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

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Abstract (395 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 compare the fire ecology of 17 orchids with diverse ecological strategies and functional traits from an isolated urban banksia and eucalypt woodland, and develop fire response monitoring methods and management criteria.

Methods: A 72-year fire record was intersected with ~1000 orchid locations and 4.5 km of transects to measure fire effects on orchid abundance and diversity. Key traits such as plant size, flowering, pollination, tuber depth, clonality and population dynamics were also compared using 7-11 years of baseline data.

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 orchids revealed 5 species usually lost to fire and 6 with substantial fire impacts, while 6 others benefited from fire, including 3 with strongly enhanced flowering, but even the latter could be killed by unseasonal fire. Pollination varied from moderate decreases to substantial increases, but three orchids produced seed primarily after 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 inter-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, since may orchids 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 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; Brundrett 2014). 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 after 10 years. Reiter and Pollard 2013 found *Caladenia disjuncta* was severely impacted by a bushfire and Jasinge et al. (2018) reported that spring or summer fires were less damaging than autumn to winter fires for a *Pterostylis* species. 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 (pyrogenic) 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 *Caladenia 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. However, Marquart (2018) found limited consequences of fire on orchid pollinators in eucalypt woodlands of South Australia, while Phillips et al. (2024) found specific wasp pollinators and mycorrhizal fungi of *Caladenia tessellata* were still present after fires 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 variations in the reproduction and spread of orchids and the impacts of climate extremes on them.

Methods

1. Study site and species

This study occurred in Warwick Bushland, an isolated naturally vegetated urban reserve of 63 hectares. It is located in the City of Joondalup in Perth in 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). This study focussed primarily on 17 species which had the most observations (Fig. 1). 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 large areas of very good or excellent condition vegetation. Data presented in Figures 2 and 3 extends a 1952-2005 fire map made by manually tracing fire scars from contact prints of aerial photographs housed in the former WA Department of Land Administration (Clarke & Brundrett 2005). For fires post 2000, 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 (3.34, Prizren). 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, direct mapping 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 years when arson was common. Mapped major 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 where major fire damage was visible on imagery, so these fires sometimes occurred late in the previous year. These major fires usually occurred in late spring, summer, or early autumn (November - April) and 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 (fires managed reduce litter and understory vegetation while limiting tree canopy impacts) lit in autumn or winter also occurred (Fig. 2A). These were excluded from fire history analyses because they were less intense and more patchy than major fires and the second one (June 2019) deliberately avoided areas where orchids were common.

3. Survey methods

Comprehensive monitoring of the abundance, flowering and pollination orchids in the study area began in 2015 and increased from 2018 onwards (Brundrett 2019). Fire studies began after a very large fire in 1/3 of the study area (18 ha) and impacted orchid groups with 3 to 7 years of existing data (Table S1). This included 200 burnt and 335 unburnt groups, both containing ~3000 flowering plants (Table 2). Monitoring continued for 3 years to confirm orchids lost to fire, as some may have initially 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 from a fuel reduction fire in June 2019 (1.3 ha), as well as small hot fires in 2023 (0.3 ha) and 2024 (0.1 ha). Observations designated as “post-fire” occurred within a year of a fire and long unburnt areas had over 22 years since the last 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 habitats. There were more transects in unburnt areas (17) than areas burnt in 2022 (13), but their total length was similar (2.3 or 2.4 km). The distance 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 of some orchids are primarily of clonal origin, but seeding orchids were also often 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 and reference photos made with a mobile phone using the SW Maps Android phone app (3-10 m accuracy). They were visited multiple times per year to count flowering plants, non-flowering plants, seedlings, flowers per spike and capsules (all had a single spike per flowering plant). Fire impacts on plant height were also measured in 2022.

4. Measurement of responses and traits

Fire response data are primarily from the large fire in 2022 and two smaller fires in 2023 and 2024 for the same orchid groups extending 3 or more years before and after fires (Table 2). Representative groups of common orchids and most locally present individuals of less common species were included (Tables S1, S3). Traits measured for ecological comparisons included seed production, seedlings, group sizes, clonality, aggregation and dispersion, as well as tuber size, depth and abundance (Table 4). 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). 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 presented here are part of an ongoing study investigating the lifespans, turnover and propagation of these orchid species.

5. Data analysis

Measurements from orchids in recently burnt and long unburnt areas were compared graphically with 95% confidence intervals (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 to intersect orchid group locations or transects with fire history polygons. This produced new point layers for each of these including the time since fire and the number of fires for each location as a data matrix. 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 intersect grids with 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.

Measured fire responses were converted into discrete response scales extending from catastrophic impacts to very major benefits, and converted to a common numeric scale (-3, -2, -1, 0 1, 2, 3) in Table 5A. These nine response indexes, which summarise direct and indirect fire responses, were then combined to produce an overall Fire Response Index (FRI, Table 5A). Separate indices for important ecological or biological traits (Tables S1-4) were also calculated as explained in Table 4 and standardised to a common scale (0-10). These represent the capacity of orchids to spread locally or distally by clonal or seed propagation, aggregation of plants, orchid abundance trends 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 data and divided by the average size of groups to estimate turnover rates (Table S4). Correlations between fire responses and traits were calculated and P values shown on graphs. Fire tolerances for orchid species were summarised using safe fire thresholds (FAST) and optimum fire ages, as explained in Table 4. Fire response data from this study was also compared with existing ecological information (Table 1).

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) 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 narrow zone visible in Figure 2B. Fires were generally smaller after 1995, with only the main 2022 fire exceeding 10 ha, while many earlier fires consumed entire compartments bounded by tracks (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. Fires included some less impacted areas due to patchiness or suppression by firefighters especially near edges. Lower intensity fuel reduction burns 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).

On average, 1.1 severe fires occurred annually after 1972, and 5.6 ha was burnt each year (Fig. 3A). In total, 58 major fires covered a cumulative area of 289 ha (4.6 x the reserve area). There was a major fire on 30 out of the 52 years (often more than one) and a maximum of seven per year (Fig. 3B). In some years there also were numerous small fires (< 100 m^2) that are not included in maps. 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 summarised using a 25 m virtual point grid revealed the average fire frequency and time since fire by area (Figs. 2B, C, 3C, D). Fire frequency had a normal distribution with an average of 5 fires per location and a maximum of 10 (Fig. 3C), and the largest areas were 1-5 years (35%) or 26-30 years post-fire (26%). This bimodal fire age distribution provided similar areas of recently burnt or long unburnt habitats for comparison (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 in the study area, which are spreading locally despite some having low rates of seed production (Brundrett 2019, Table S4). Grazing by rabbits was more severe after fire, but was only substantial for *L. fimbria*, which had similar grazing rates 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 growing 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 recovered substantially after seven years. *Pterostylis orbiculata* (banded greenhood) was less productive in burnt areas but still common (see below). This orchid also forms subterranean shoots in autumn (Fig. 4G) so is also vulnerable to unseasonal 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 much more widespread in the study area since 42 plants in three groups were discovered 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 lost 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, when one additional plant was found. Overall, only 11% of plants of this species survived in fire areas and all of these were located near fire boundaries where 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 groups were found each year (Fig. 6, Table S1). The smaller blue sun orchid *T. graminea* also 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 areas with many 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 (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), but fire was less important than seasonal variations in rainfall. This orchid has a strong density effect on pollination which is smaller after fire (Fig. 9A). Overall, increased seed production post-fire results from greater flower production rather than increased rates of pollination. Thus, flying male *Myrmecia* ants survived in or dispersed into 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 can form clumps and 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 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 1/2 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 using habitat photos and markers. This orchid gradually recovered flowering capacity after fire over a decade (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 are known to reduce the likelihood of subsequent flowering by small orchids (Shefferson et al. 2020).

Pterostylis orbiculata 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 likely to be 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 (Fig. 9D). It may also 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 was also regulated by climatic factors (Fig. S1).

Diuris magnifica (pansy orchid) is one of many very similar donkey orchid species in the *D. corymbosa* complex. Pollination of this species and its close relatives is by visual deception of native bees that primarily visit Fabaceae flowers (Scaccabarozzi et al. 2020). Pansy orchid plants were substantially smaller after fire (Fig. 7A) and pollination 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 plants that support its pollinators need to gradually recover 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 and seed than those in unburnt areas (average 9.5 vs. 15.5). Pollination was strongly regulated 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. Some unburnt plants 5-10 m from the fire edge flowered in 2022 (34 plants). This confirms the flowering stimulus is air-borne and not heat. It is likely to be ethylene gas (Dixon & Barrett 2003). 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 counted formed capsules (Table 2). The higher rates of pollination of *P. nigricans* in 2019 may result from lower 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. *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 and has relatively high pollination rates.

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 their absence or scarcity in burnt areas. These included all three self-pollinating species (*D. bracteata, M. media* and *T. benthamiana*). 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 the pyrogenic species *P. nigricans* and *L. menziesii* (Table 2).

4. Indirect fire effects

The fire in 2022 provided 18 ha of 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). 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) leading to orchid recolonisation over time.

Four extremely fire intolerant species were small, relatively short-lived and spread rapidly (*T. graminea*, *M. media, D. bracteata* and *P. ectypha*). These orchids prefer fairly open habitats with intermediate levels of disturbance including some weeds. They should be able to rapidly colonise burnt areas by seed

dispersal, provided substantial refugia exist nearby. However, their minimum fire age for recolonisation was 15 years and peak abundance occurred after several decades (Table 3). In jarrah forest, close relatives of *P. ectypha* were most abundant several decades after fire (Cargill 2015) and started to colonise in restoraytion 5 years post mining (Collins & Brundrett 2015).

The fire intolerant sun orchids *T. macrophylla* and *T. graminea* (Fig. 11) 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 more shade and leaf litter (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 first appeared 3 years after fire (Fig. 4M). There also was evidence of increasing productivity with time since fire for *D. magnifica* (Fig. 12E).

Orchids lacking a clear relationship with time since fire include *Caladenia flava*, which had fire promoted flowering and increased in abundance after fire (Figs. 11, 12D) and *E. brunonis*, which had similar abundance in burnt and unburnt areas (Fig. 11). *Caladenia arenicola* was found more often after fire (Fig. 11B), but had a flat response to time since fire (Fig. S2F). 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 strongly enhanced seed production, reproduction primarily from seed, relatively short lifespan and shade intolerance. It has a bimodal fire age relationship like the entire site (Figs. S2A, S2J).

In theory, the pyrogenic orchids *P. nigricans* and *L. menziesii* should have 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* flowered substantially more after fire, but its distribution also had a significant bias towards long unburnt areas (Figs. 11, 12A). Resolving fire age trends for these species is difficult because of inherently large variations in group sizes, but all prefer very long fire intervals.

5. Comparing fire responses and traits for orchids

Overall fire effects on orchid diversity and abundance were dramatic, but substantial differences in fire responses between orchid species required classification in a consistent manner. The approach taken here was to test the validity of exiting fire tolerance scales and develop more comprehensive rankings with consistent criteria. These criteria were based on 10 fire response indexes and 12 ecological traits for each species (Table 4). The indexes, which used common numeric scales, were combined into a comprehensive overall fire response index (FRI) for each orchid (Tables 5A, 6). The FRI, score (-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) and fire intolerant (-13 to -18). Orchids identified as fire intolerant in 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 harmed by fire than benefited from it (Figs. 15, 16H).

Indexes provided in Table 5 summarise fire response indexes and key biological and ecological traits of orchids, which are based on data in Tables S1 to S5. Comparisons between orchids revealed that fire

responses were highly correlated with biological traits such as flowering, seed production, clonality, tuber depth, aggregation and lifespan (Table 7, Fig. 14). One exception was tuber size which was regulated by the size of orchids. Thus, fire susceptibility is deeply integrated into orchid ecology, especially traits that regulate dispersal and local persistence (Fig. 16). Comparisons of non-fire traits revealed that flower and seed production were inversely correlated with clonality, aggregation and lifespan indexes. The strongest relationship was an inverse correlation between lifespan and colonisation indexes (Fig. S5A, correlation coefficient = 0.95). Thus, orchids which reproduce primarily by seed are most effective at local dispersal, as would be expected. For similar reasons, indexes for aggregation and dispersion are also inversely correlated (Fig. S5B, correlation coefficient = 0.65). The dispersion index compares results from monitoring locations chosen to maximise orchid diversity, and unbiased sampling of orchids on transects (Table 5B). This index summarises the uniformity of orchid distribution, and was also correlated with the overall fire response index (Table 7).

Due to shared habitat preferences, there were positive correlations between 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), revealing disparate habitat preferences (Table 7B).

6. Determining fire age safe thresholds

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 (Fig. 12). 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, 13, S2). FAST is highly correlated with the overall fire trait index (FRI), which is dominated by short term fire responses (Fig. 16H). Peak fire ages for orchid species, where diversity and abundance are maximised, could be as important than FAST ages, but were less precisely estimated due to limited areas with fire ages over 40 years, a time when orchid abundance and diversify may still be increasing (Fig. 13).

Some orchids may lack FAST periods due to similar abundance in recently burnt and long unburnt areas (Figs. 11, 12, 14). Thus, the designation of fire tolerance for orchids with intermediate FRI categories may vary with circumstances. These orchids 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 preference for relatively open areas. However, even low FAST age orchids may require long unburnt areas for seedling establishment, since 86% of seedling nurseries were found there. Thus, there are very few if any orchids that are fully fire promoted or neutral when relationships between habitat fire 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 compared 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* which has 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. 15, Box 1) are similar to those used by others (e.g. Jones 1988, Duncan 2012, Adams 2018), but formed a continuum from obligate fire flowering to fully fire intolerant species, so it was difficult to assign some species to specific categories (see Figs. 14, 16H). 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 also identifying orchids which are highly susceptible to unseasonal fires (Box 1).

Text Box 1. Orchid fire response summary

a) Comparisons of recently burnt and long unburnt areas revealed clear winners and losers after fire (Table 6, Fig. 15).
b) Four orchids had major fire benefits, while two others had minor benefits. In contrast, six species experienced minor or major harm from fire due to reduced productivity and five orchids rarely survived fire or were entirely absent from recently burnt areas (Fig. 15).
c) 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).
d) Orchids intolerant of fire 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).
e) 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).
f) 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 5A).

In this study, orchid diversity and abundance increased with time since fire, which was more important than the total number of fires impacting an area. Thus, fire impacts diminished over time, presumably due to gradual recovery of suitable habitat conditions. This study demonstrates the importance of long-term orchid monitoring to provide data from orchids before and after fire. There are very few scientific studies that try 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 their fire responses. These relationships were revealed using trait indexes, many of which are correlated with each other (Table 7A). Fire tolerant or intolerant species had divergent index profiles for these traits, which are central to orchid ecology. In particular, fire tolerant orchids were more likely to be aggregated, have long lifespans, reproduce clonally and have relatively deep tubers (Figs. 14, S5). In contrast, fire intolerant orchids tended to have greater flower and seed production, reproduce primarily by seed and spread more rapidly (after sufficient time post-fire). They also had less localised distributions, shallower tubers, shorter lifespans and preferences for 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 would 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).

