Article

Remarkable Resilience of Forest Structure and Biodiversity Following Fire in the Peri-Urban Bushland of Sydney, Australia

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Abstract: In rapidly urbanizing areas, natural vegetation becomes fragmented, making conservation planning challenging, particularly as climate change accelerates fire risk. We studied urban forest fragments in two threatened eucalypt-dominated (scribbly gum woodland, SGW, and ironbark forest, IF) communities across ~2000 ha near Sydney, Australia, to evaluate effects of fire frequency (0–4 in last 25 years) and time since fire (0.5 to >25 years) on canopy structure, habitat quality and biodiversity (e.g., species richness). Airborne lidar was used to assess canopy height and density, and ground-based surveys of 148 (400 m^2) plots measured leaf area index (LAI), plant species composition and habitat metrics such as litter cover and hollow-bearing trees. LAI, canopy density, litter, and microbiotic soil crust increased with time since fire in both communities, while tree and mistletoe cover increased in IF. Unexpectedly, plant species richness increased with fire frequency, owing to increased shrub richness which offset decreased tree richness in both communities. These findings indicate biodiversity and canopy structure are generally resilient to a range of times since fire and fire frequencies across this study area. Nevertheless, reduced arboreal habitat quality and subtle shifts in community composition of resprouters and obligate seeders signal early concern for a scenario of increasing fire frequency under climate change. Ongoing assessment of fire responses is needed to ensure that biodiversity, canopy structure and ecosystem function are maintained in the remaining fragments of urban forests under future climate change which will likely drive hotter and more frequent fires.

Keywords: Cumberland Plain; disturbance; Eucalyptus; fire regime; habitat; leaf area index; lidar; sclerophyll; succession; woodland; urbanization

1. Introduction

Globally, climate change is creating more extreme conditions resulting in longer fire seasons associated with more extensive and intense fires in many fire-prone environments. An especially dangerous bushfire future is projected for Australia's temperate forest regions [1], as warming intensifies the decline of southern Australia's winter rainfall and increases the number of extreme heat events [2]. This combination will drive greater likelihood of intense forest fire conditions [3], with more hot, dry, windy weather, such as recently witnessed during the "Black Summer" of 2019–2020, which resulted in the most extensive forest fires in Australia's recorded history [1,4,5]. These mega-fires pose increasing risks to human life, biodiversity and socioeconomic wellbeing in Australia and other

fire-prone regions globally [6,7] (Figure 1). As extreme fire conditions increase in frequency near urban areas, the probability of damage to life and property has risen exponentially in recent years [5,8].
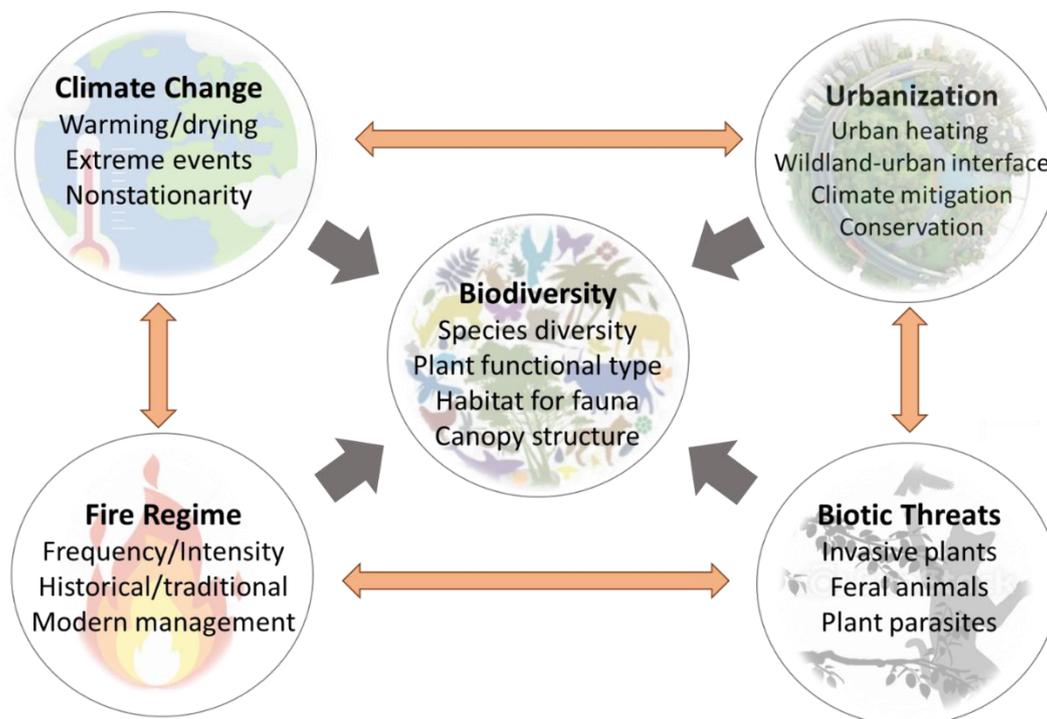

