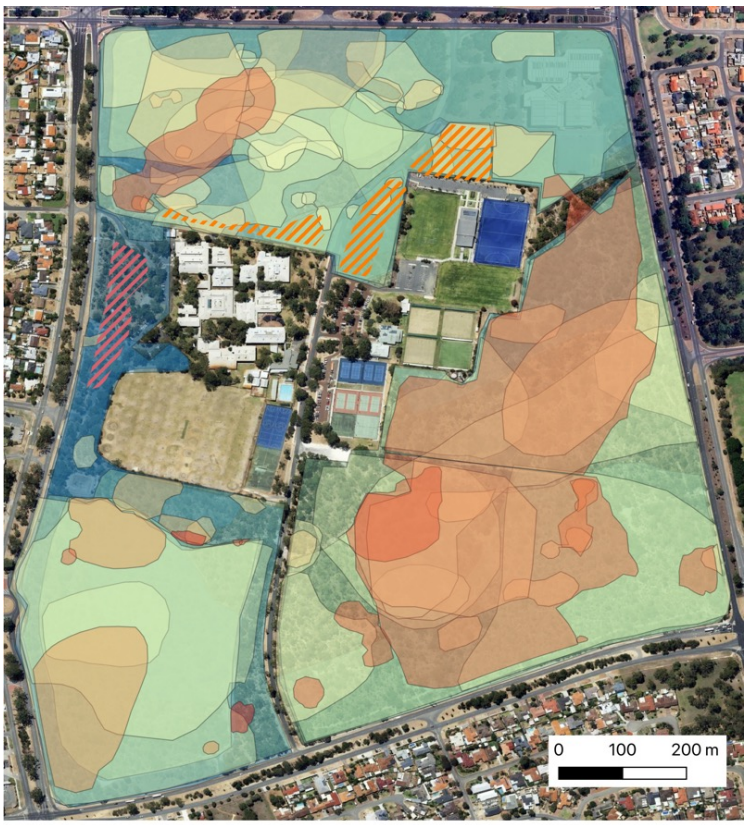


Figure 2. Warwick Bushland Fire History (C & D are 25m grids)

A. Location

B. Major fires after 1952

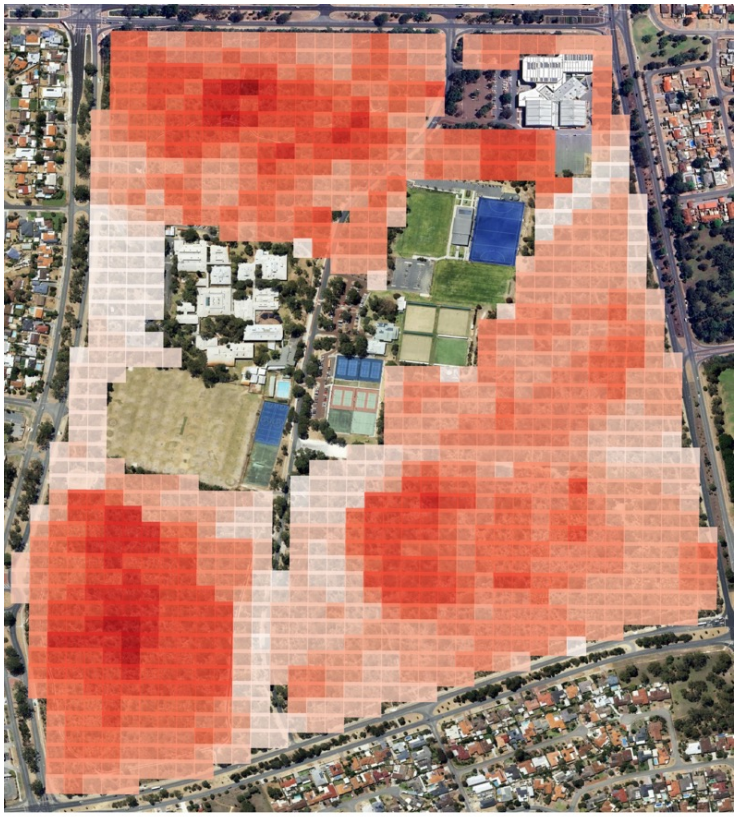


Fuel Reduction Burns
- 2016
- 2019

Fire History
- 1973 - 1978
- 1978 - 1983
- 1983 - 1988
- 1988 - 1993
- 1993 - 1998
- 1998 - 2003
- 2003 - 2008
- 2008 - 2013
- 2013 - 2018
- 2018 - 2023
- 2023 - 2028