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 for 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 variability (measured by FAST and FRI) as a keystone of Australian orchid ecology. 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 was observed to dramatically modified habitat suitability for orchids due to increased light from canopy loss, loss of organic matter and increased dominance of major environmental weeds, especially veldt grass (*Ehrharta calycina*). Most orchid species were substantially less common in relatively poor condition vegetation with many weeds, but some persisted in these areas. Increasing weed abundance is likely to be a major factor limiting the productivity of relatively fire-resilient orchids. However, 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 can be associated with coarse soil organic matter (Brundrett et al. 2003), and micro-habitats suitable for their germination are limited to small patches in soils in banksia woodland (Batty et al. 2001). Thus, orchid habitats are often 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 orchid seedlings were found in long unburnt areas, except *P. orbiculata,* which first emerged three years after fire, but only 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 often in forest than in restored areas, where they were 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 (see Introduction).

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, and avoid mortality, but their fecundity and recruitment may increase or decrease. 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 smaller, or more isolated patches of suitable habitat. New orchid species occasionally arrive from distant sites into urban areas like Warwick Bushland, where five new species were discovered recently, but may fail to persist. These "vagrant" species include *Caladenia falcata*, a common species in areas further east, which temporarily appeared five separate times.

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 impacts of unseasonal fires which impact orchids when they are most vulnerable.

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 their population dynamics, and essential resources including symbiotic organisms required to grow and such as mycorrhizal 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 can be resilient in the short term, but this makes it challenging to detect impacts of adverse factors such as fire 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, these approaches have not 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 (Box 2). Correlations between fire age and orchid diversity also occur 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 (Brundrett 2014). 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 at least 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 due to increasing fire frequency. 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, effective weed management, providing artificial shade, etc., but this would 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 (Box 2). 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 these core habitat areas (see Brundrett 2016), but this study 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 (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 (Box 2). 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 (Box 2). These approaches are especially important for habitats of rare orchids, but would also protect focal points for tourism and protect 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 fire age safe 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 or exclusion from natural areas when conditions are dangerous and not locating schools near 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 important, but is expensive and difficult.
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 recruitment.
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 declined substantially after inclusion in 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. However, 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 man-made 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 integrated with other key aspects of their ecology and biology, such as tuber depth, clonality, dispersion and disturbance tolerance. Fire traits allowed orchids to be classified into distinct risk categories defined by tolerance indices (e.g. FRI and FAST), but also revealed an ecological spectrum that requires further investigation. These indexes should also help predict future risks 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.

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References

Adams PB (2018) Destructive effect of fire on terrestrial orchid populations at Warrandyte, Victoria. *The Victorian Naturalist,* **135**, 171–177

Batty AL, Dixon KW, Brundrett M, Sivasithamparam K (2001) Constraints to symbiotic germination of terrestrial orchid seed in a mediterranean bushland. *New Phytologist* **152**, 511–520

Bergstrom DM, Wienecke BC, van den Hoff J, Hughes L, Lindenmayer DB, Ainsworth TD, Baker CM, Bland L, Bowman DM, Brooks ST (2021) Combating ecosystem collapse from the tropics to the Antarctic. *Global Change Biology* **27**, 1692–1703.

Bower C (2019) Post-Fire Survey of Terrestrial Orchids in the Mount Canobolas State Conservation Area. NSW National Parks and Wildlife Service, (Bathurst, NSW, Australia) https://savemtcanobolassca.com/wp-content/uploads/2019/10/mt-canobolas-orchid-survey-report-final.pdf

Bradshaw SD, Dixon KW, Lambers H, Cross AT, Bailey J, Hopper SD (2018) Understanding the long-term impact of prescribed burning in mediterranean-climate biodiversity hotspots, with a focus on south-western Australia. *International Journal of Wildland Fire* **27**, 643–657

Brown J, York A (2016) Fire, food and sexual deception in the neighbourhood of some Australian orchids. *Austral Ecology* **42**, 468–478

Brundrett M (2014) 'Identification and Ecology of Southwest Australian Orchids'. (Western Australian Naturalists' Club Inc.: Perth, Western Australia)

Brundrett MC (2016) Using vital statistics and core habitat maps to manage critically endangered orchids in the West Australian wheatbelt. *Australian Journal of Botany* **64**, 51–64.

Brundrett MC (2019) A comprehensive study of orchid seed production relative to pollination traits, plant density and climate in an urban reserve in Western Australia. *Diversity* **11**, 123.

Brundrett MC (2021) One biodiversity hotspot to rule them all: southwestern Australia—an extraordinary evolutionary centre for plant functional and taxonomic diversity. *Journal of the Royal Society of Western Australia* **104**, 91–122

Brundrett M, Longman V (2016) Recovery of Banksia Woodland after Fire. *Western Wildlife* **20**, 10–12.

Brundrett MC, Ladd PG, Keighery GJ (2024) Pollination strategies are exceptionally complex in Southwestern Australia—a globally significant ancient biodiversity hotspot. *Australian Journal of Botany* **72**, 1–70. doi:10.1071/BT23007

Brundrett M, Scade A, Batty A, Dixon K, Sivasithamparam K (2003) Development of *in situ* and *ex situ* seed baiting techniques to detect mycorrhizal fungi from terrestrial orchid habitats. *Mycological Research* **107**, 1210–1220.

Cargill J (2005) Impact of fire on geophyte abundance, diversity and composition in the Jarrah Forests of South-West Western Australia. https://ro.ecu.edu.au/theses_hons/383/.

Clarke KA, Brundrett MC (2005) History of Warwick Bushland. *Friends of Warwick Bushland*. https://friendsofwarwickbushland.com/wp/wp-content/uploads/2020/06/History-of-Warwick-Bushland-Web.pdf.

Collins M, Brundrett MC (2015) Recovery of terrestrial orchids in natural ecosystems after severe disturbance. 'Mining in Ecologically Sensitive Landscapes'. pp. 141–158. (CSIRO Publishing: Canberra)

Collins M, Brundrett MC, Koch J, Sivasithamparam K (2007) Colonisation of jarrah forest bauxite-mine rehabilitation areas by orchid mycorrhizal fungi. *Australian Journal of Botany* **55**, 653–664.

Coates F, Duncan M (2009) Demographic variation between populations of *Caladenia orientalis*–a fire-managed threatened orchid. *Australian Journal of Botany* **57**, 326–339

Coates F, Lunt ID, Tremblay RL (2006) Effects of disturbance on population dynamics of the threatened orchid *Prasophyllum correctum* DL Jones and implications for grassland management in south-eastern Australia. *Biological Conservation* **129**, 59–69.

Commonwealth of Australia (2016) 'Banksia Woodlands of the Swan Coastal Plain: a nationally-protected ecological community' (Commonwealth of Australia: Canberra)

Dixon K, Barrett R (2003) Defining the role of fire in south-west Western Australian plants. 'Fire in Ecosystems in south-west Australia: Impacts and management'. (Eds I Abbott, N Burrows) pp. 205–223. (Backhuys Publishers: Leiden, The Netherlands)

Doherty TS, Macdonald KJ, Nimmo DG, Santos JL, Geary WL (2024) Shifting fire regimes cause continent-wide transformation of threatened species habitat. *Proceedings of the National Academy of Sciences* **121**, e2316417121

Duncan M (2012) 'Response of Orchids to Bushfire: Black Saturday Victoria 2009: Natural Values Fire Recovery Program.' (Department of Sustainability and Environment Heidelberg, Victoria, Australia.

Duncan M, Pritchard A, Coates F (2005) Major threats to endangered orchids of Victoria, Australia. *Selbyana* 189–195

Edens-Meier R, Westhus EJ, Bernhardt P (2013) Floral biology of large-flowered *Thelymitra* species (Orchidaceae) and their hybrids in Western Australia. *Telopea* **15**, 165–183.

Enright NJ, Fontaine JB, Westcott VC, Lade JC, Miller BP (2011) Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. *Plant Ecology* **212**, 2071–2083.

Fowler WM, Standish RJ, Enright NJ, Fontaine JB (2023) Extinction debt varies in two threatened Mediterranean-type woodland communities undergoing rapid urbanisation. *Australian Journal of Botany*.

Gallagher RV, Allen SP, Mackenzie BDE, Keith DA, Nolan RH, Rumpff L, Gosper CR, Pegg G, Van Leeuwen S, Ooi MKJ, Yates CJ, Merow C, Williams RJ, Nikolopoulos EI, Beaumont LJ, Auld TD (2022) An integrated approach to assessing abiotic and biotic threats to post-fire plant species recovery: Lessons from the 2019–2020 Australian fire season. *Global Ecology and Biogeography* **31**, 2056–2069.

Government of Western Australia. 2000. 'Bush Forever: Keeping the Bush in the City, Volume 2: Directory of Bush Forever Sites' (Department of Environmental Protection: Perth, Western Australia)

Groom PK, Lamont B (2015) 'Plant life of southwestern Australia: adaptations for survival.' (De Gruyter Open Ltd: Warsaw/Berlin)

Hobbs RJ, Atkins L (1990) Fire-related dynamics of a Banksia woodland in south-western Western Australia. *Australian Journal of Botany* **38**, 97–110.

Hopper SD, Gioia P (2004) The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual review of ecology Evolution and Systematics* ***35***, 623–650.

Hutchings MJ (2010) The population biology of the early spider orchid *Ophrys sphegodes* Mill. III. Demography over three decades. *Journal of Ecology* **98**, 867–878.

Jasinge NU, Huynh T, Lawrie AC (2018) Consequences of season of prescribed burning on two spring-flowering terrestrial orchids and their endophytic fungi. *Australian Journal of Botany* **66**, 298–312.

Jones DL (1988) 'Native Orchids of Australia.' (Reed Books Pty Ltd: Frenchs Forest, NSW, Australia)

Kuiter RH (2024) 'Orchid Pollinators of Victoria.' (Aquatic Photographics: Seaford, Victoria)

Lambers H, Brundrett MC, Raven JA, Hopper SD (2010) Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil* **334**, 11-31

Lamont BB, Downes KS (2011) Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecology* **212**, 2111–2125.

Lamont BB, He T (2012) Fire-adapted Gondwanan angiosperm floras evolved in the Cretaceous. *BMC Evolutionary Biology* **12**, 1–11.

Marquart AE (2017) Insects, orchids and fire: the effects of fire on orchid pollinators in eucalypt woodlands of South Australia. PhD Thesis. https://digital.library.adelaide.edu.au/dspace/handle/2440/113388.

Martín-Forés I, Bywaters SL, Sparrow B, Guerin GR (2022) Simultaneous effect of habitat remnancy, exotic species, and anthropogenic disturbance on orchid diversity in South Australia. *Conservation Science and Practice* **4**, e12652.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* ***403***, 853–858.

Pate JS, Dixon K (1982) 'Tuberous, cormous and bulbous plants.' (University of Western Australia Press: Nedlands, Western Australia)

Pierce S, Vagge I, Brusa G, Cerabolini BE (2014) The intimacy between sexual traits and Grime's CSR strategies for orchids coexisting in semi-natural calcareous grassland at the Olive Lawn. *Plant Ecology* **215**, 495–505.
Phillips RD, Hatley J, Li X, Dimon RJ, Reiter N (2024) Resilience to summer bushfire in the threatened orchid, *Caladenia tessellata*, in terms of pollination success, herbivory, and mycorrhizal associations. *Botanical Journal of the Linnean Society* **205,** 365–378.
Ramalho CE, Laliberte E, Poot P, Hobbs RJ (2014) Complex effects of fragmentation on remnant woodland plant communities of a rapidly urbanizing biodiversity hotspot. *Ecology* **95,** 2466–2478.
Ramsay RR, Dixon KW, Sivasithamparam K (1986) Patterns of infection and endophytes associated with Western Australian orchids. *Lindleyana* **1**, 203–214.
Reiter N, Pollard G (2013) The response of Grampians Duck-orchid and Grampians pincushion lily in Victoria to wild fire. *Australasian Plant Conservation: Journal of the Australian Network for Plant Conservation* **22**, 15–17
Ritchie AL, Svejcar LN, Ayre BM, Bolleter J, Brace A, Craig MD, Davis B, Davis RA, van Etten EJ, Fontaine JB (2021) A threatened ecological community: research advances and priorities for Banksia woodlands. *Australian Journal of Botany*.
Scaccabarozzi D, Cozzolino S, Guzzetti L, Galimberti A, Milne L, Dixon KW, Phillips RD (2018) Masquerading as pea plants: behavioural and morphological evidence for mimicry of multiple models in an Australian orchid. *Annals of Botany* **22**, 1061–1073
Scaccabarozzi D, Guzzetti L, Phillips RD, Milne L, Tommasi N, Cozzolino S, Dixon KW (2020) Ecological factors driving pollination success in an orchid that mimics a range of Fabaceae. *Botanical Journal of the Linnean Society* **194**, 253–269.
Scaccabarozzi D, Guzzetti L, Pioltelli E, Brundrett M, Aromatisi A, Polverino G, Vallejo-Marin M, Cozzolino S, Ren Z-X (2024) Evidence of introduced honeybees (*Apis mellifera*) as pollen wasters in orchid pollination. *Scientific Reports* **14**, 14076.s
Shefferson RP, Jacquemyn H, Kull T, Hutchings MJ (2020) The demography of terrestrial orchids: life history, population dynamics and conservation. *Botanical Journal of the Linnean Society* **192**, 315–332.
Thomsen AM, Davies RJP, Ooi MKJ (2024) The impacts of inter- and intra-seasonal burns on the terrestrial orchid *Pterostylis curta*. *Plant Ecology*.
Tremblay RL, Perez M-E, Larcombe M, Brown A, Quarmby J, Bickerton D, French G, Bould A (2009) Dormancy in *Caladenia*: a Bayesian approach to evaluating latency. *Australian Journal of Botany* **57**, 340–350.
Udy DG, Vance TR, Kiem AS, Holbrook NJ, Abram N (2024) Australia's 2019/20 Black Summer fire weather exceptionally rare over the last 2000 years. *Communications Earth & Environment* **5**, 317.
Wraith J, Pickering C (2019) A continental scale analysis of threats to orchids. *Biological Conservation* **234**, 7–17

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 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. Data from 30 transects for abundance and distribution of 17 orchid species in recently burnt or long unburnt areas.