Figure 1. Conceptual figure showing the compound/interacting threats to biodiversity, including species composition, plant functional type, habitat and canopy structure, in peri-urban forests of southeast Australia and globally. In mid-latitudes climate warming, drying and extreme events are becoming more common, leading to nonstationarity, in which future conditions cannot be predicted from the past. Fire regimes have become more intense, while recognition of traditional (indigenous) management is increasing. Urbanization is associated with challenges of development at the wildland–urban interface and urban heat islands, but these can be mitigated with adaptive conservation planning and policies. Biotic threats may require more aggressive management in some cases. The biggest uncertainties for biodiversity protection may be related to the interactive nature of all these threats.

Altered fire regimes pose major threats to forest ecosystems worldwide [9], and the recovery of ecosystem structure and function may be inhibited by low resilience [10]. However, many Australian forests and woodlands (collectively termed bushland) are resilient to fire owing to millennia of co-evolution [11]; they are adapted to recover from fire and indeed a number of native plant species rely on fire to complete their life cycle [12]. For instance, many species require fire cues such as smoke [13,14] or heat [15] to germinate seed, induce flowering or release seed [16]. The passage of fire also creates a post-fire environment with higher light and soil nutrient availability [14] and reduced ground-cover competition, increasing opportunities for many species to regenerate and thus increase local vegetation diversity [17]. Within Australian eucalypt communities approximately 70% of plant species resprout following fire from stems or roots, while 27% are obligate seeders unable to resprout and reliant on regeneration after fire from seed. The remainder are killed by fire and do not reappear following fire until re-dispersed back into the area [18]. Despite these traits, the increased risk of extreme fires brought about by climate change [1] may exceed the resilience and adaptive capacity of some Australian ecosystems [12], with potentially negative impacts on native biodiversity and ecosystem function. However, the resilience and recovery of biodiversity—including numbers of species, plant functional

types, habitat quality, etc. (Figure 1)—and ecosystem functioning in response to increasingly frequent and extreme fires in communities which comprise species of differing functional types, particularly seeders and resprouters, has not been well studied [6]. Our study investigated responses to fire frequency and time since fire in two contrasting communities.

Monitoring recovery of ecosystem structure and function following disturbance so as to evaluate resilience has traditionally involved time consuming on-ground biodiversity surveys [10]. These enable detailed tracking of responses by plant functional types, growth forms and individual species such as invasive weeds or threatened species. Recently, remote sensing technology, particularly application of light detection and ranging (lidar) methods, has dramatically expanded the spatial extent and the temporal resolution of vegetation monitoring [19] at a broader scale, but with some loss in specific plant species or functional group responses. Forest canopy structure can be characterized using lidar in areas of different burn severities or frequencies to evaluate effects of fire (and its management) on recovery over varying times since burning [20,21]. Moreover, the three-dimensional ecosystem structure can be a key predictor of ecosystem function, if morphological traits such as height, canopy cover and structural complexity are calculated in a straightforward and reproducible manner [22,23]. High resolution maps of the three-dimensional structure of forest canopies can inform biodiversity conservation efforts [23], because structurally complex canopies (such as those with several layers, or with a high variance of heights) indicate diverse species composition and plant ages and create a wide range of habitats supporting wildlife [24]. Spatially explicit maps of forest structure recovery following fires of different age, severity or intensity at high spatial resolution are increasingly used to inform fire management planning [25,26].