Google Satellite

C. Number of fires after 1952

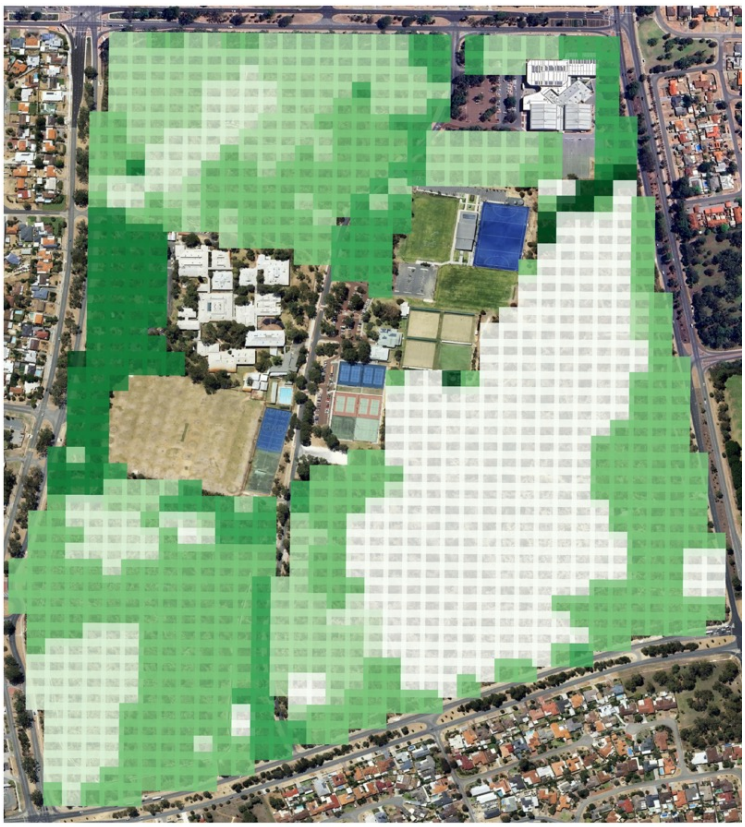


0 100 200 m

Number of Fires
- 1
- 2
- 3
- 4
- 5
- 6
- 7
- 8
- 9
- 10

Google Satellite

D. Years since a major fire

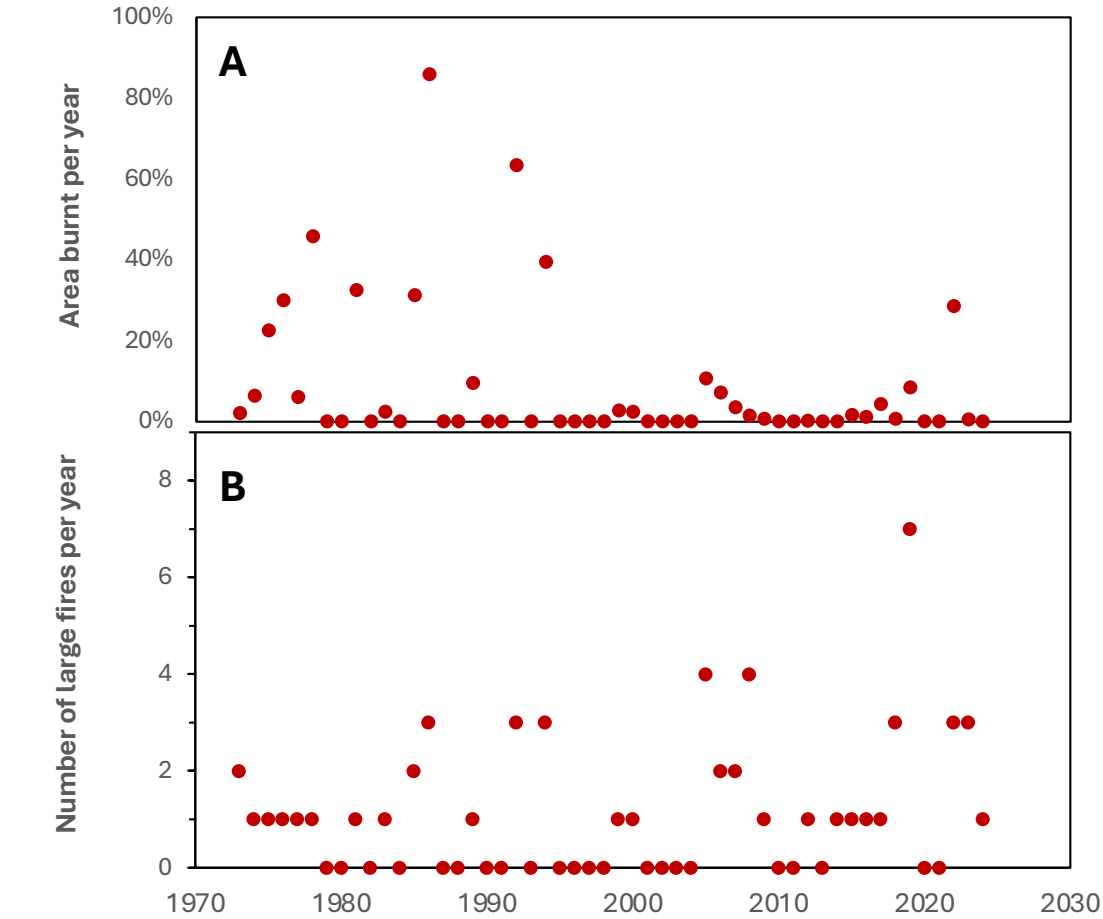


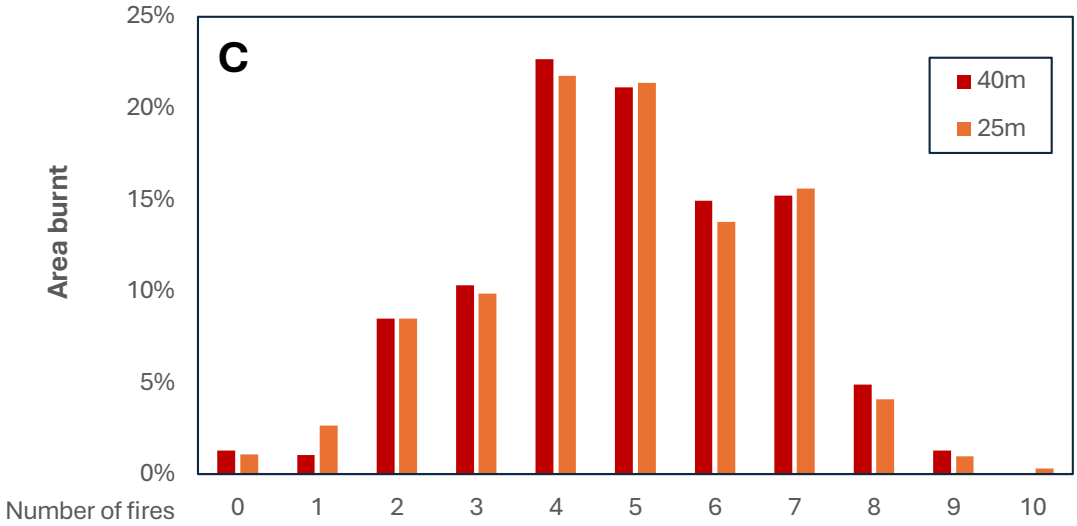
0 100 200 m

Fire Age
- 0 - 2
- 2 - 12
- 12 - 24
- 24 - 32
- 32 - 39
- 39 - 49
- 49 - 72

Google Satellite

Figure 3. Fire area totals and frequency in Warwick Bushland





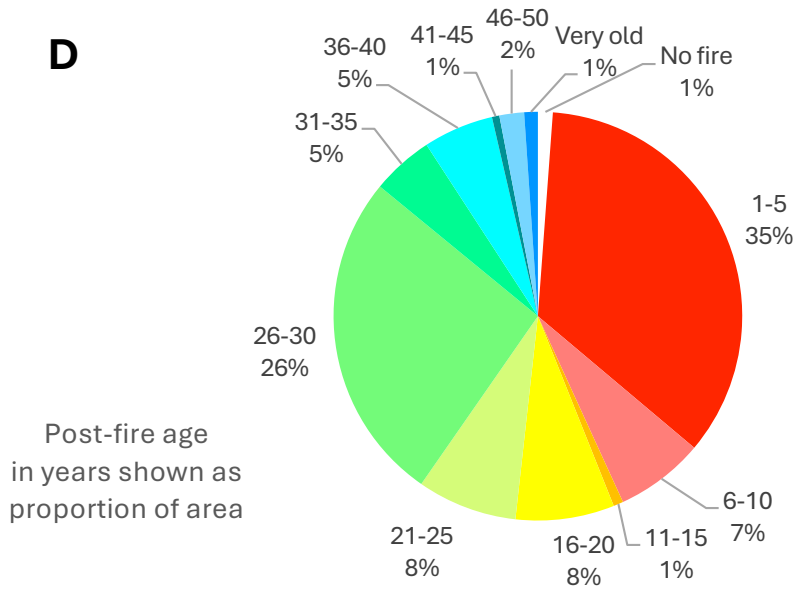
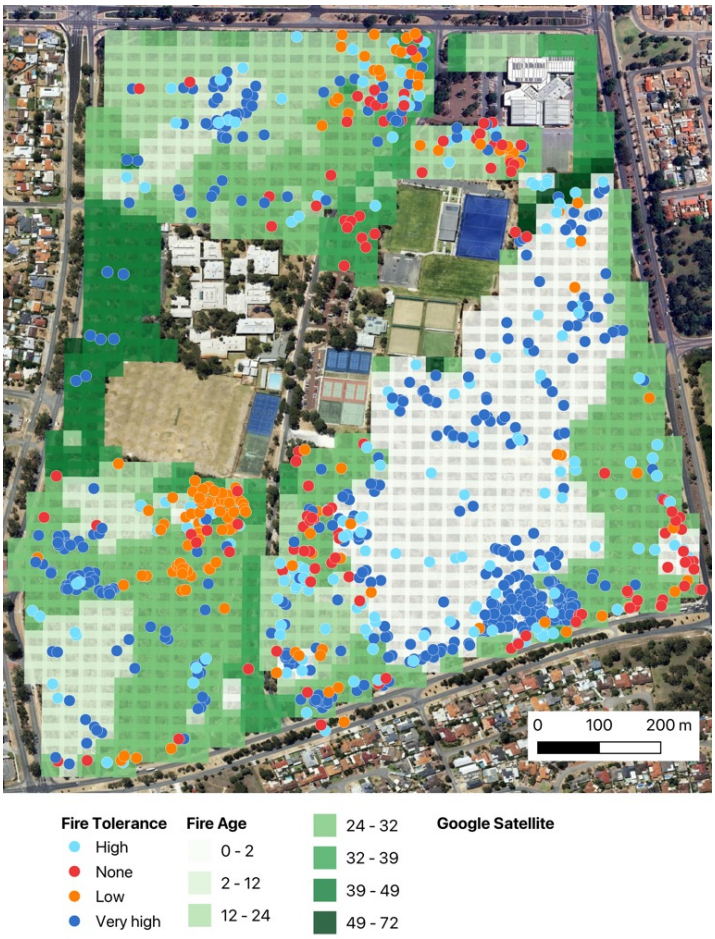


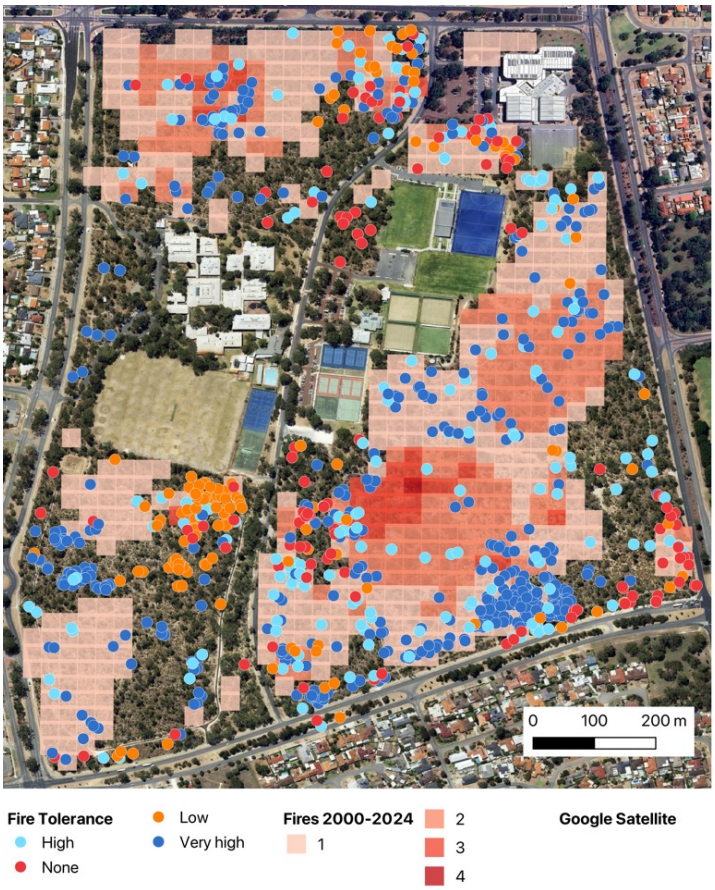
Figure 4. Observations

Figure 5. Locations of orchids relative to recent fires

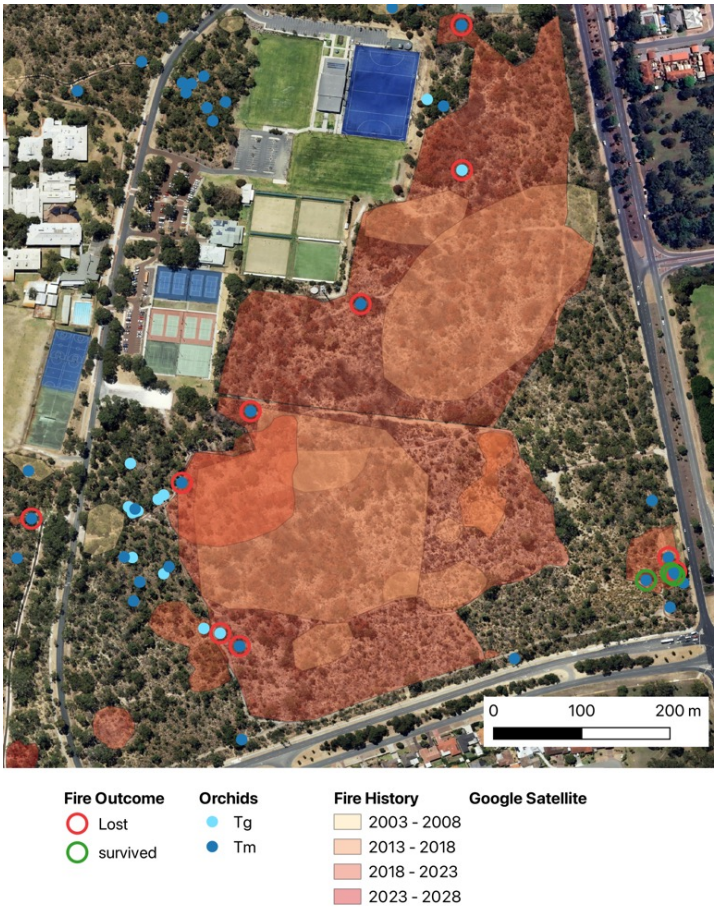
A. Orchid distributions and time since fire