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

Table S4. Data used to measure clonality, tuber size, lifespans, etc. (see 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. Location of Warwick Bushland. **B.** All major fires and fuel reduction burns in Warwick Bushland between 1973 and 2023. Colour shading is from the most recent in red to oldest in blue. **C**. The total number of fires in each 25 m grid square. **D**. Time since the most recent fire in each 25 m grid square. Background map is by Google.

Figure 3. Fire history for Warwick Bushland summarising data in Figure 2. Total major fire area (**A**) or frequency (**B**) by year. Fire frequency (**C**) or 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 (stars) to orchids by unseasonal fire in late autumn for *Leporella fimbria* (**D**) and *Pyrorchis nigricans* (**E**). **F.** Scorching of *Thelymitra macrophylla* by the fuel reduction burn (stars). **G**. *Pterostylis orbiculata* tubers sprout several months before emerging. **H**. *Caladenia flava* seed capsules after fire. **I**. *Pheladenia deformis* seed formed after fire. Seedlings of *Diuris magnifica* (**J**), *Thelymitra benthamiana* (**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.

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 of six orchid species in long unburnt or post-fire areas (see labels).

Figure 10. *Pheladenia deformis* pollination ecology. **A**. Pollination of burnt or unburnt plants. **B**. Changes to flowering capacity after fire. **C.** Transitions between vegetative, flowering or missing plants.

Figure 11. A. The relative abundance of 17 orchids in recently burnt (<3 years) or long unburnt (>20 years) areas on transects. **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 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 using data from transects with regression equations and correlation probabilities (see species labels).

Figure 13. Orchid density (**A**) and diversity (**B**) relative to time since fire on transects.

Figure 14. The average fire frequency and fire age where orchids occur (data from Table S4, name codes in Table 1). The average fire history for the entire site is also shown (red dot).

Figure 15. Overall fire tolerance rankings for 17 orchid species.

Figure 16. Correlations between tuber depth (**A**) or size (**B**) or key ecological trait indices (**C-F**) with the overall fire response index for 17 orchid species.

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, where it is a focus of education activities (friendsofwarwickbushland.com/walk-trails/jt020).

Figure S1. *Caladenia flava* flowering trends over two years. Graphs compare flowering (**A-B**) or pollination (**C-D**) 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 in monitored areas (**A-I**). The frequency distribution of fires by area is also shown (**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 also shown (**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 also shown (**J**).

Figure S5. Additional trait correlation graphs. **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	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 of 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	Ratio of plants in groups 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	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**
Average or total*	**-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	

Notes: 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

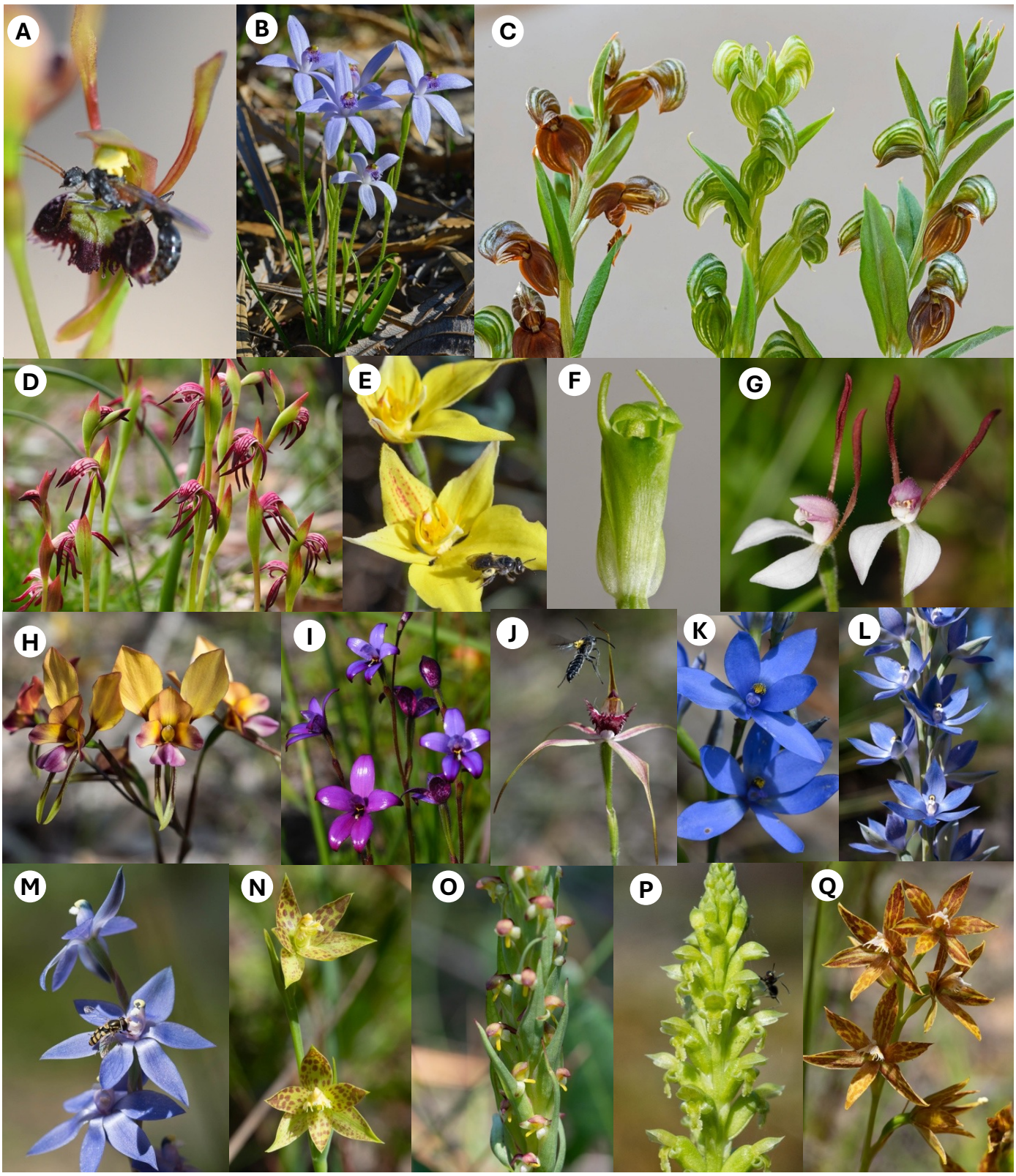
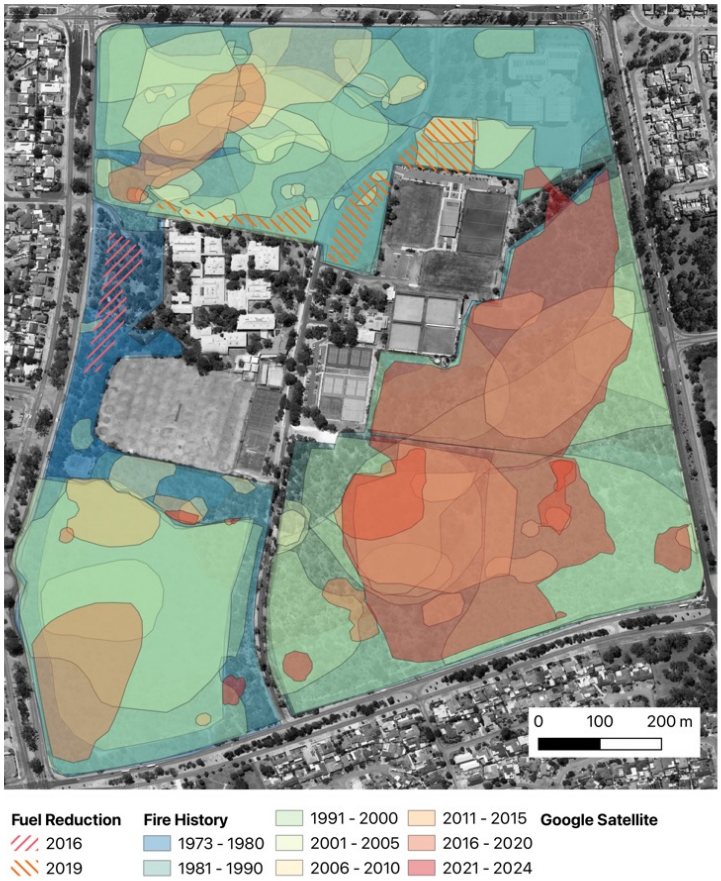


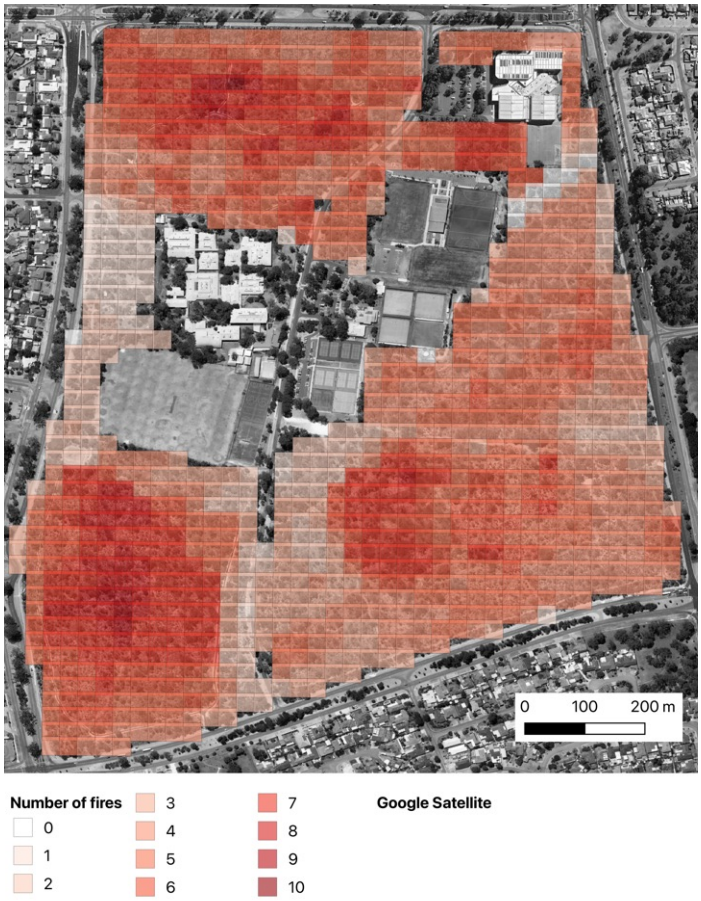
Figure 2. Warwick Bushland Fire History (C & D are 25m grids)

A. Location

B. Major fires



C. Number of fires



D. Years since a major fire

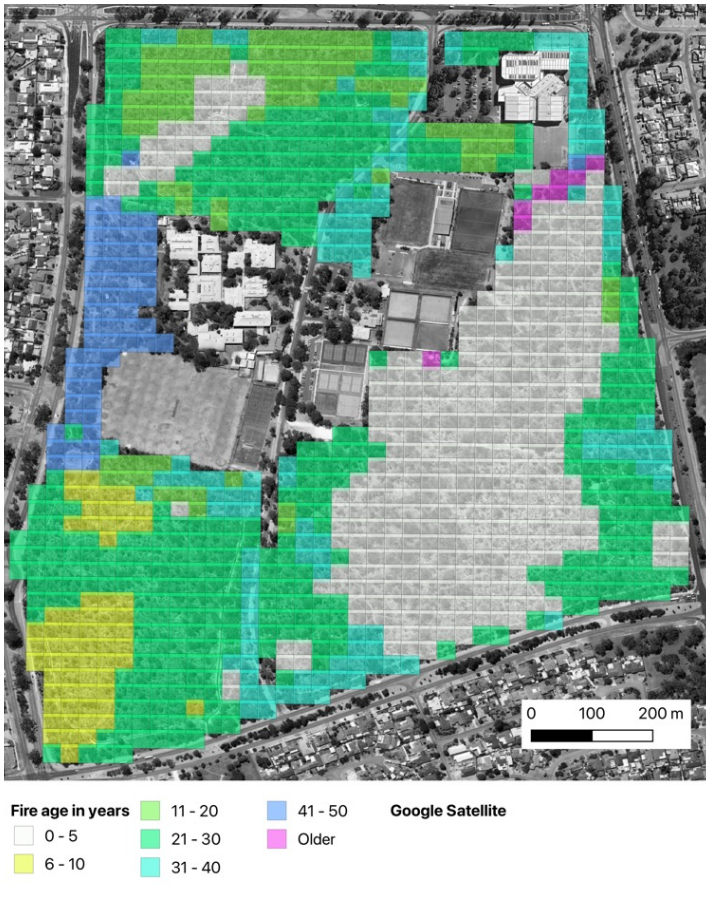
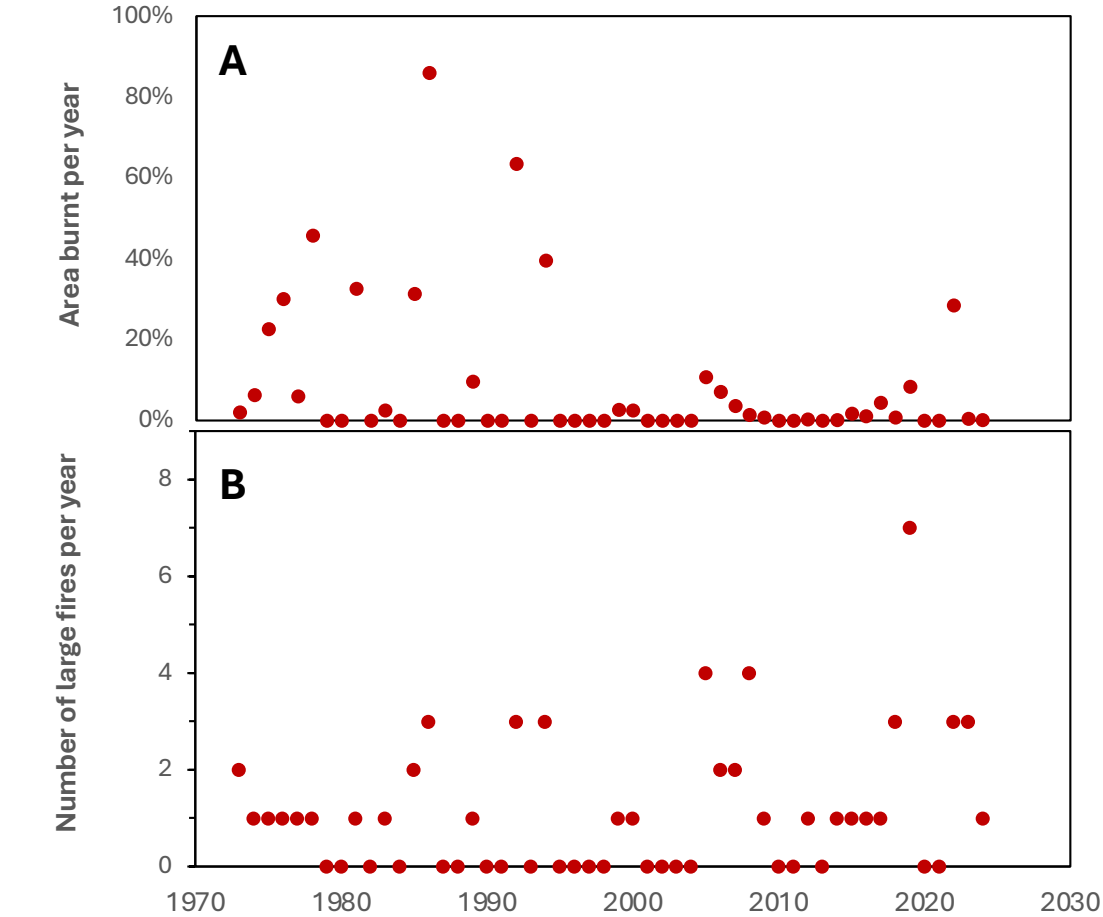
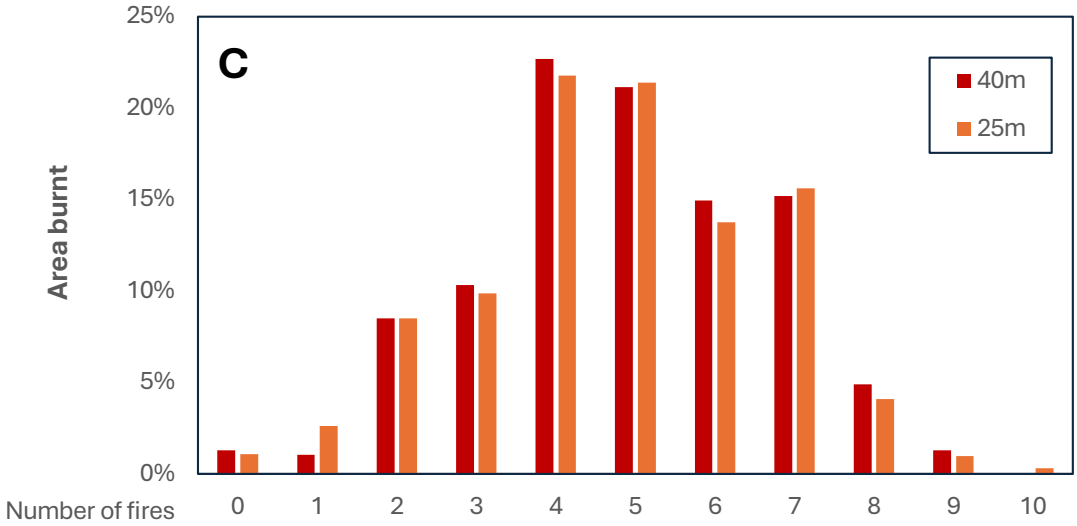