Healthy natural environments within urban settings are recognized as critical to mitigate the effects of climate change and improve livability [27,28]. However, urban development situated alongside fire-prone ecosystems pose challenges to landholders and authorities aiming to conserve biodiversity while minimizing threats to life and property [29,30]. The wildland–urban interface (WUI) has expanded globally, posing increasing needs for interdisciplinary research and knowledge transfer [31]. Colonization and urbanization in Australia and elsewhere have also disrupted Indigenous land management practices where fire was previously more frequently used to manage natural resources [32]. However, large uncertainties remain regarding pre-European ecology and fire regimes [33], especially in densely settled areas such as the Sydney basin where Aboriginal people were forcibly removed and displaced from their land [34]. Prior to European settlement, regular burning of some communities is believed to have resulted in lower tree and shrub cover and higher grass, sedge and forb cover in some Australian woodlands and forests, a pattern which is thought to have been reversed since Indigenous land management ceased [33]. However, debate around this topic is ongoing [34], and more research is needed on fire resilience and management at the WUI in the context of Australia's highly diverse forest biomes [35].

Sydney's threatened bushland provides important habitat for native plant and animal species, many now rare and significant at regional, state and national levels [36,37]. Over 200 years of land clearance for agriculture, forestry, mining and urbanization in the Sydney basin had reduced native vegetation cover to 8.8% of its pre-European extent by the late 1990s [37]. Development and urbanization are continuing across peri-urban areas of greater Sydney, whose human population is expected to grow from 5 million residents in 2020 to over 9 million by 2050 [38]. With ongoing urbanization, fire risk mitigation becomes increasingly difficult as options for fuel hazard reduction are reduced, while the WUI and probability of ignition grow. Reducing fuel loads through hazard reduction burns for the protection of life and property whilst ensuring that fire intervals are suitable for species persistence in these fire-dependent ecosystems is an ongoing challenge. Disturbances that are too frequent to allow plants to reach reproductive maturity and re-establish between fires, or so infrequent as to exhaust seed banks, can each cause population decline and potential local extinction [12,39,40].

We used a space-for-time experimental design employing remote sensing lidar and detailed on-ground surveys to evaluate effects of fire on canopy structure, habitat quality and plant diversity in two eucalypt-dominated Threatened Ecological Communities (TECs). We hypothesized that canopy leaf area, height and fauna habitat value (e.g., woody debris, litter and tree hollows) would increase with time since the last fire, and that vascular plant species richness (i.e., number of species) would respond to fire differently in the two communities. Specifically, we expected that higher fire frequencies and/or decreased fire intervals would be associated with reduced species richness and cover in the Scribbly Gum Woodland (SGW) community, because of the predominance of the shrub and herbaceous cover growth forms and higher numbers of species (both resprouters and obligate seeders). Conversely, we expected the Castlereagh Ironbark Forest (IF), with its lower shrub and herbaceous ground cover but greater tree cover and height, would have a more rapid post-fire canopy recovery and more stable richness and cover scores under higher fire frequencies. We expected that abundance of resprouting eucalypts in both communities would be associated with recovery of canopy structure over time since fire, and that the cover of obligate seeders, shrubs and exotic weeds would decrease in both communities with fire frequency. The findings from this case study may inform local conservation and management decisions and provide insights for biodiversity conservation in other fire-dependent regions undergoing rapid urbanization and increased fire activity associated with climate change.