B. Orchid distributions and recent fires (2000-)



C. Sun orchids impacted by recent fires



D. Transect locations

Figure 6. ***Thelymitra macrophylla*** **fire impacts and control groups**

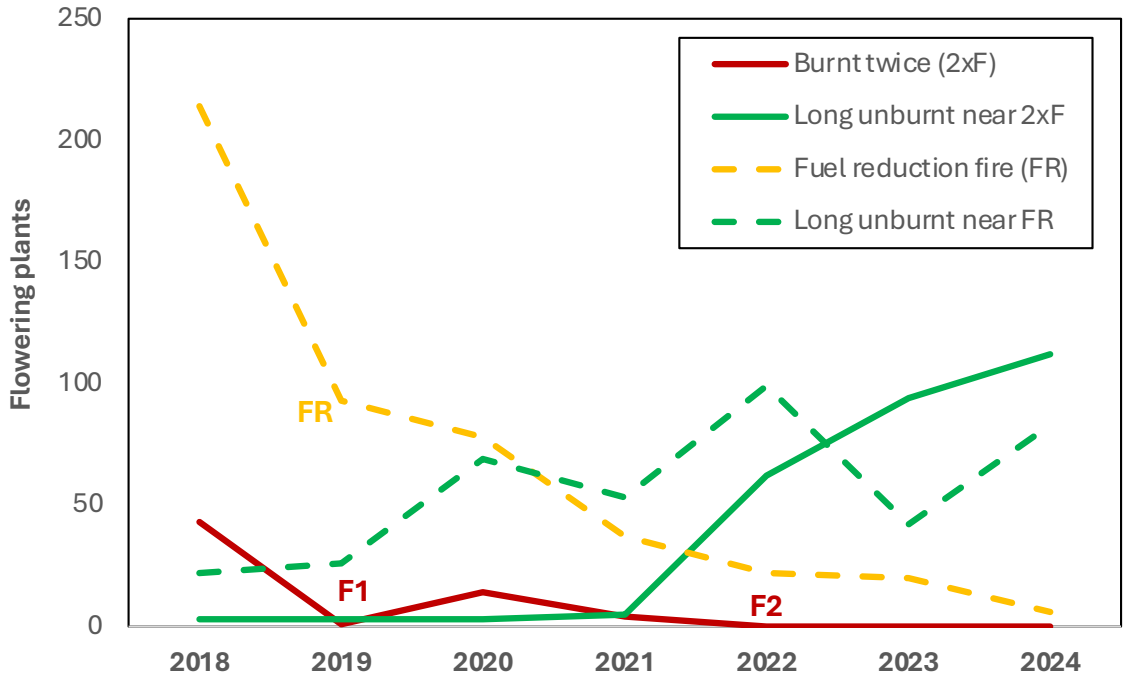
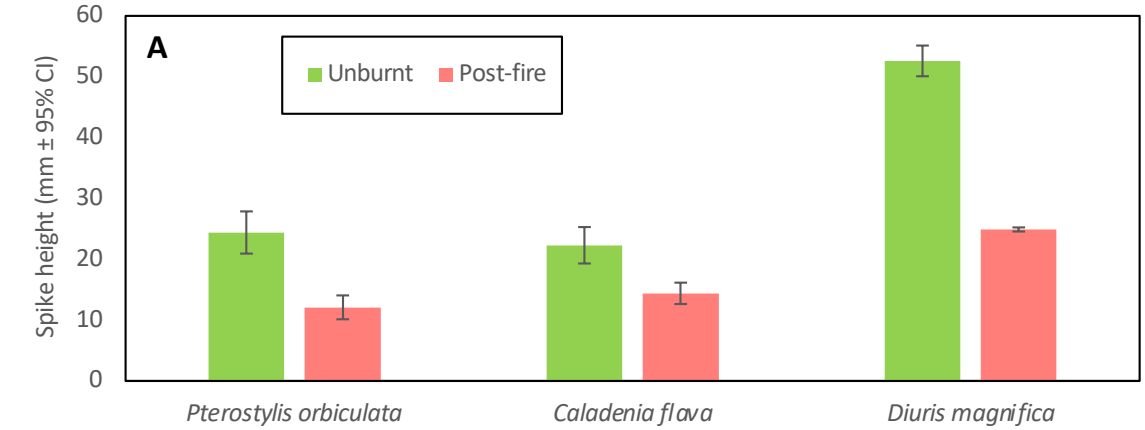
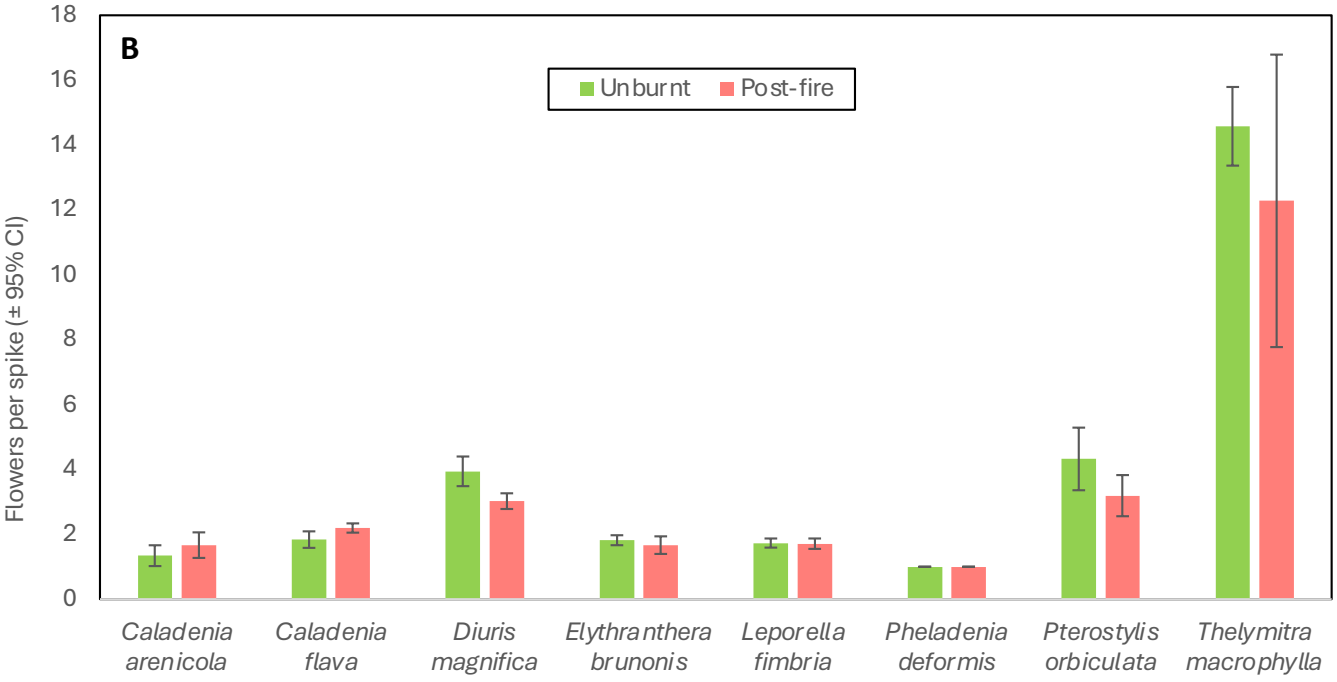