Figure 3. Fire area totals and frequency in Warwick Bushland





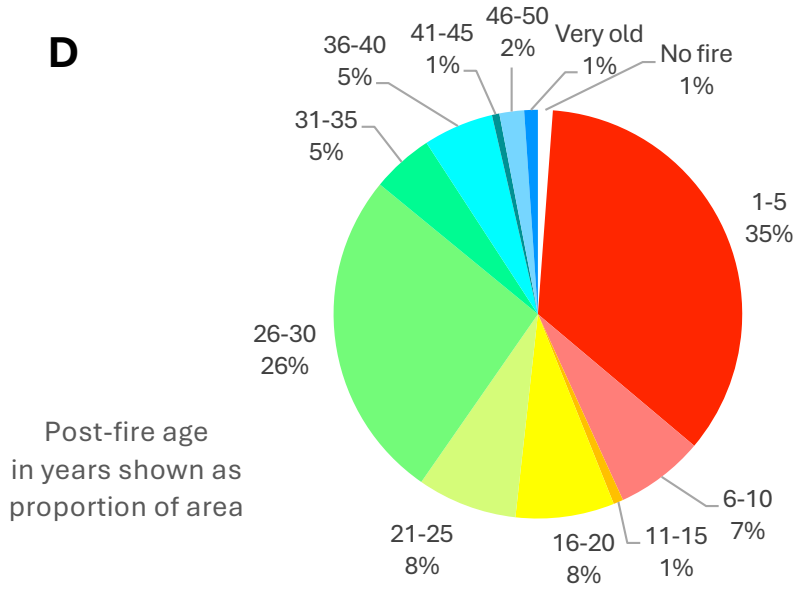
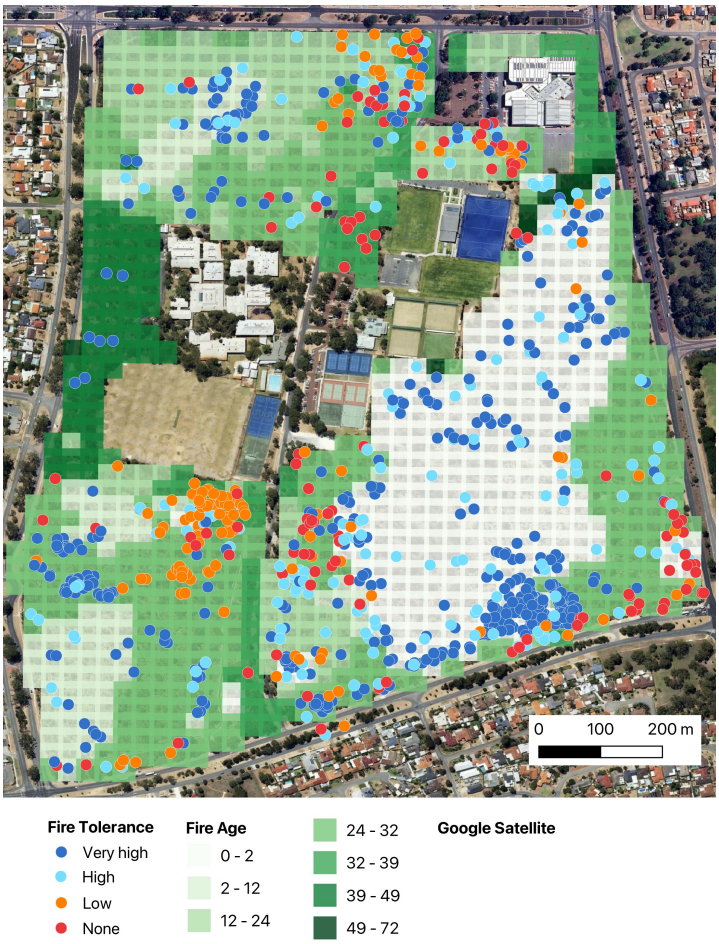


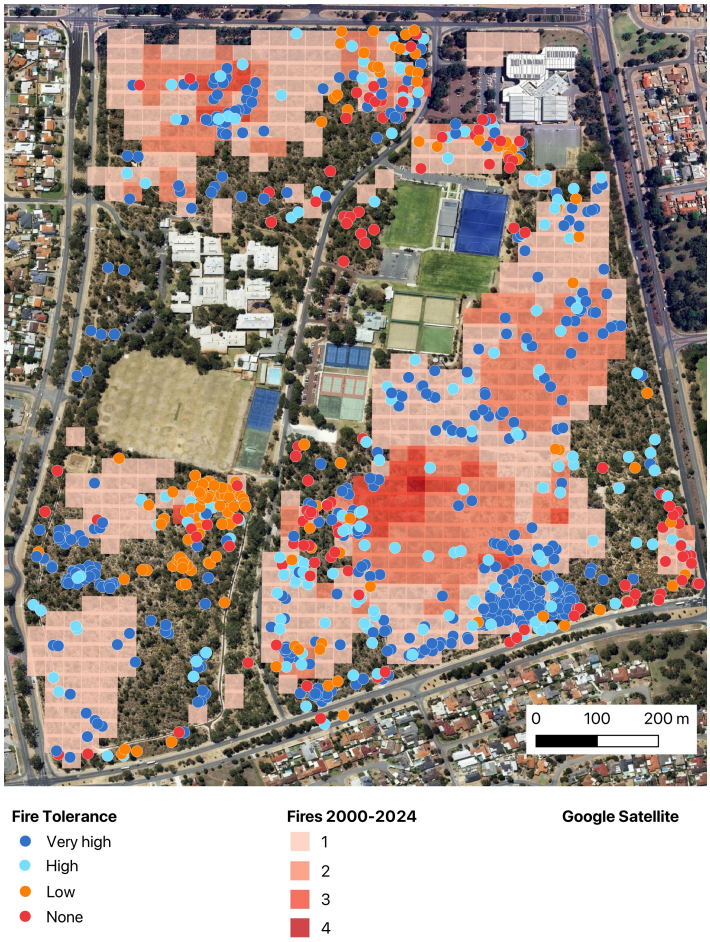
Figure 4. Observations

Figure 5. Locations of orchids relative to recent fires

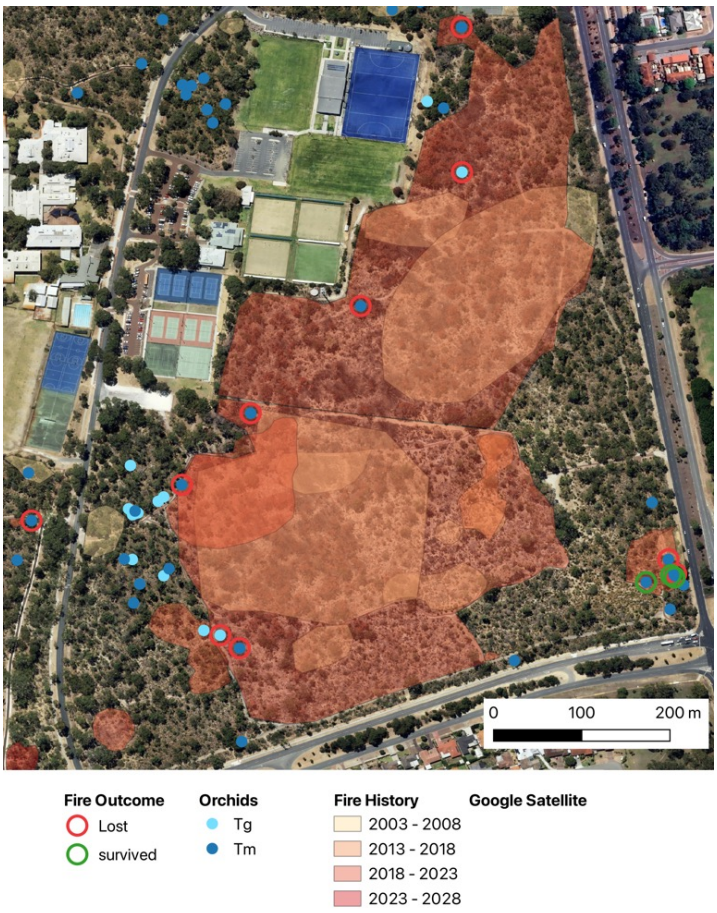
A. Orchid distributions and time since fire



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**

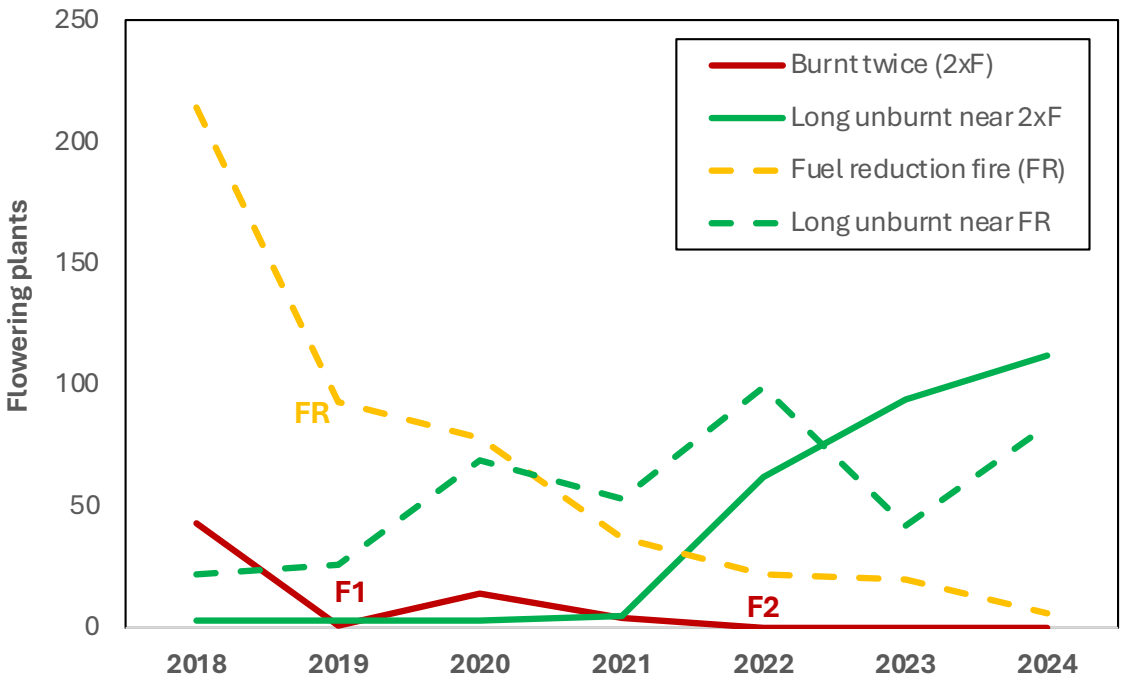
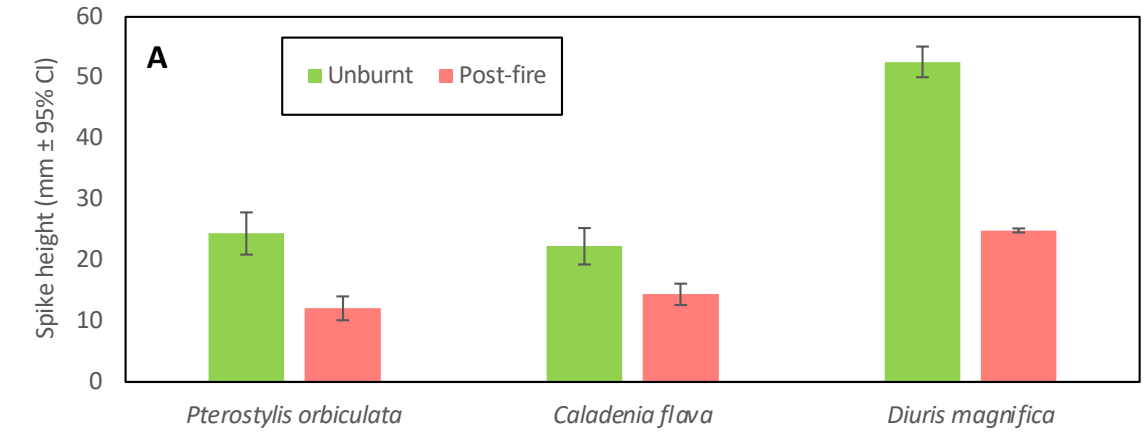
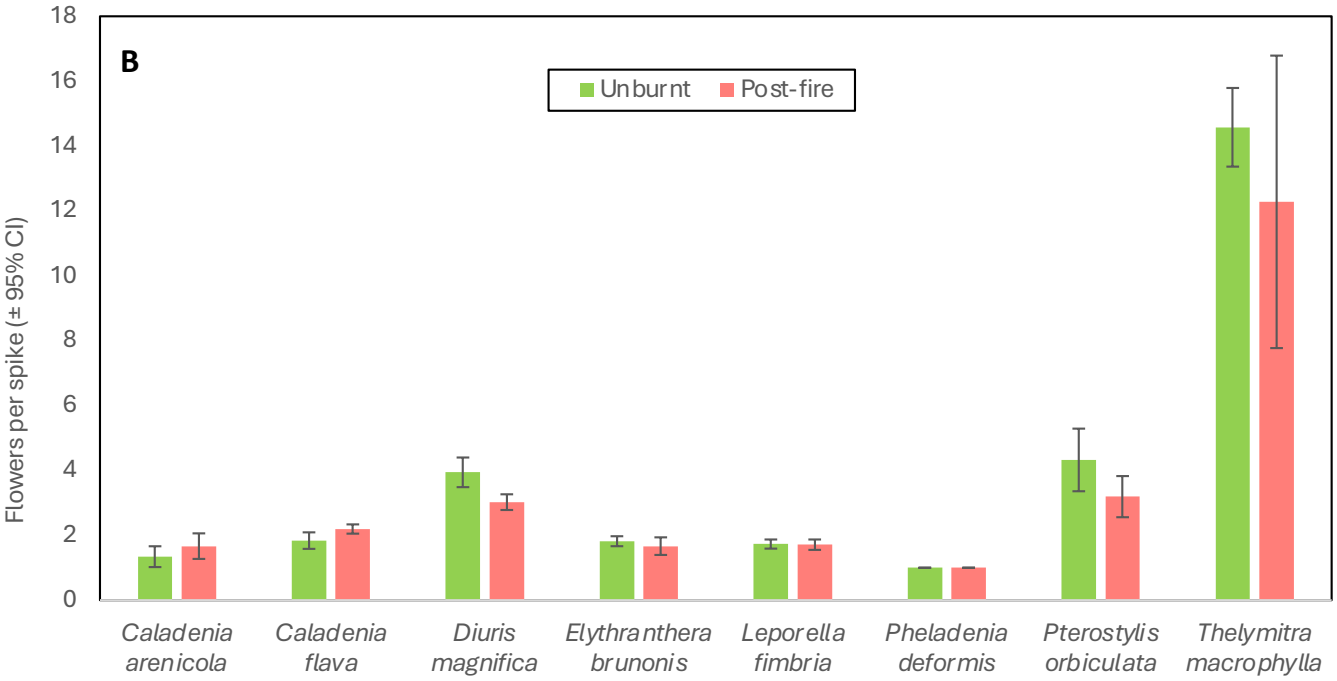