2. Study Area

The western portion of the broader Cumberland subregion in Sydney, NSW [41] (Figure 2) lies between the Kurrajong-Ebenezer rise to the north-west, Woronora Plateau to the south-east, Hornsby Plateau to the north-east and the Blue Mountains Plateau to the west and southwest. It consists of generally low-lying (20–80 m asl), gently undulating country with low hills on Wianamatta Group finer grained sediments and Tertiary and Quaternary alluvium [41,42]. Mean annual rainfall of our study area is approximately 840 mm; average January maximum temperature for the area is 31.2 °C and average July minimum temperature is 5.3 °C (Bureau of Meteorology station 067113). Summer heat waves have recently intensified in Western Sydney, owing to dense urban development and distance from cooling sea breezes [43]. Future projections for this area indicate up to a 50% increase in the number of very hot days in the near future [44], increasing the number of days of more severe fire weather [1,45].
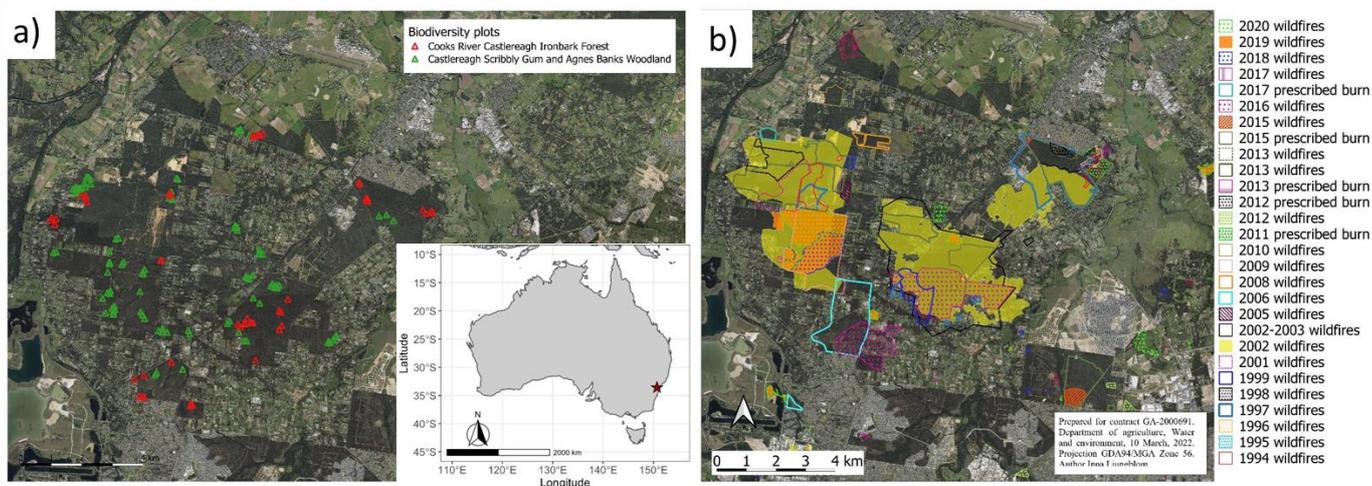

Figure 2. Study area showing (**a**) biodiversity plots and (**b**) fire boundaries, sourced from NSW Rural Fire Service and National Park and Wildlife Service. Inset shows location of study in southeast Australia.