Figure 7. Fire effects on plant growth and flower production





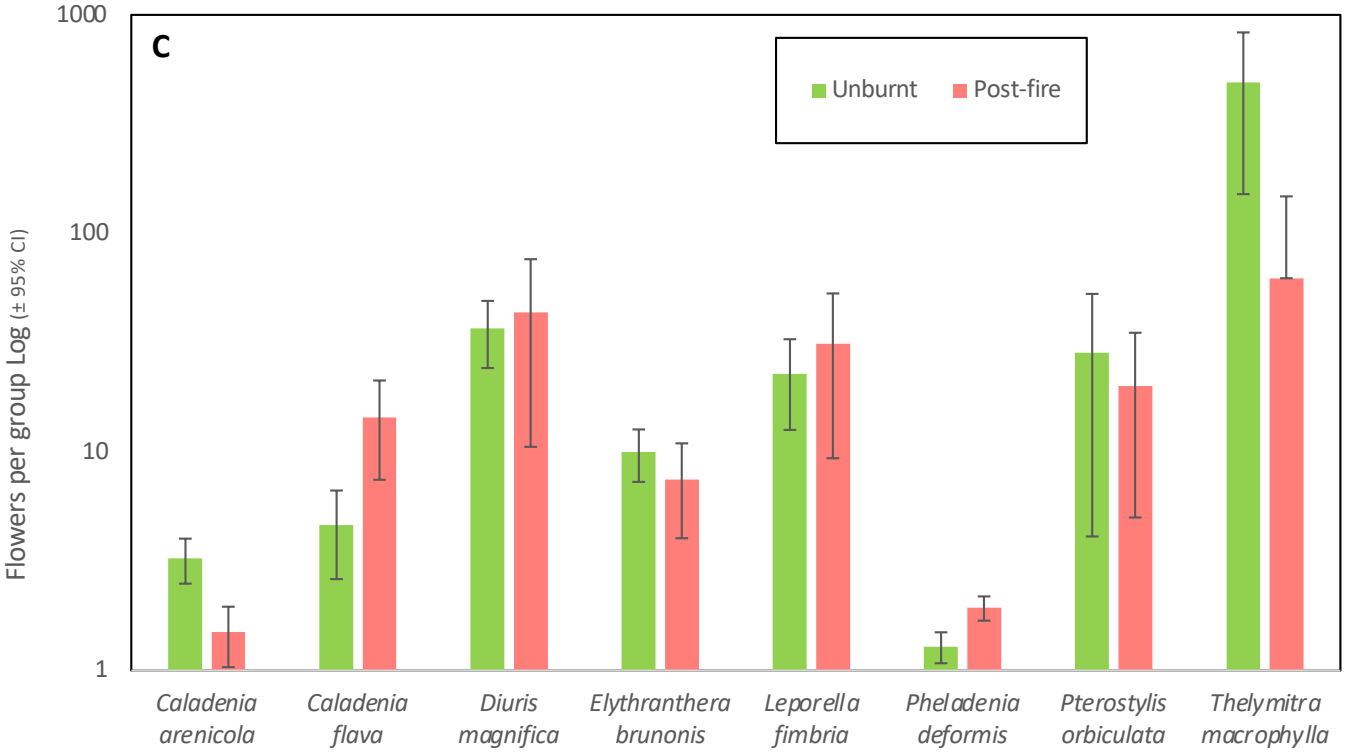


Figure 8. Fire effects on pollination

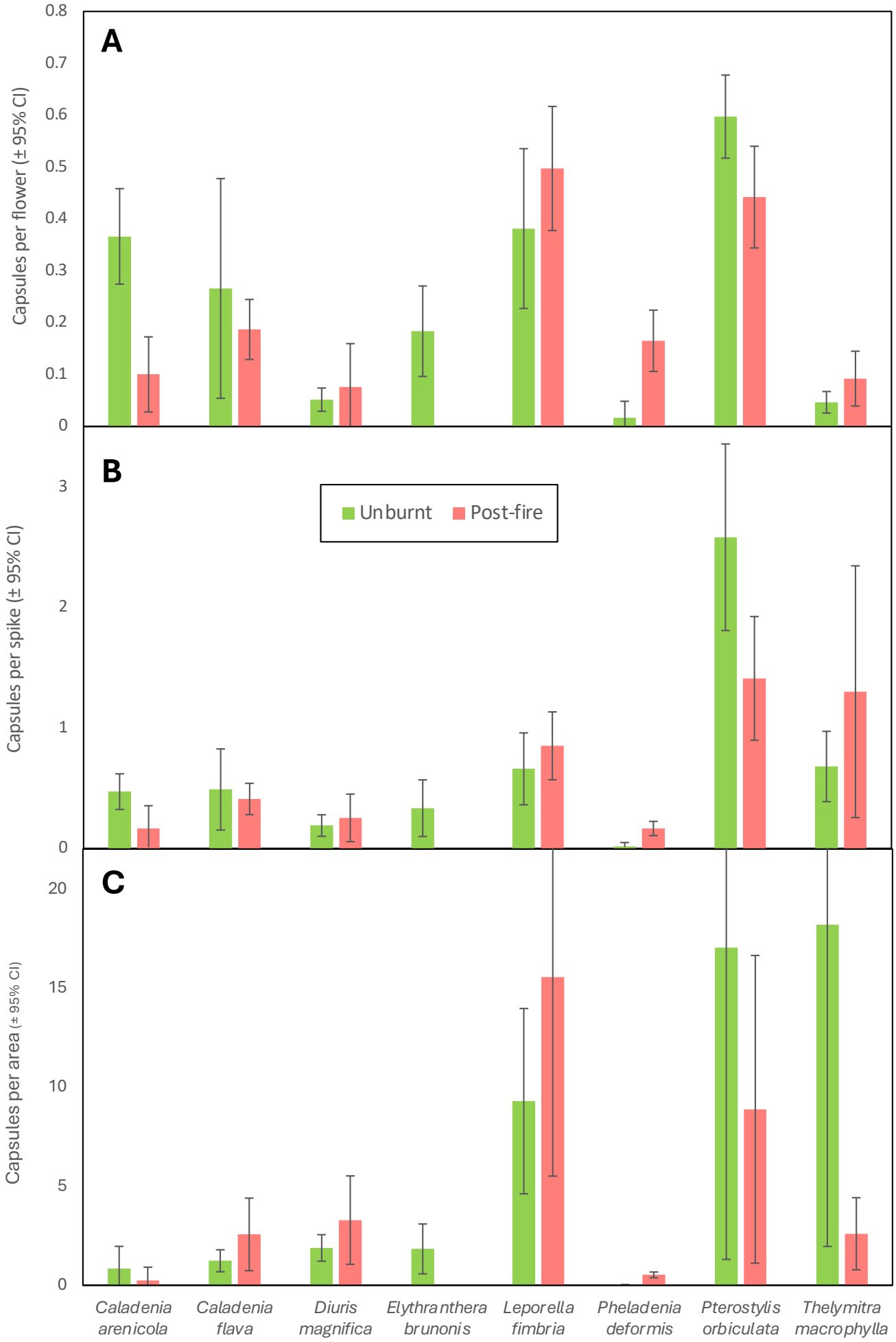


Figure 9. Density effects on pollination due to fire

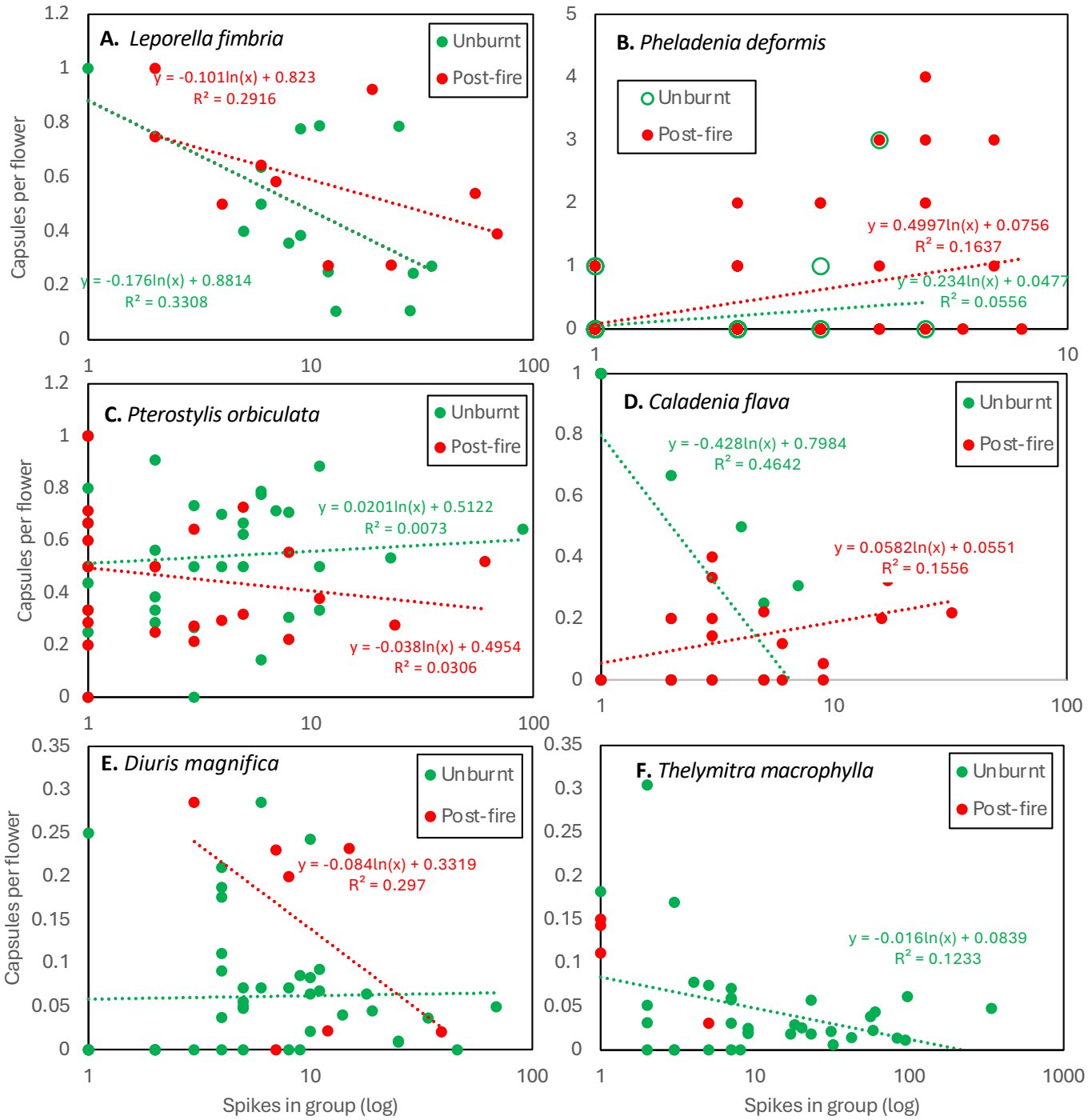


Figure 10. Blue beard orchid case study