Figure 7. Fire effects on plant growth and flower production





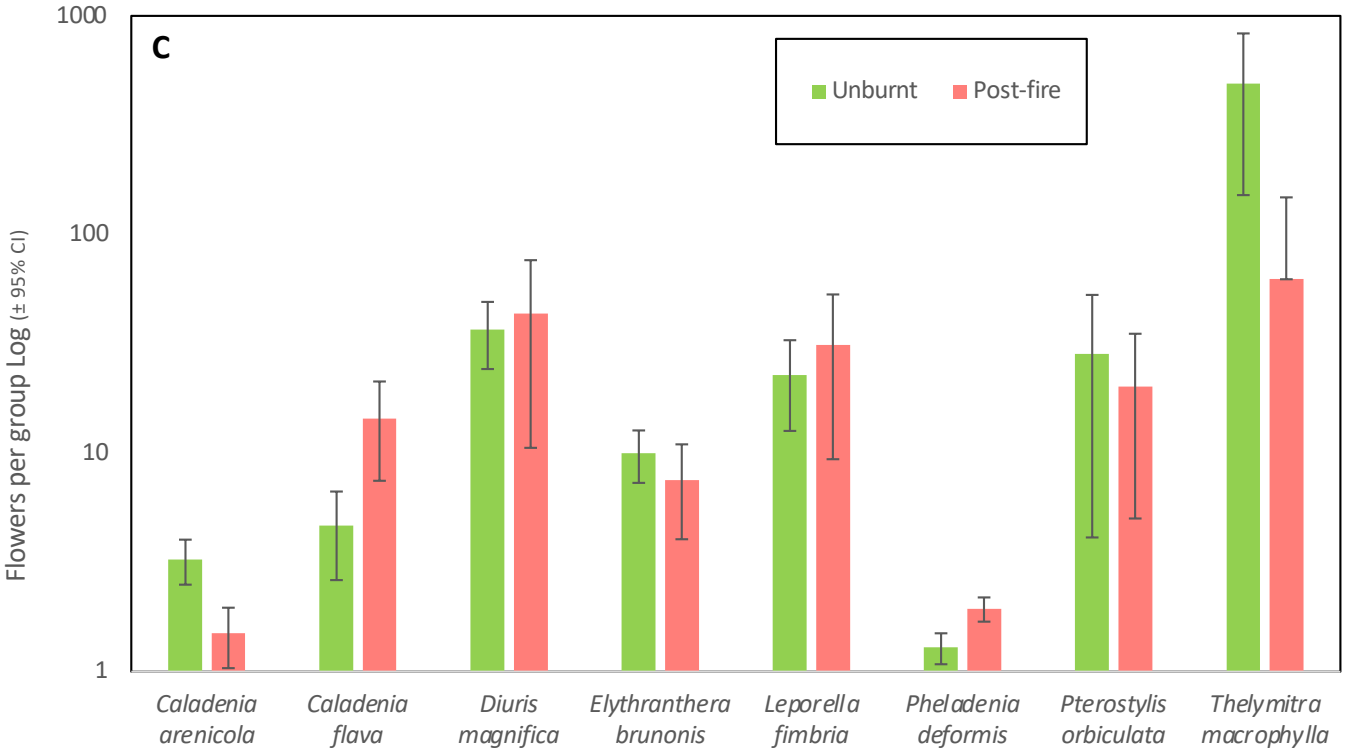


Figure 8. Fire effects on pollination

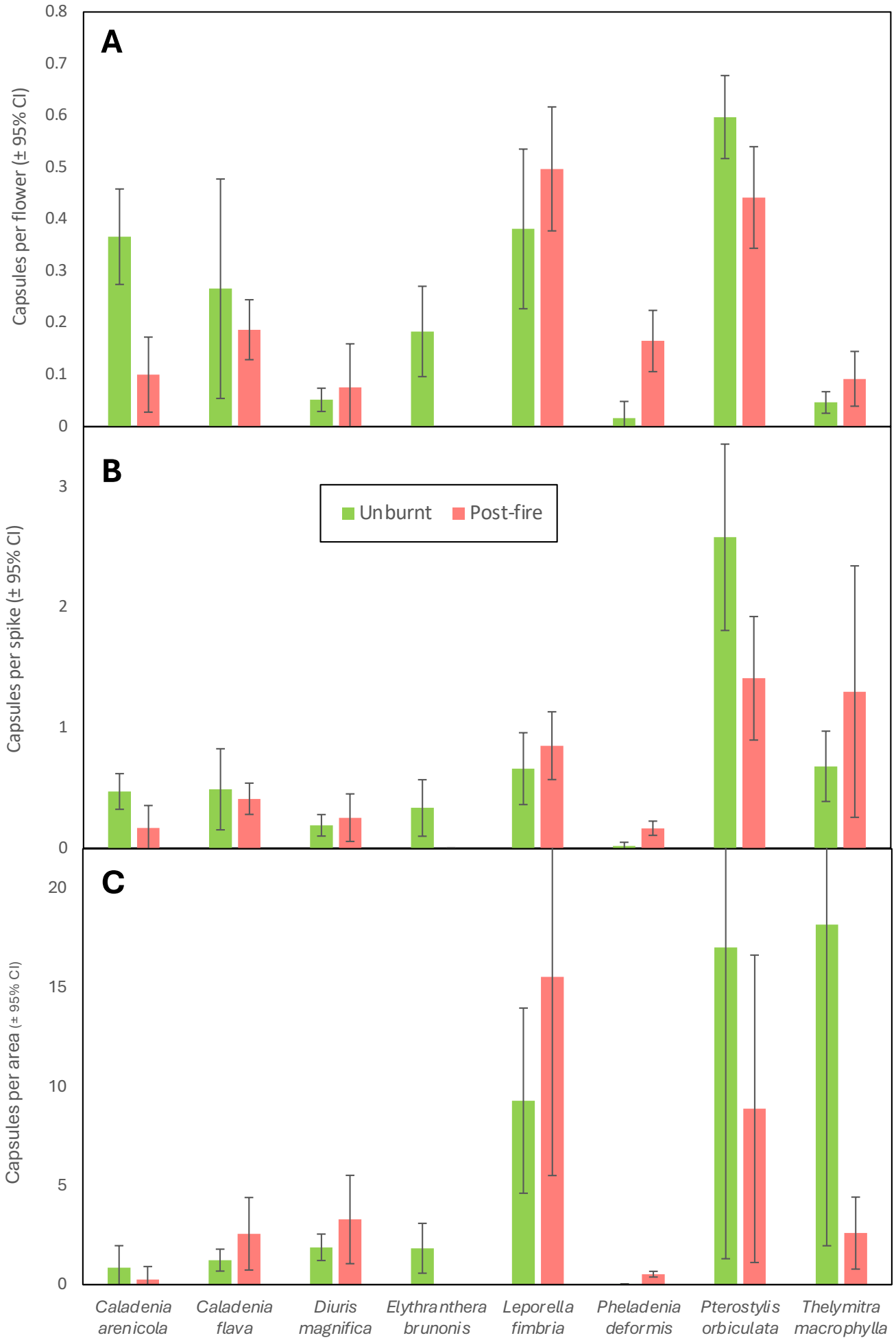


Figure 9. Density effects on pollination due to fire