Two Commonwealth-listed eucalypt TECs were studied: *Castlereagh Scribbly Gum and Agnes Banks Woodland* (Endangered listing, EPBC Act 1999; referred to as "Scribbly Gum Woodland" or SGW) and *Cooks River/Castlereagh Ironbark Forest* (Critically Endangered listing, EPBC Act 1999; referred to as "Ironbark Forest" or IF). SGW is a low open woodland with a diverse and prominent sclerophyllous shrub layer and a patchy herbaceous ground layer of grasses and forbs [46–48], whereas IF comprises taller open forest with a moderate shrub layer and a sparse herbaceous ground layer [49,50] (Figure 3). These communities provide habitat for many native plant and animal species including threatened shrub species *Micromyrtus minutiflora*, *Acacia bynoeana*, *Dillwynia tenuifolia*, *Grevillea juniperina* subsp. *juniperina*, *Persoonia nutans*, *Allocasuarina glareicola* and *Pultenaea parviflora*. Extensive urban and rural development across the Cumberland sub-region has removed up to 95% of the original extent of these communities, and remaining fragments of bushland occur across a range of ownership and local jurisdiction [41].
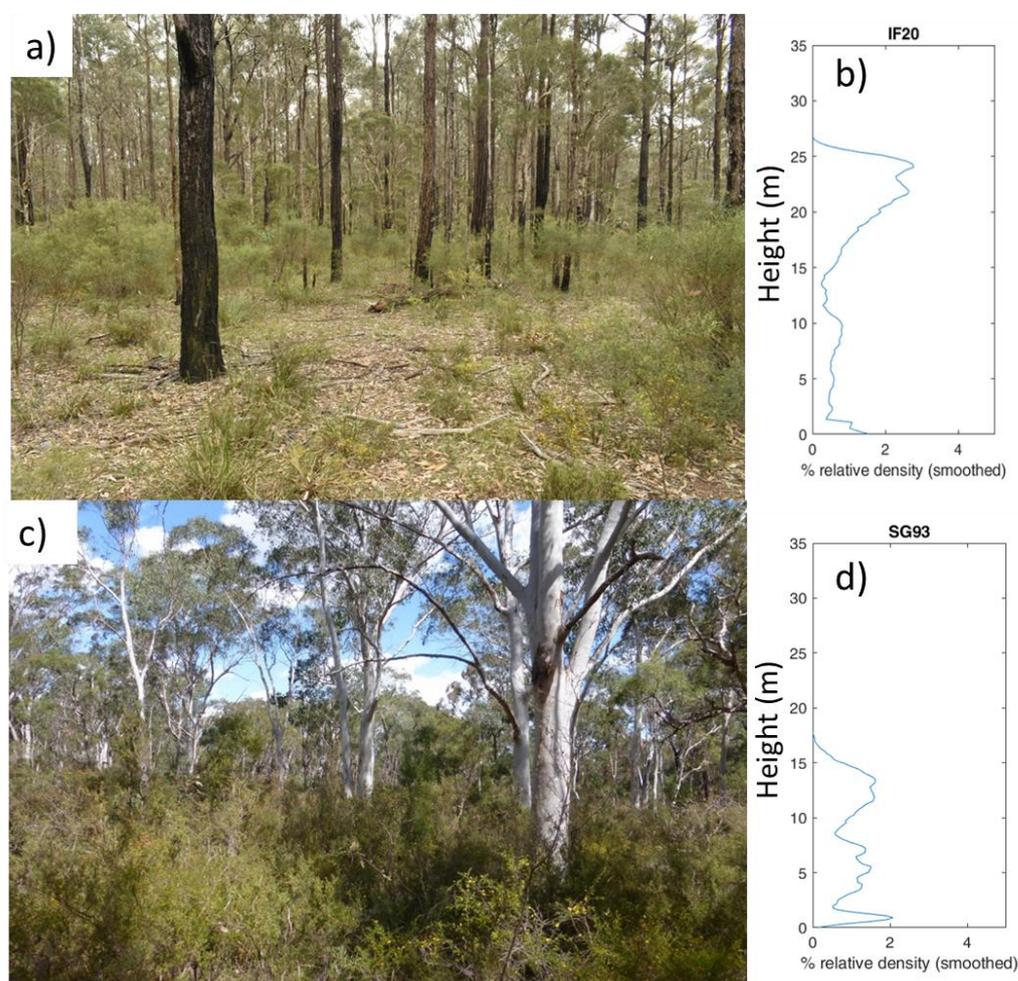
Figure 3. Typical structure of (**a**) Ironbark Forest with (**b**) an example profile of canopy density with height, and (**c**) Scribbly Gum Woodland with (**d**) an example profile of canopy density with height.

3. Methods

3.1. Study Sites

Site selection was informed by New South Wales National Parks and Wildlife Service (NSW NPWS) vegetation mapping [51]. Subsequent field observations were undertaken to confirm the mapping and TEC locations.

3.2. Disturbance Histories

Fire histories were established from NPWS and NSW Rural Fire Service (RFS) fire mapping databases, earlier research work compiled by Watson [52], NearMap aerial imagery (https://www.nearmap.com/au/en accessed on 31 May 2021) and cross-checking with the oral recall of land managers and site neighbors. Sites were included only where strong agreement between these sources was obtained to enable assignment of time-since-fire and fire frequency, or number of fires in the last 25 years. Study sites were located using handheld Garmin 6 GPS units (GDA94). All data layers were stored in QGIS (v 3.18).