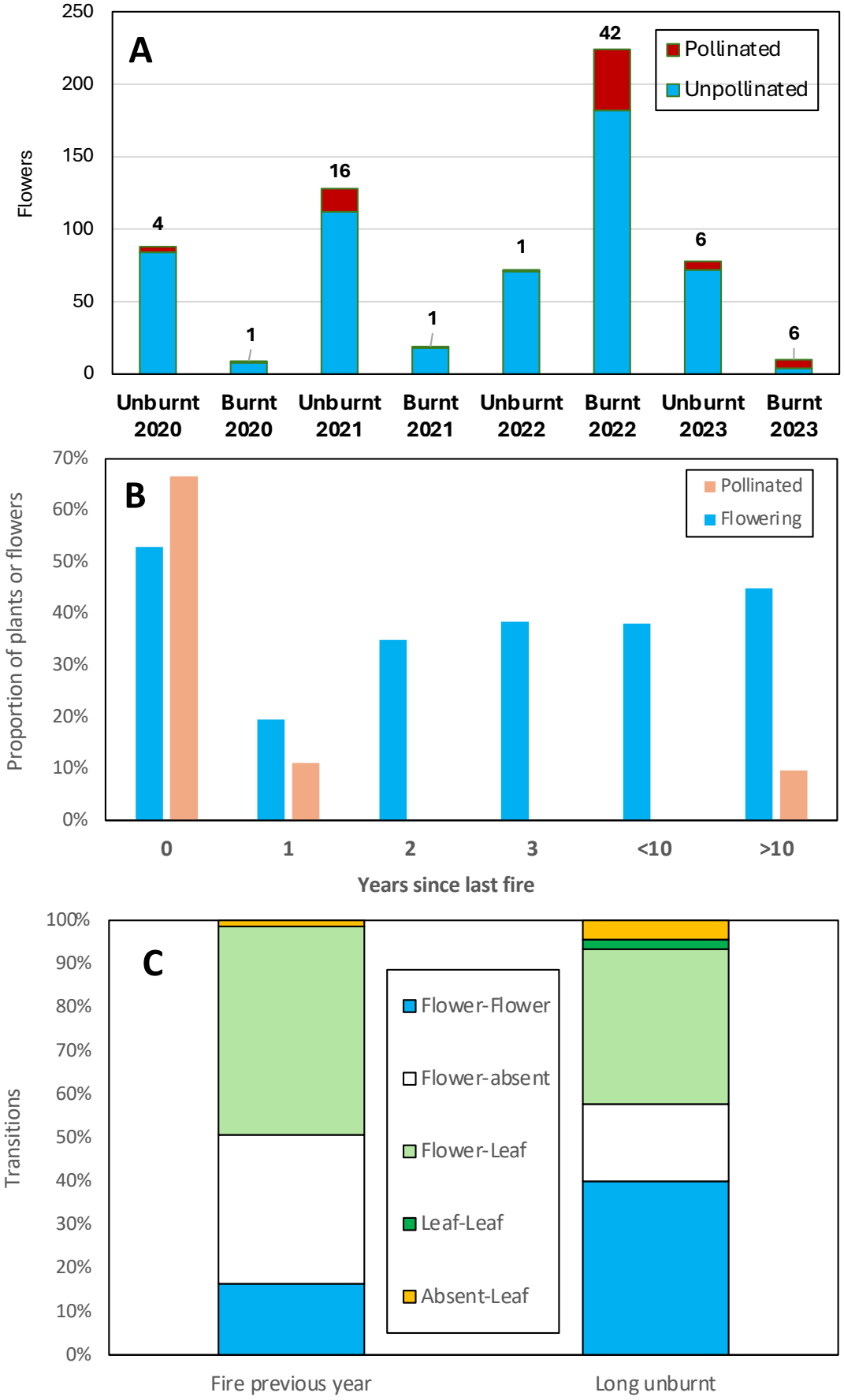


Figure 11. Fire effects on orchid abundance on transects

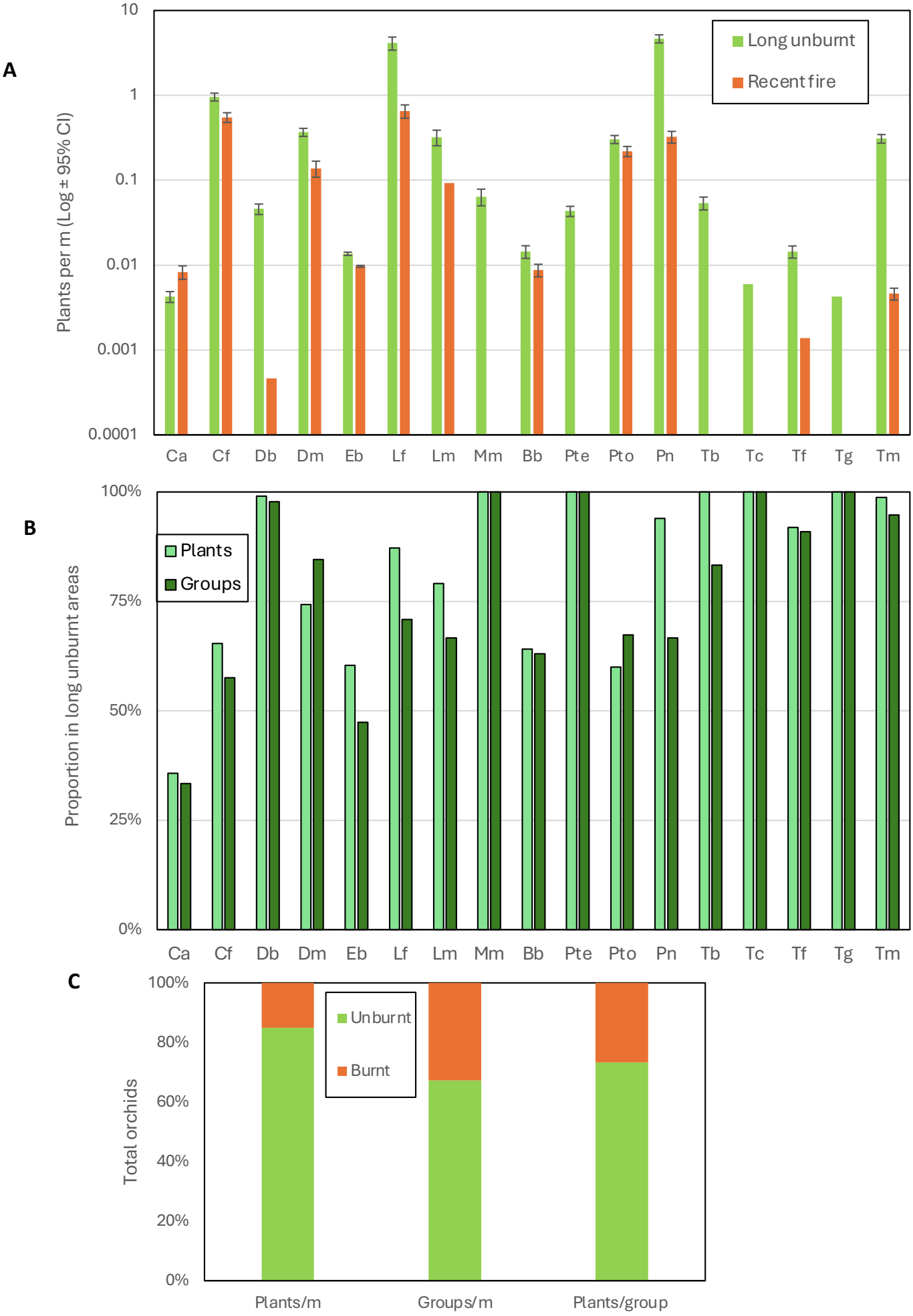


Figure 12. Fire age vs orchid abundance from transect data

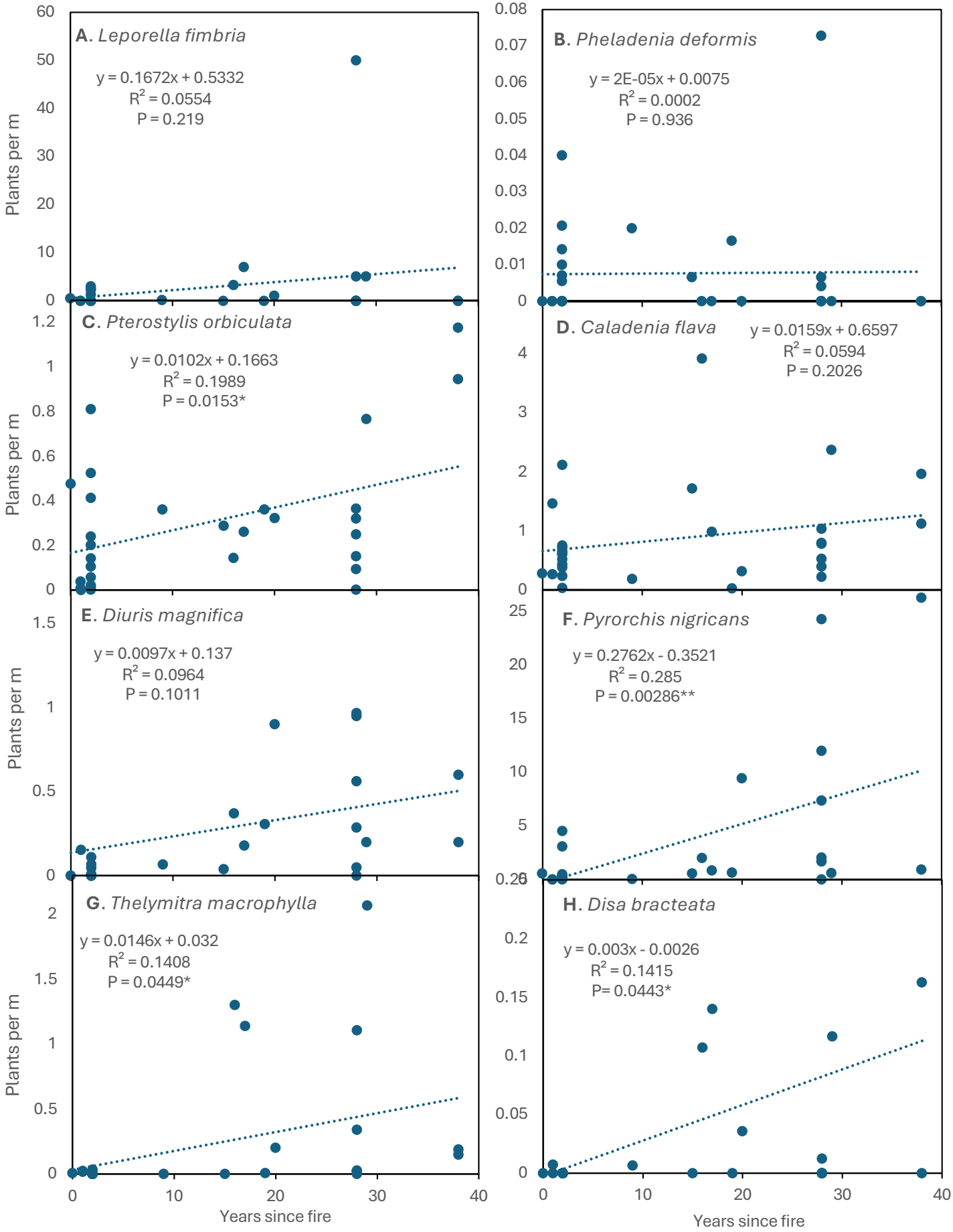


Figure 13. Fire tolerance rankings

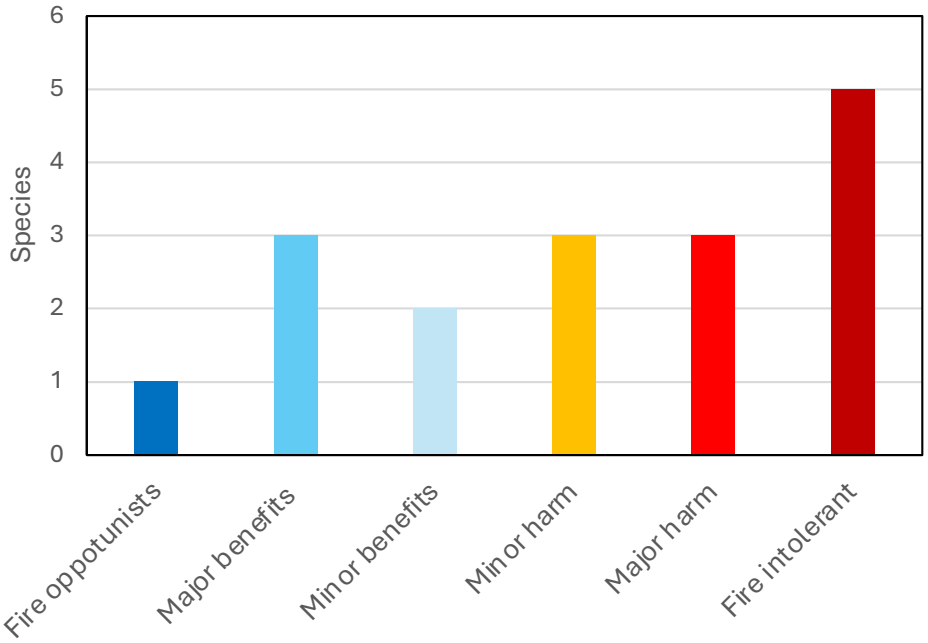


Figure 14. Fire response and trait correlations