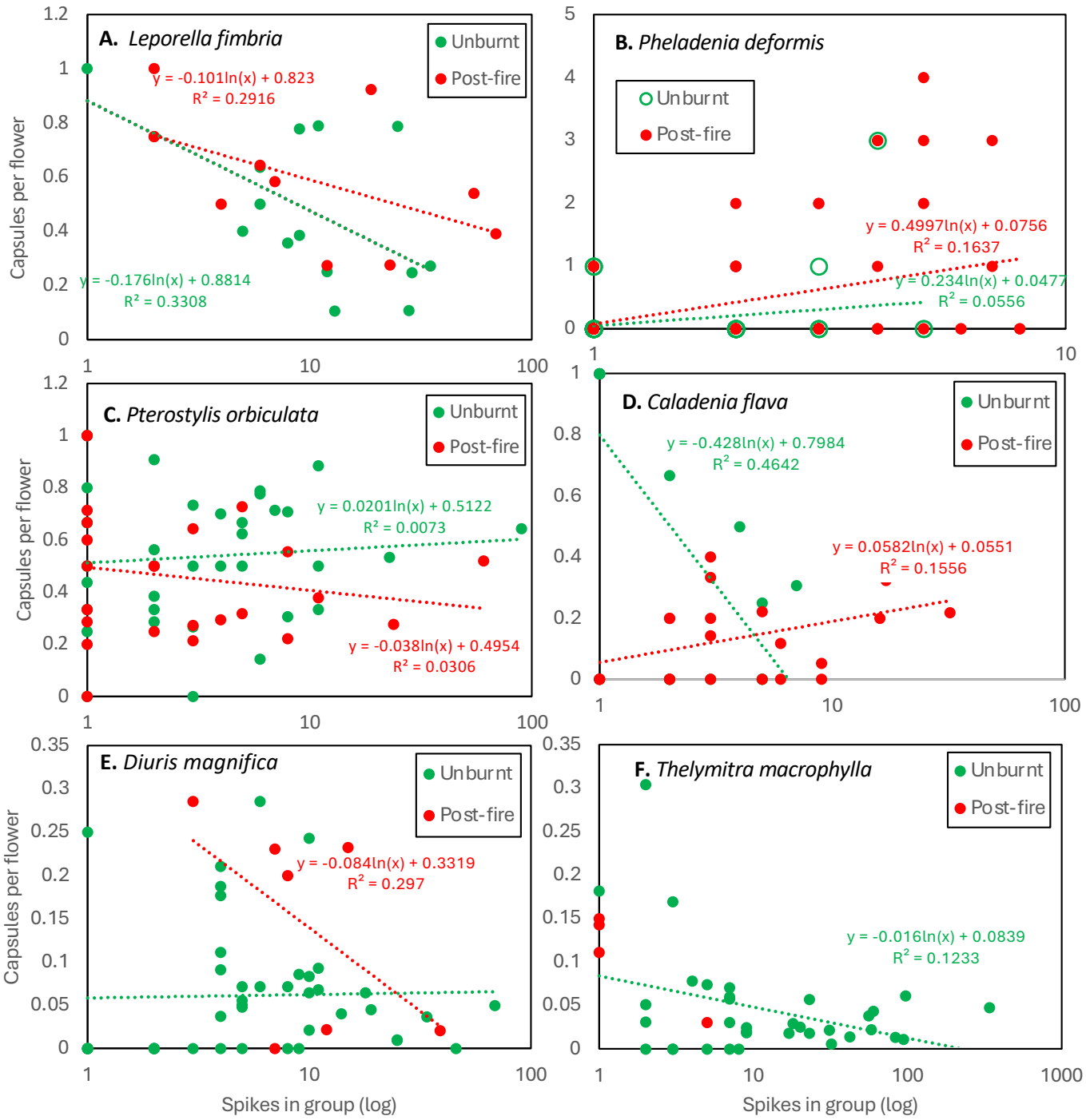


Figure 10. Blue beard orchid case study

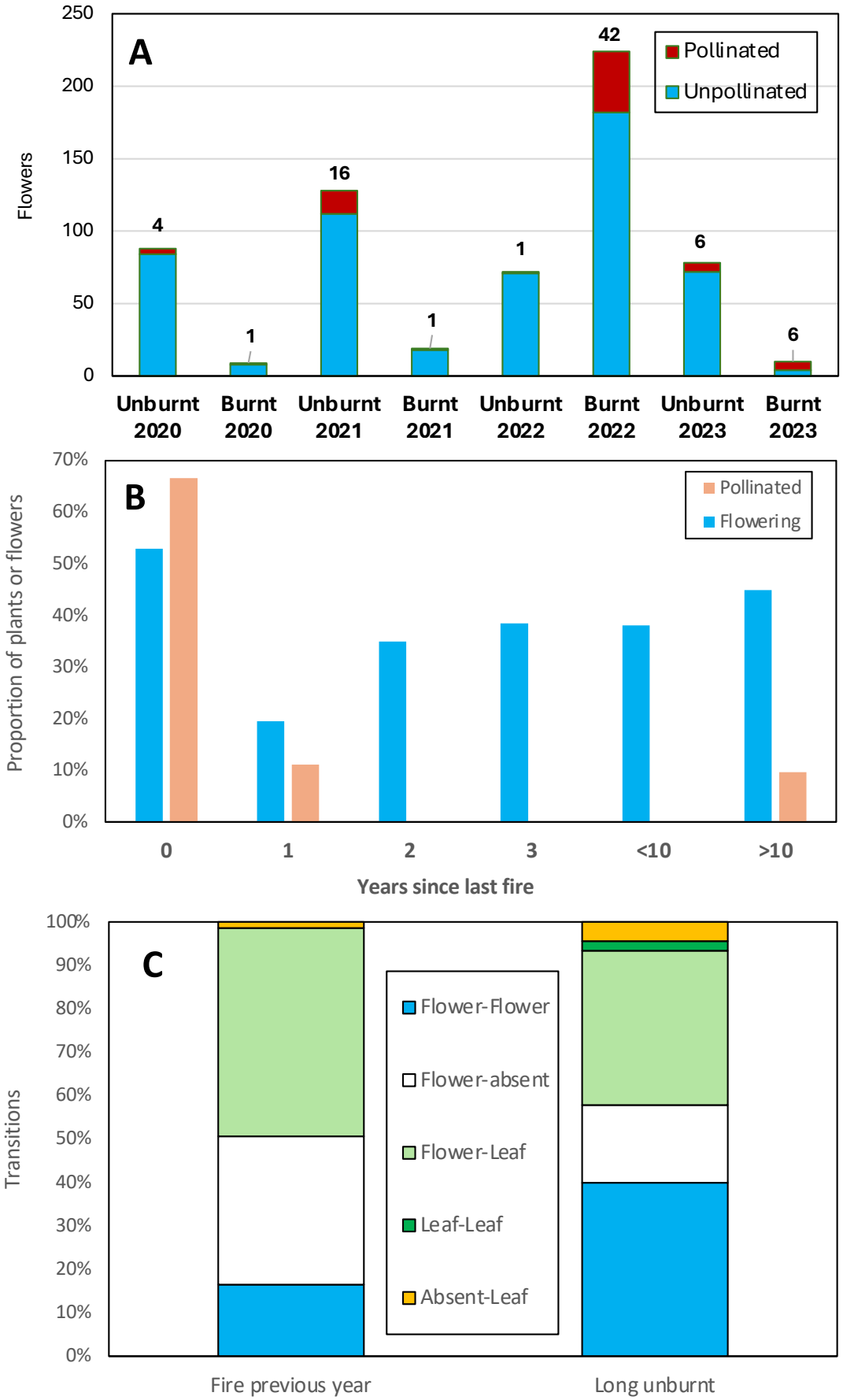
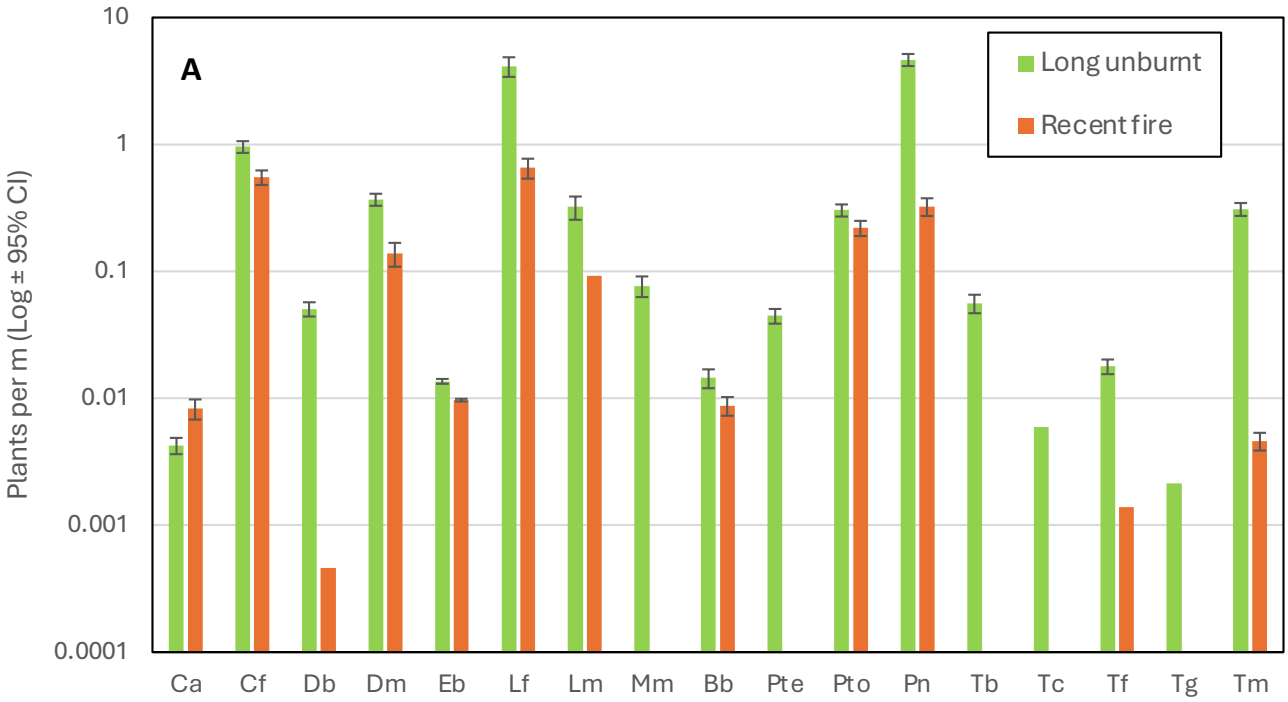
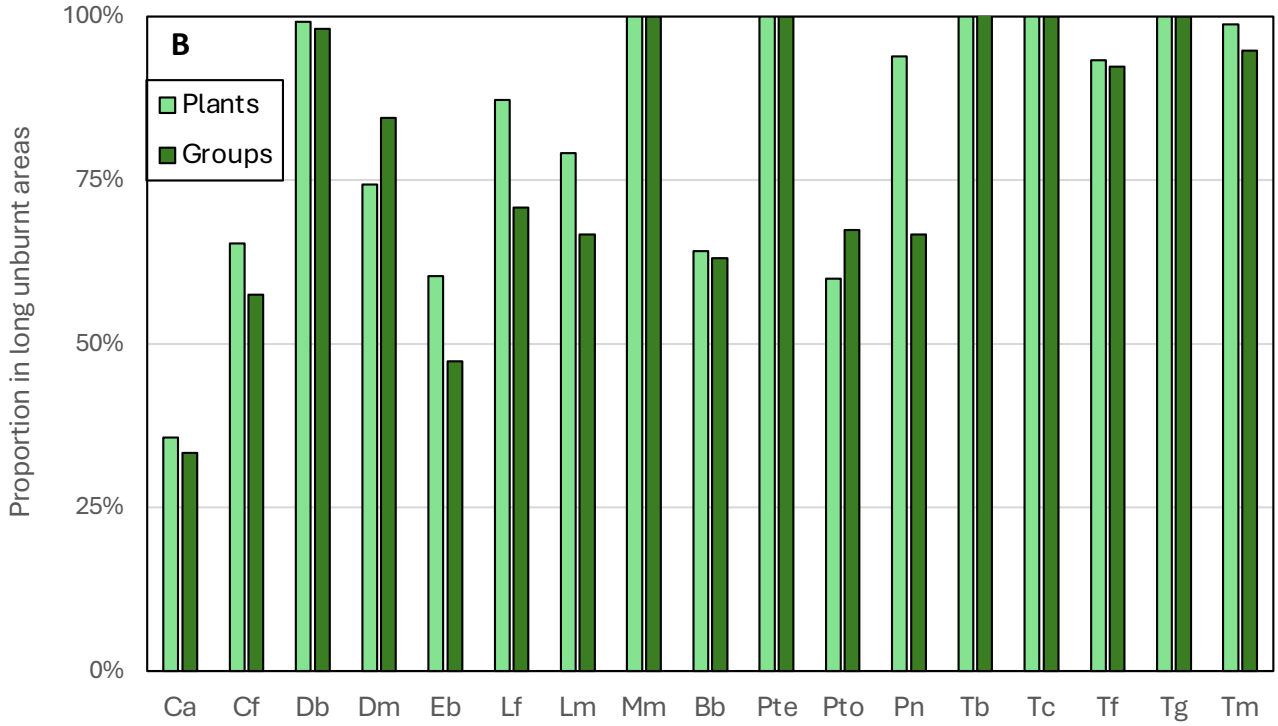