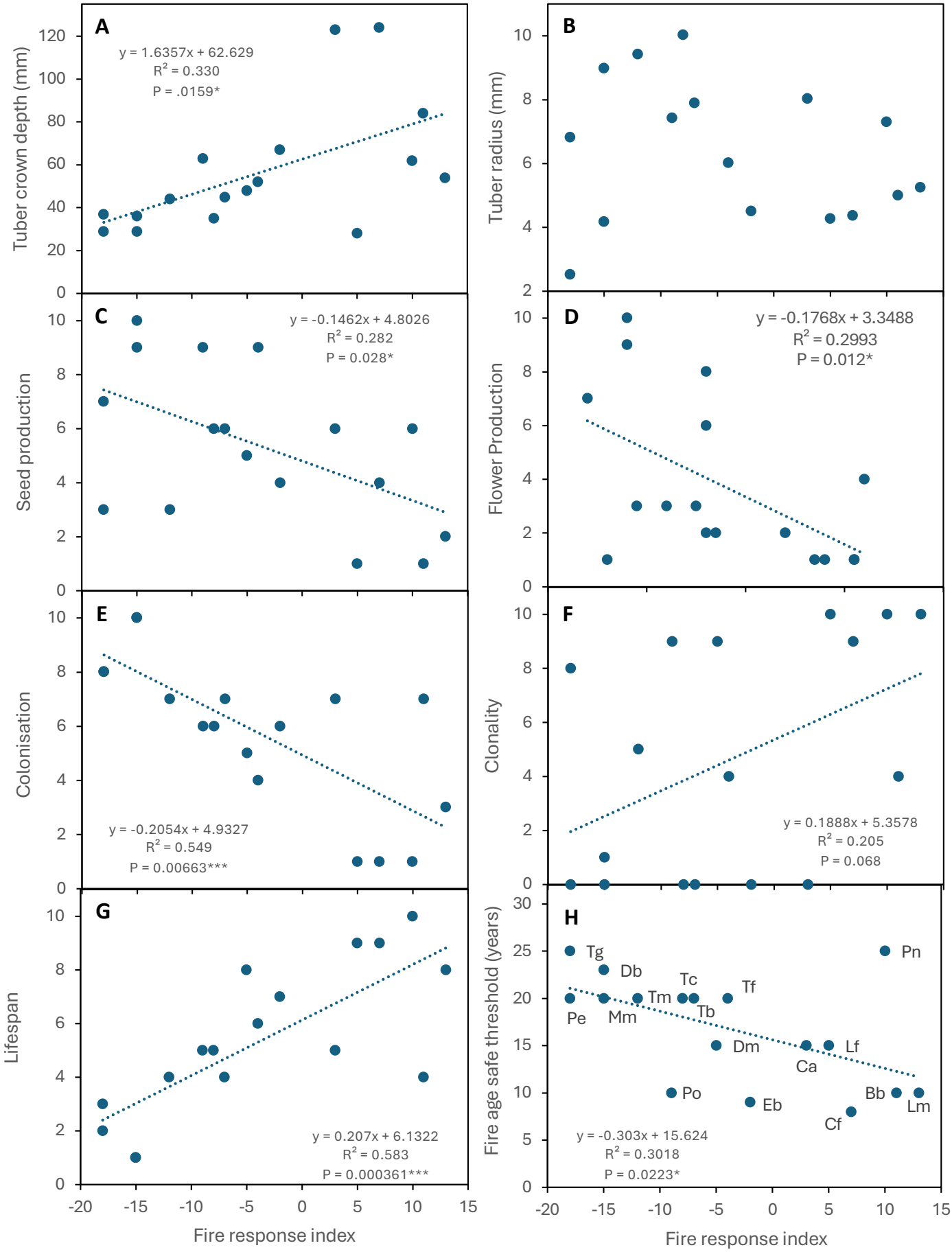


Figure 15. Orchid density and diversity relative to fire history on transects

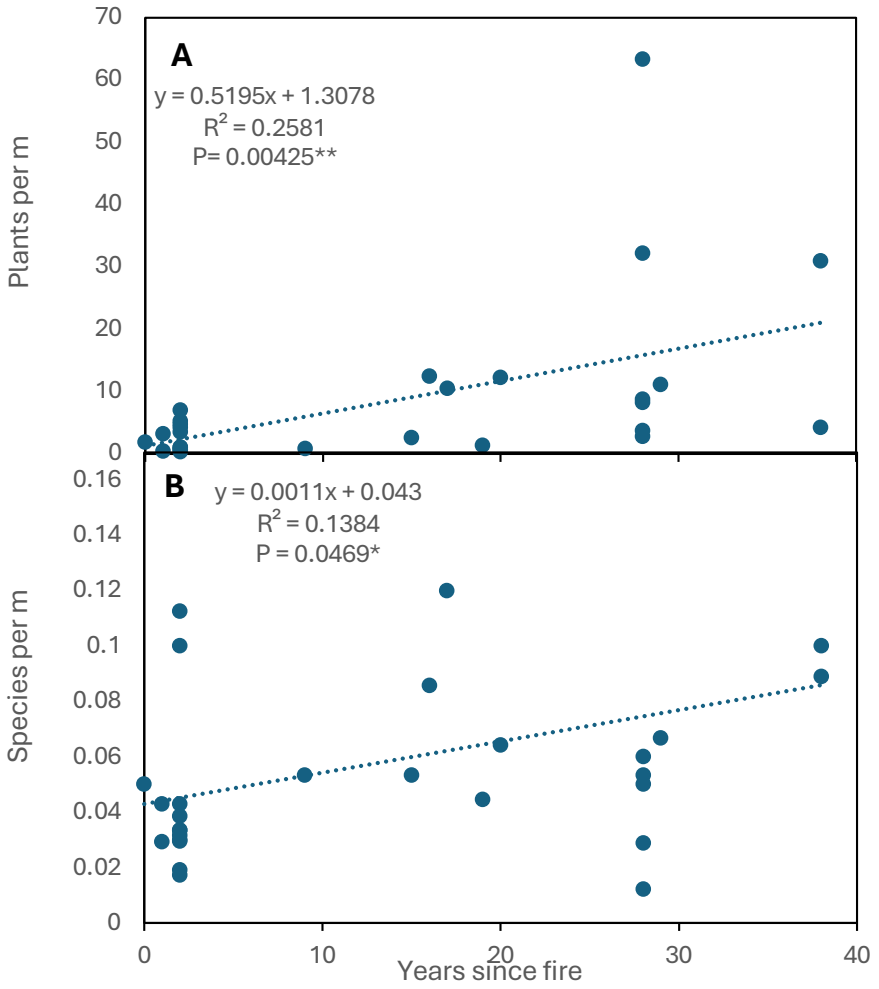


Figure 16. Orchid occurrences relative to fire history from monitoring

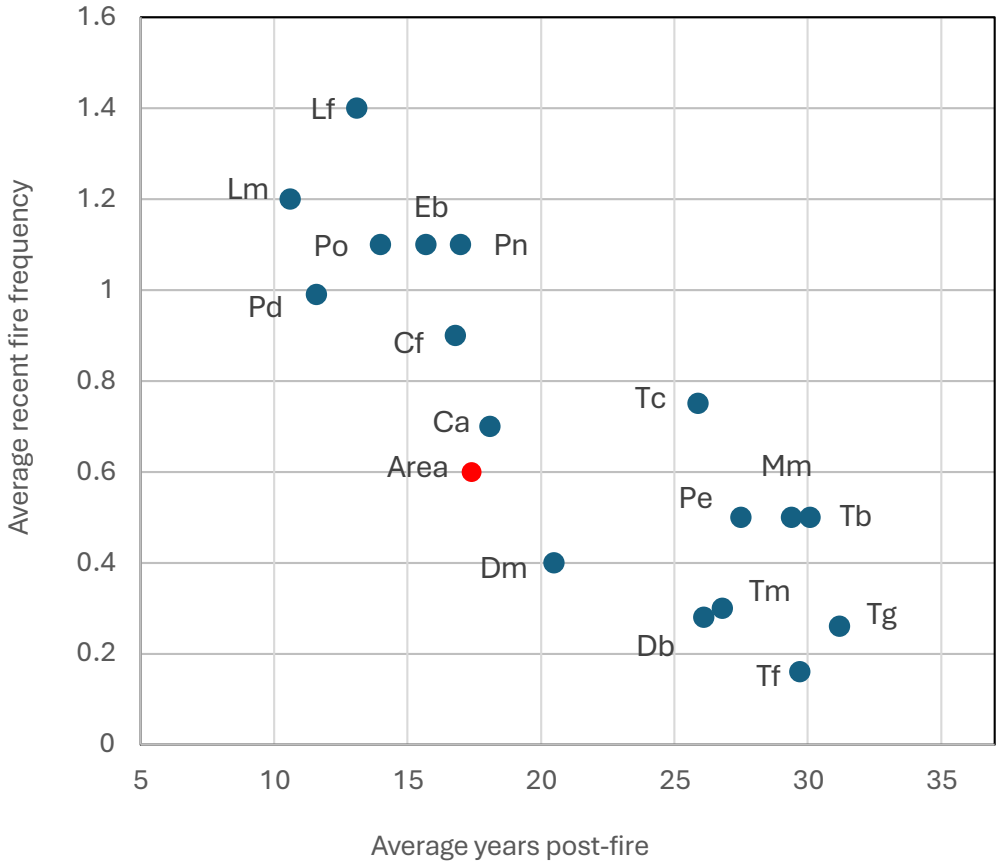


Figure 17. Blue sun orchid (*Thelymitra macrophylla*)

Figure S1. *Caladenia flava* flowering trends over two years

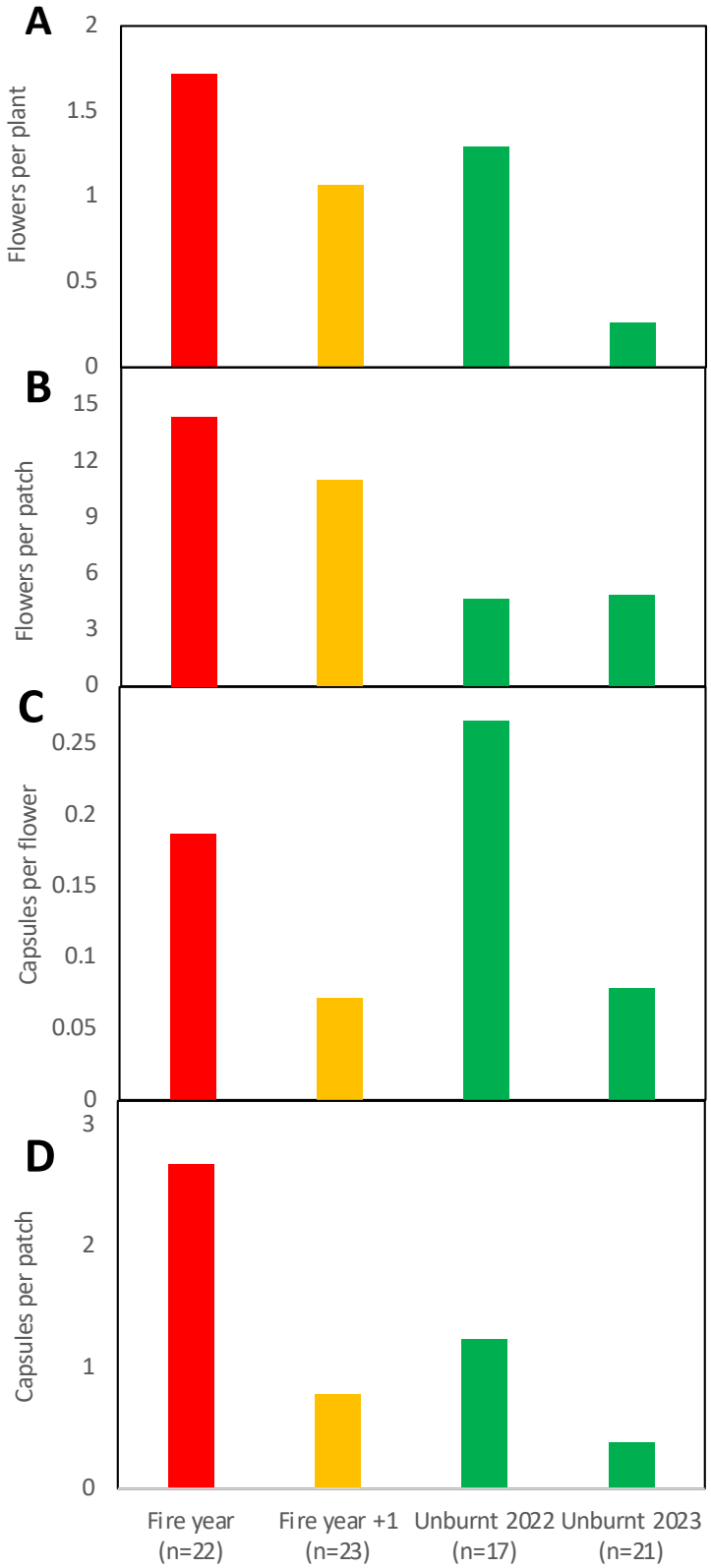


Figure S2. Time since fire & flowering productivity

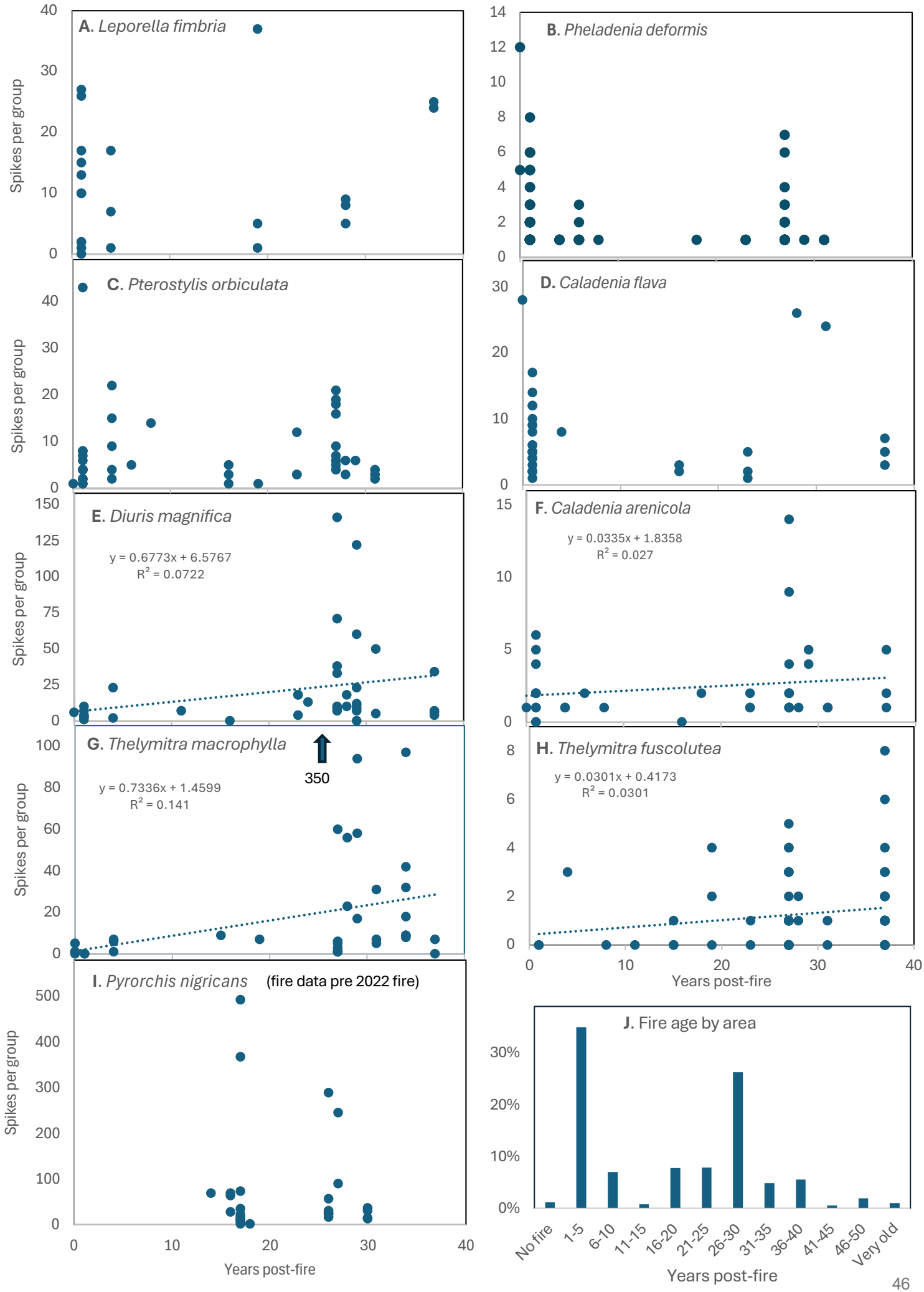


Figure S3. Flowering productivity relative to total fires