Figure 11. Fire effects on orchid abundance on transects





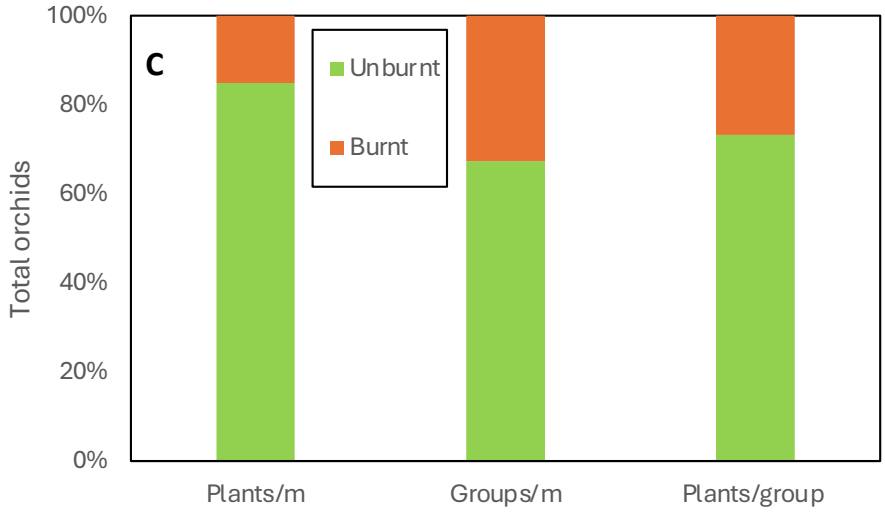


Figure 12. Fire age vs orchid abundance from transect data

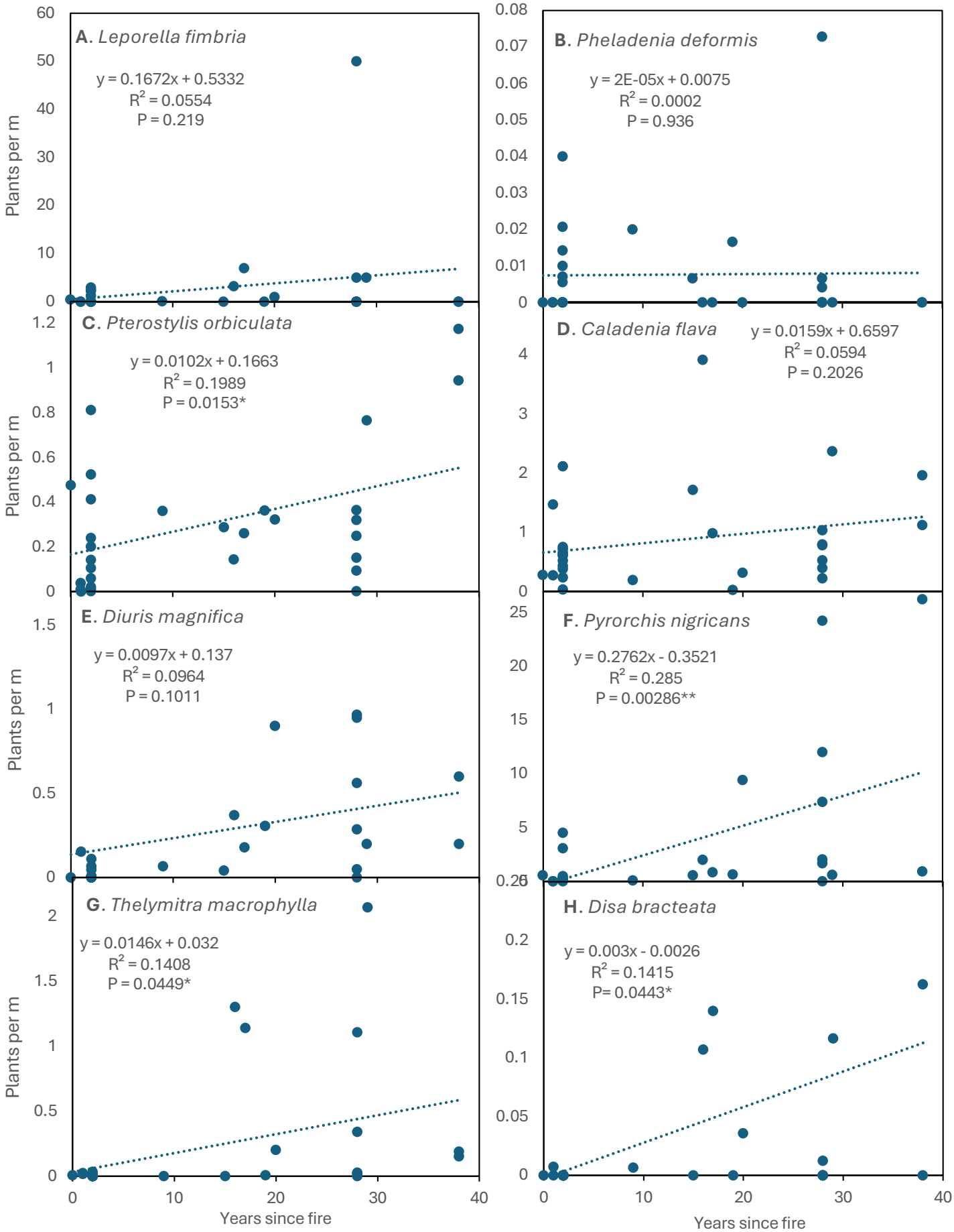


Figure 13. Fire tolerance rankings

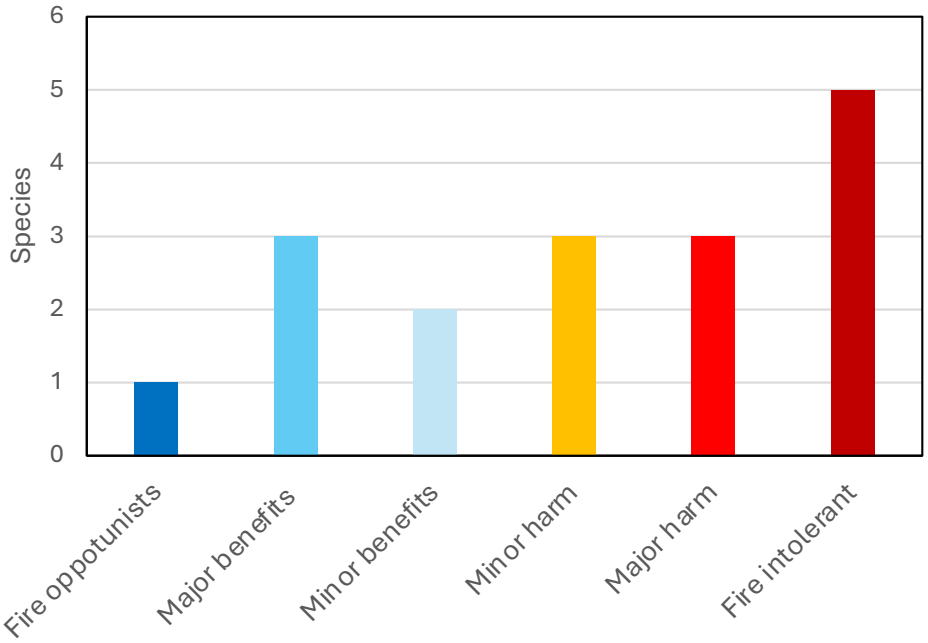


Figure 14. Fire response and trait correlations

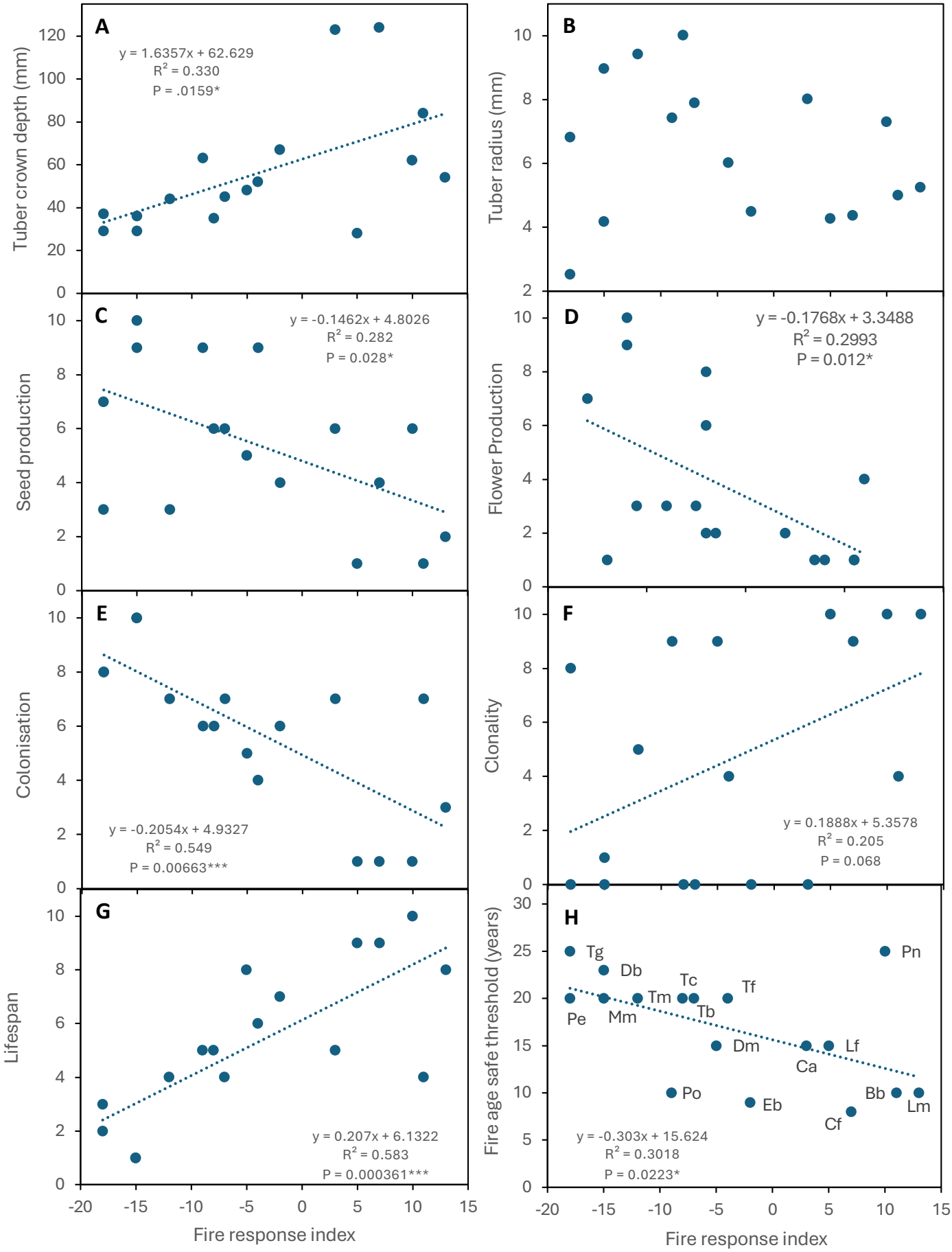


Figure 15. Orchid density and diversity relative to fire history on transects

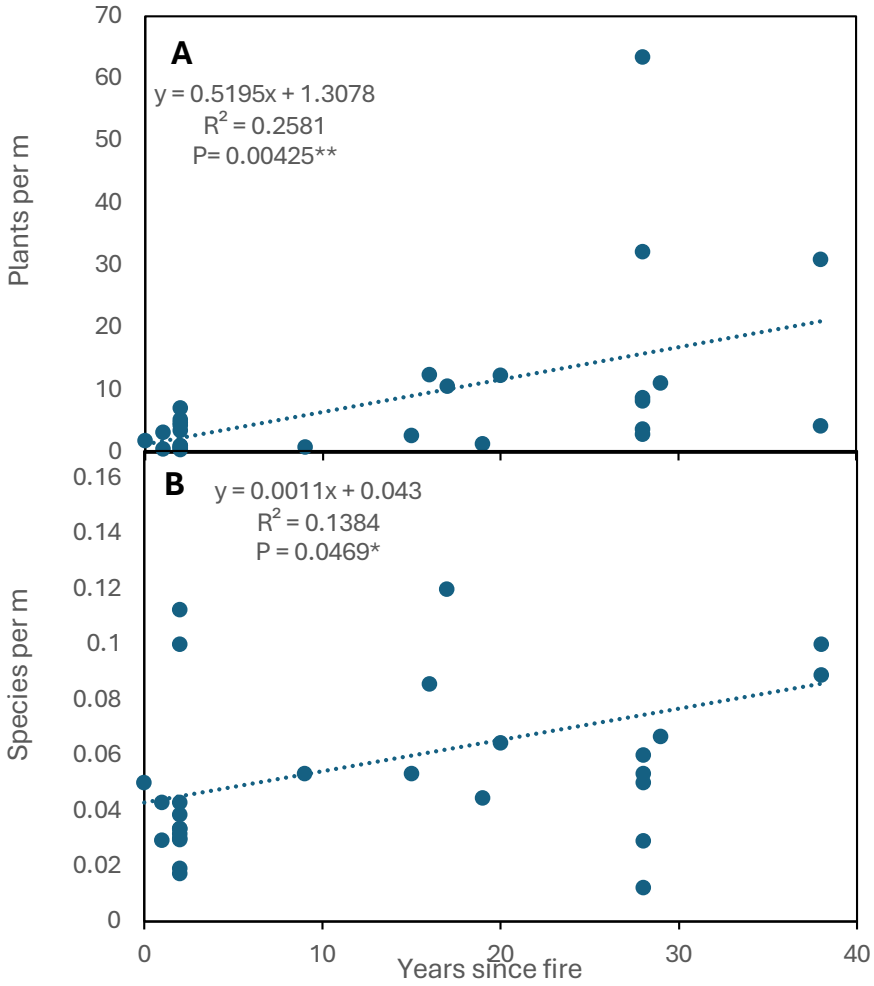


Figure 16. Orchid occurrences relative to fire history from monitoring

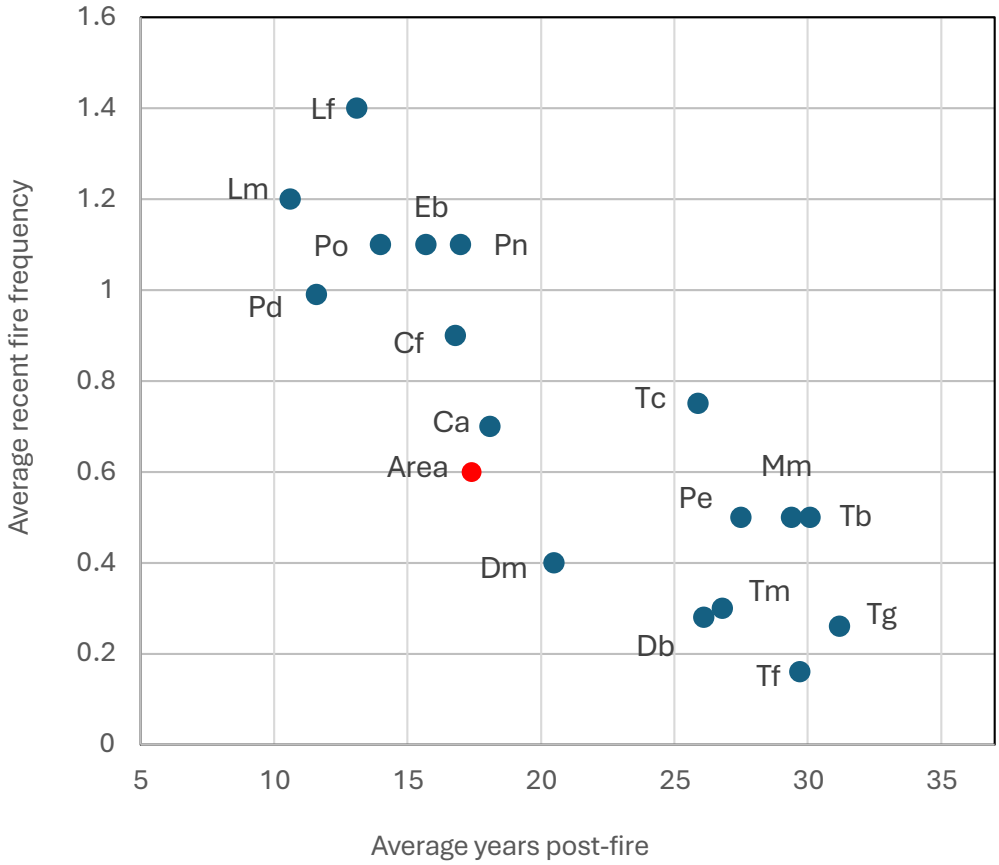


Figure 17. Blue sun orchid (*Thelymitra macrophylla*)

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

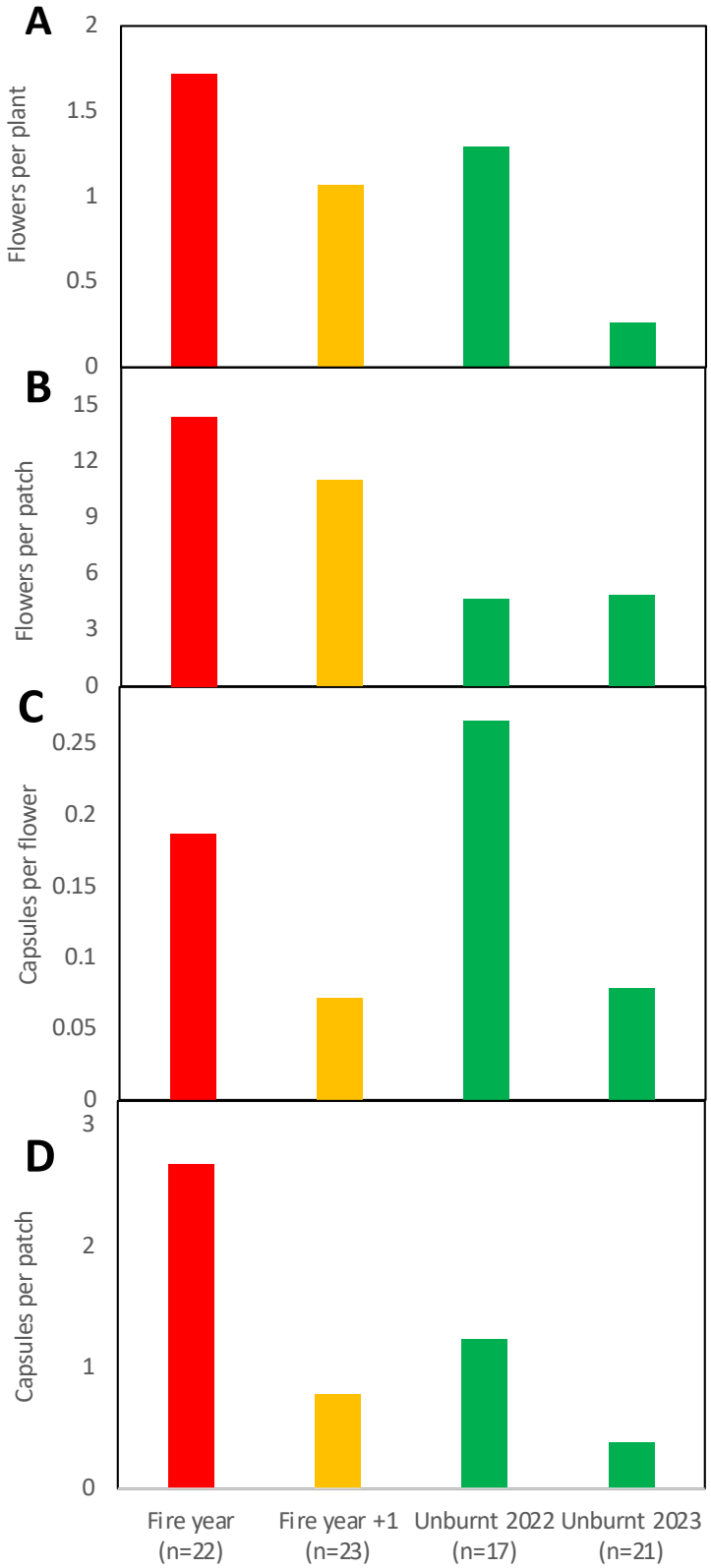


Figure S2. Time since fire & flowering productivity

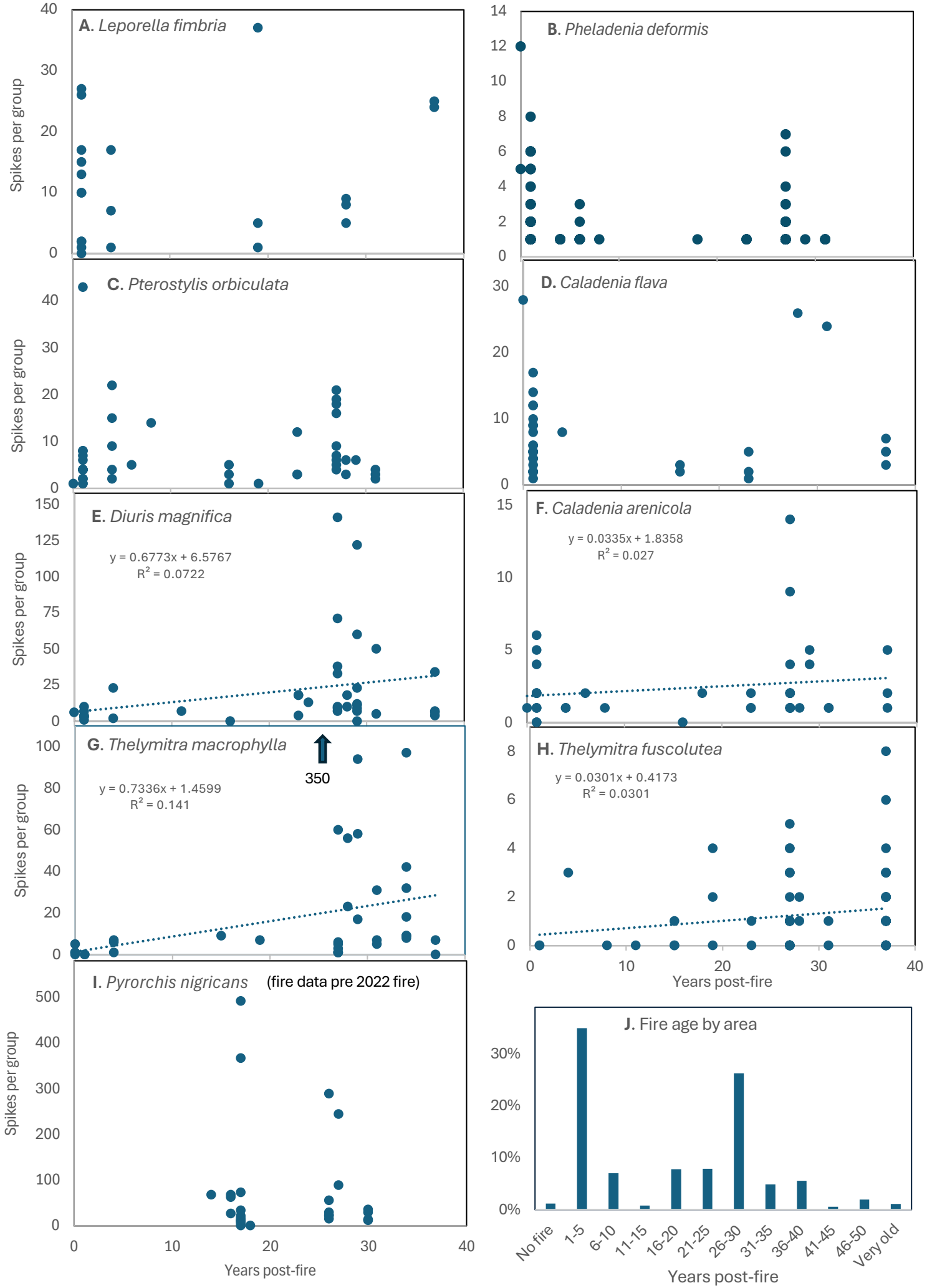


Figure S3. Flowering productivity relative to total fires

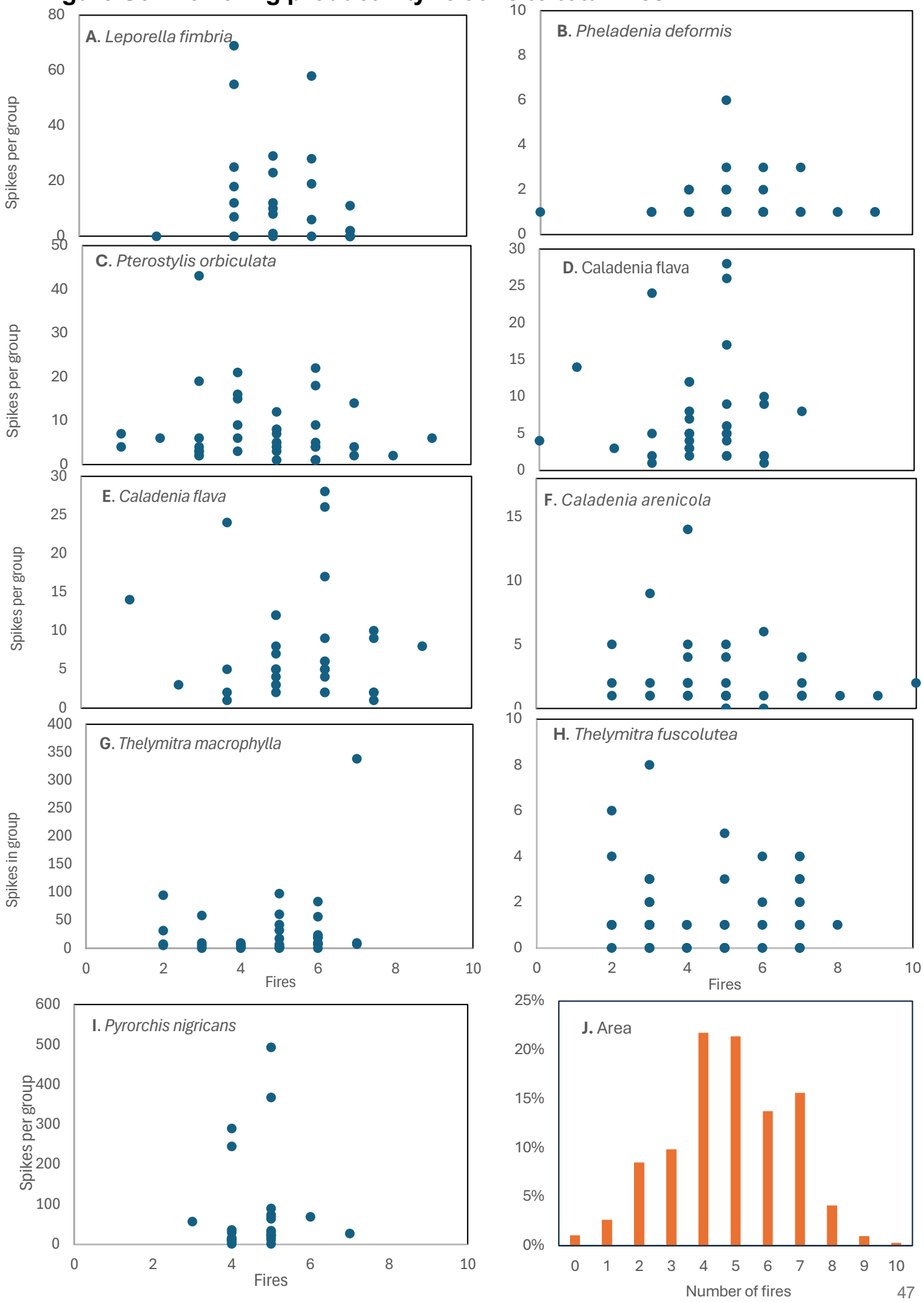


Figure S4. Flowering productivity relative to recent fires (2000-2023)

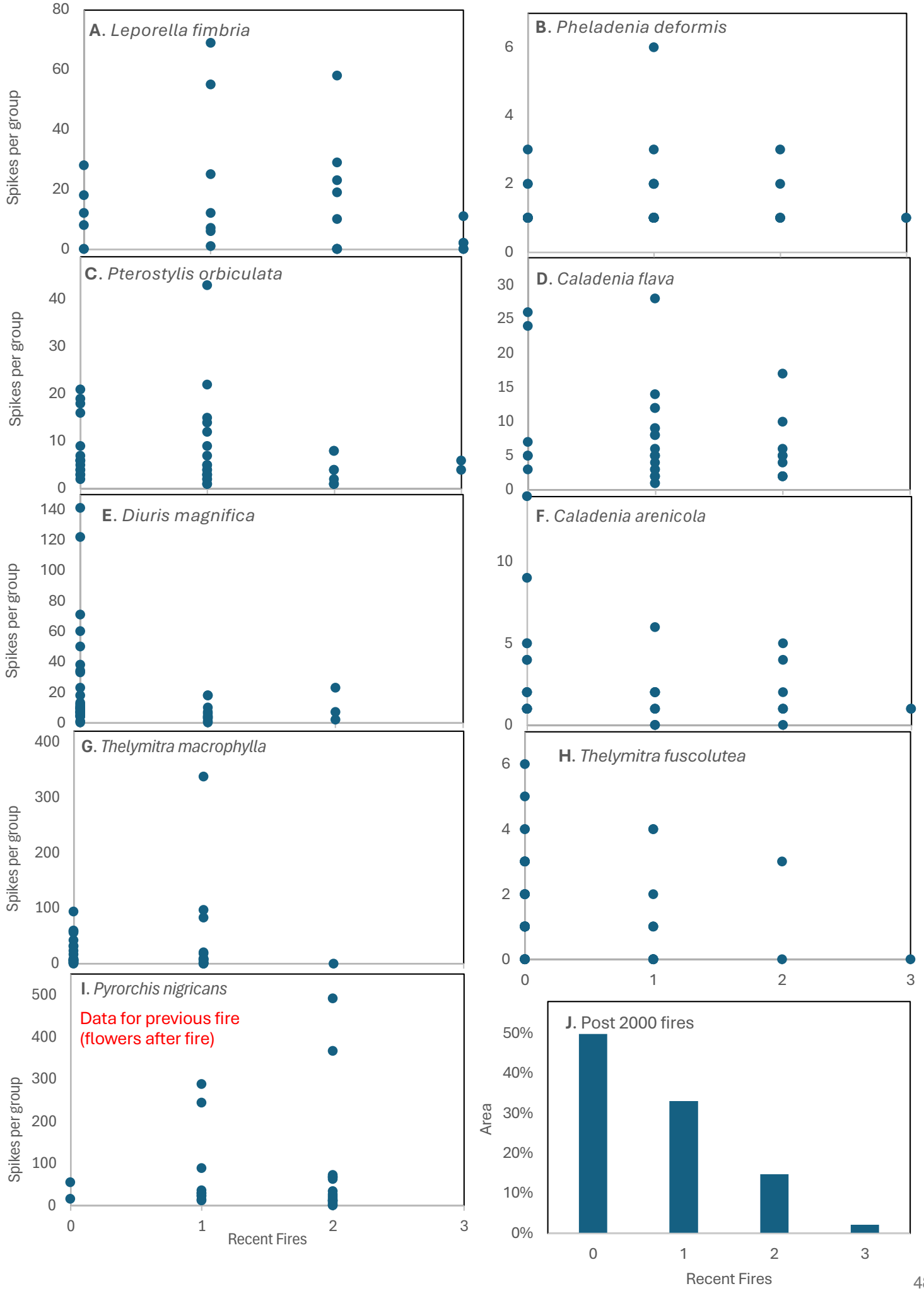
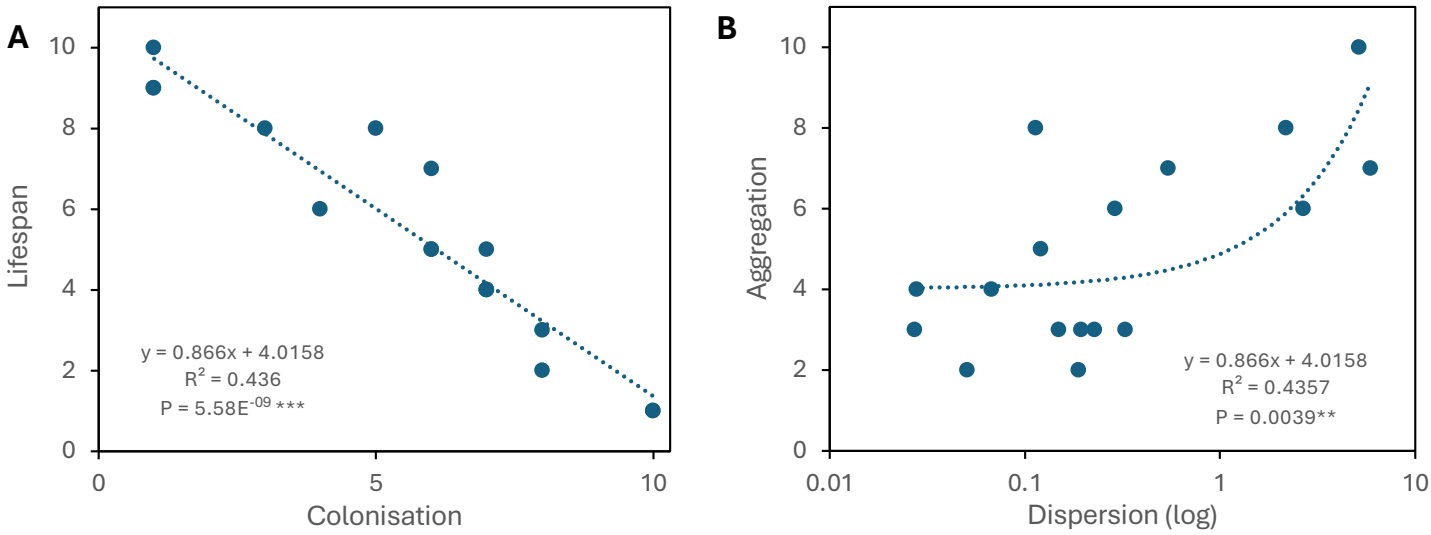



Figure S5. Additional trait correlation graphs