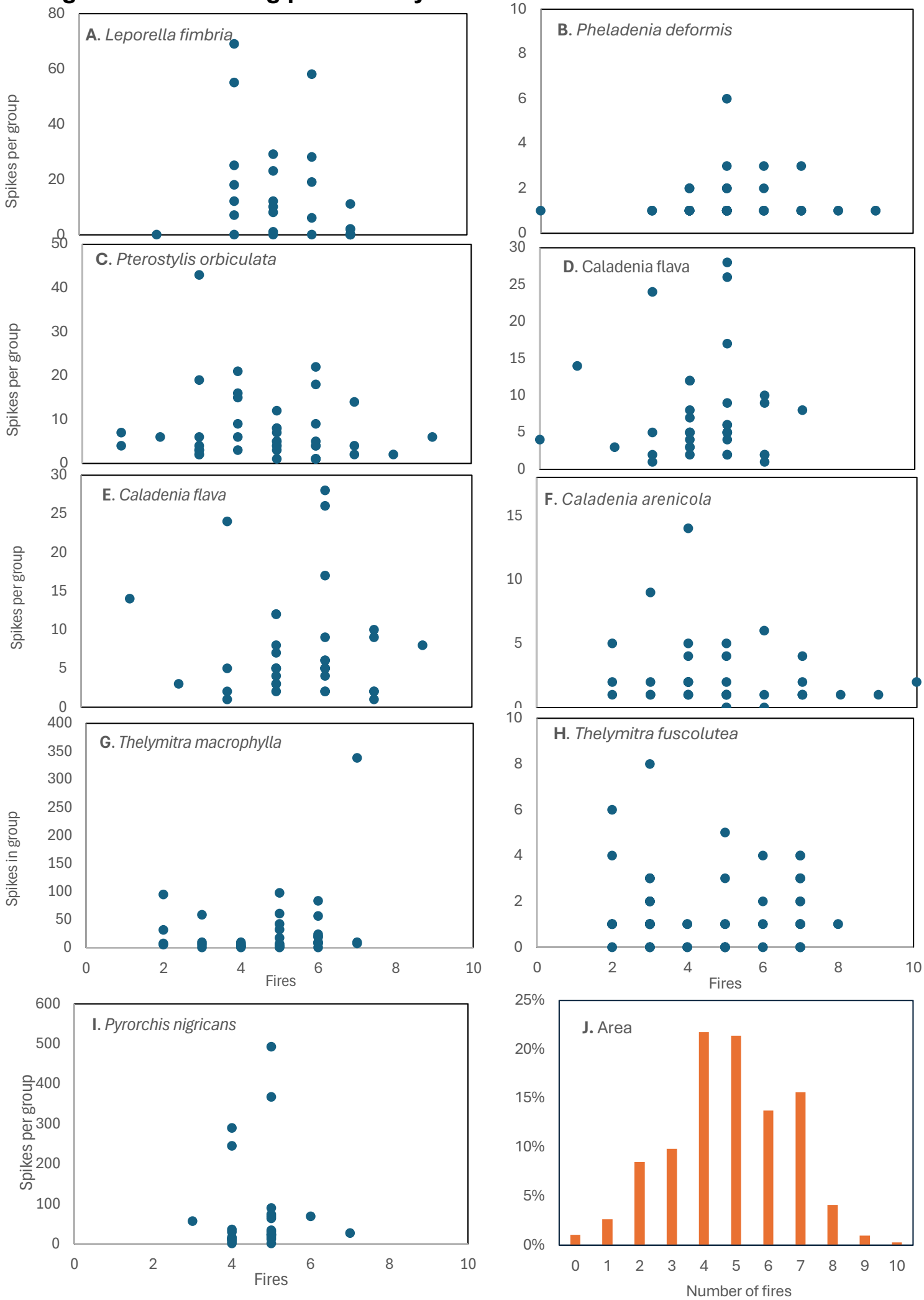


Figure S4. Flowering productivity relative to recent fires (2000-2023)

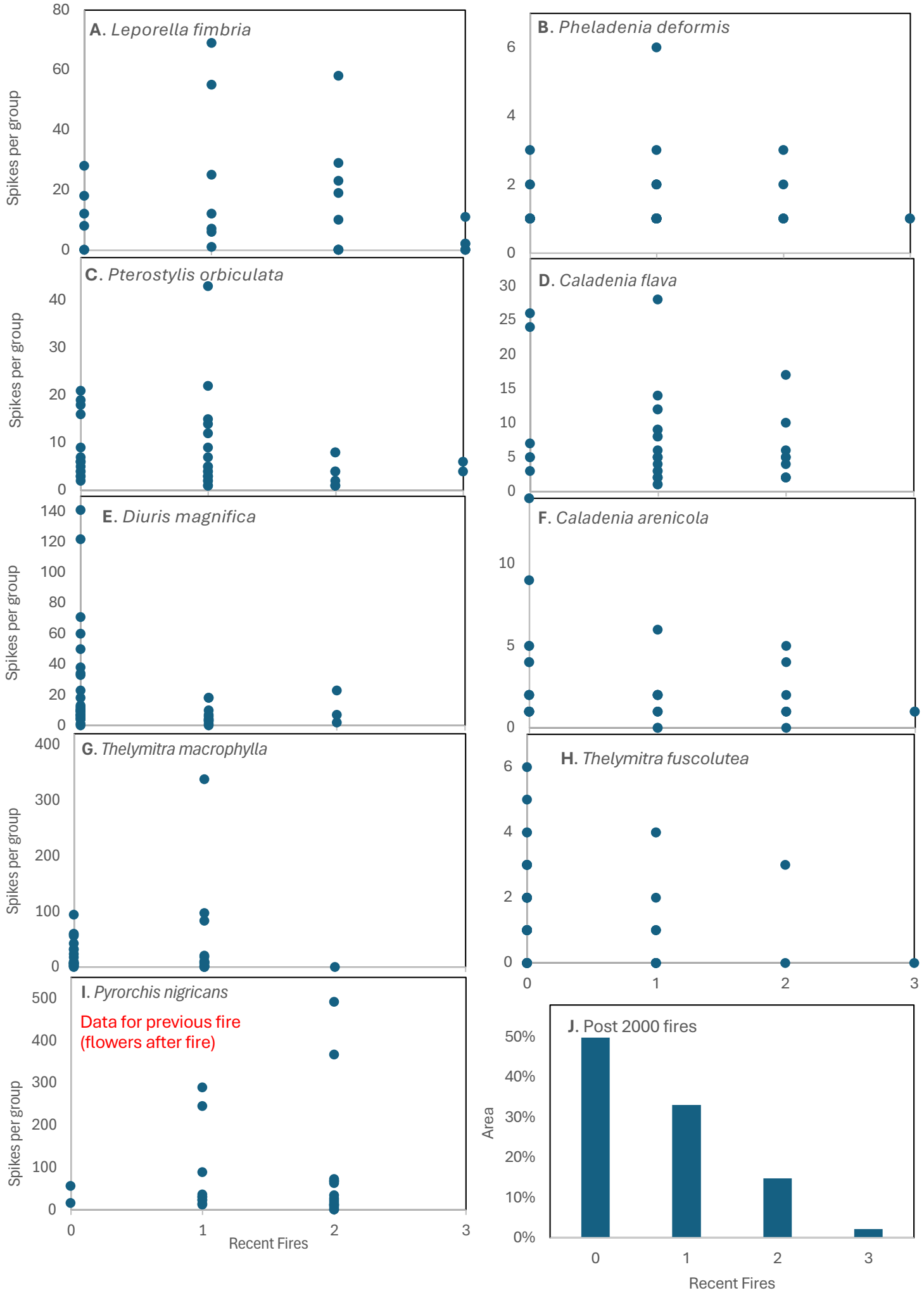
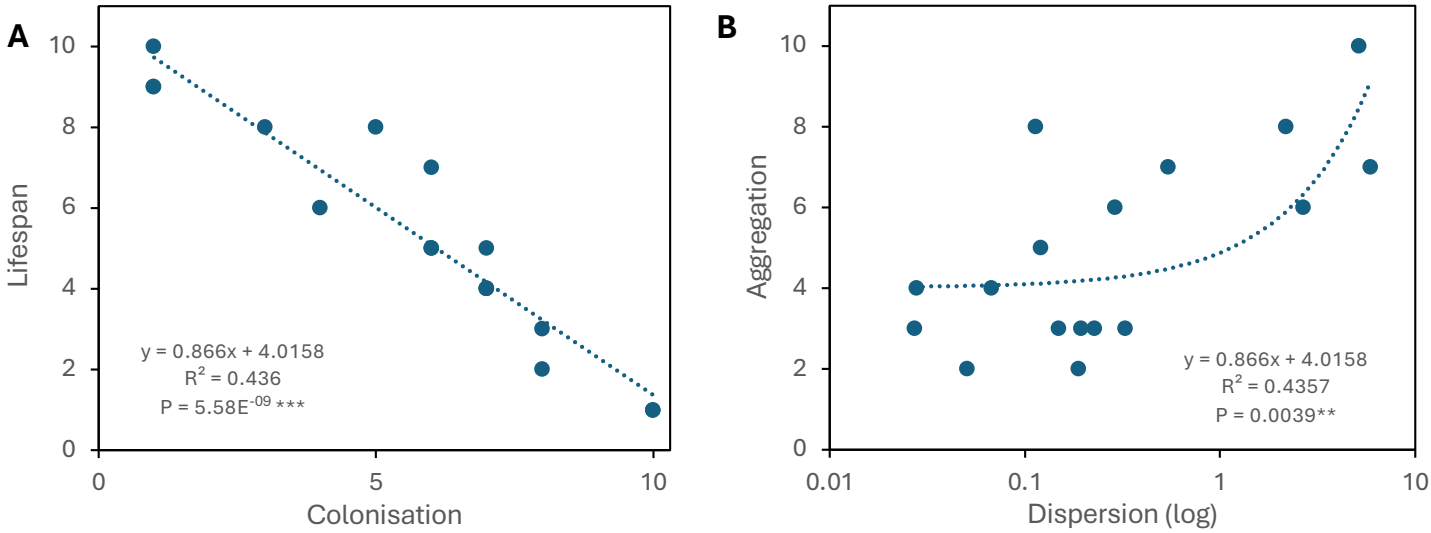



Figure S5. Additional trait correlation graphs