3.3. Biodiversity and Habitat Inventories

We conducted 148 plot surveys, using the NSW Government's Biodiversity Assessment Method (20 × 20 m plots), randomly stratified by confirmed TEC and fire history, between December 2020 and April 2021. Of these, 96 were within the more widespread SGW and 52 within IF (Figure 2). Abundance of all vascular plant species present was estimated visually as cover scores, and structural and habitat indicators included litter, microbiotic crust and bare earth cover scores, stem size diversity, the number of visible tree hollows and the total length of woody debris (fallen logs > 10 cm diameter and ≥50 cm length) [53,54].

3.4. Biodiversity Metrics

Biodiversity metrics of species richness (number of species) and evenness were derived per plot from the biodiversity inventories. Species were also grouped into functional groups by growth form (tree, shrub, grass, forb, fern, sedge/rush, vine or mistletoe) [54], fire response (resprouter, obligate seeder or other), and exotic versus native. A full species list is available in the Supplementary Materials.

3.5. Leaf Area Index

Leaf area index (LAI) was estimated from canopy photography following Macfarlane et al. [55] using a Sony NEX7 camera with a 50 mm lens. Sixty upward-looking photos per plot (15 from each corner, at 1.3 m height) were analyzed to estimate light interception by the canopy and means and standard deviations were recorded at the plot level.

3.6. Airborne Lidar Acquisition and Analysis

Lidar data was collected between December 2020 and April 2021 over ~2000 ha by the School of Aviation at UNSW using a Piper Seminole (PA44) aircraft modified for georeferenced aerial survey work. Surveys were flown at approximately 300 m above ground, with a swath of around 350 m and data density of 7 to 10 points m^{-2}. Lidar data was classified into ground and vegetation points. Derived data products include digital terrain models (DTMs), digital surface models (DSMs) and canopy structural characteristics of density and height. DTMs provided ground topography using the ground classified points from the combined swaths. Gridded DTMs and DSMs were generated with Global Mapper software and exported as height colourized GeoTIFF files. DSMs provided the maximum heights of tree canopy tops using the first returns of the vegetation classified points from the combined swaths.

Canopy density for each 20 × 20 m biodiversity plot within the lidar survey area was estimated by processing the LAS files in Matlab to calculate the average density of first return points of vegetation above 1.3 m. Average height was evaluated for each biodiversity plot by exporting raw histogram data of point height bin versus number of points from Global Mapper. Canopy profile structure was characterized from lidar point clouds with the Global Mapper profile tool; height profiles within biodiversity plots and 10-m-wide transects between given plots were exported as bitmap image files. Uniform distance scaling was used on all images.

3.7. Data Analysis

Differences between TECs were evaluated using Student's T-tests (2 samples with unequal variance, 2 tailed, alpha = 0.05), and with Mann–Whitney rank sum tests where normality and variance assumptions were not met (alpha = 0.05). Relationships between biodiversity metrics and fire history metrics were evaluated using Spearman rank order correlations and linear and nonlinear regression. Averages ± standard deviations (SDs) are reported throughout. Non-metric multidimensional scaling ordination was conducted in PC-Ord Version 7. To reduce sparsity (88.9% zeros or empty cells in the original species-by-plot matrix) some species were combined to genus level if their growth form and native versus exotic status were the same, e.g., *Glycine*, *Mitrasacme*, *Rytidosperma*, *Drosera*. Low-frequency species (recorded in fewer than 4 plots) were then removed to improve homogeneity resulting in 160 plant taxa in the response matrix. An outlier analysis (cut-off of 2.0 standard deviations from the grand mean) indicated skew in one plot with two species with unusually large cover scores. Data was therefore relativized in plots (rows) by total abundance so that species retained their rank but were scored as a proportion of the plot total and normality was improved. City-block (Sorensen's) distance measures were applied. Analyses were conducted on the main matrix of plot species by cover scores and a second matrix of environmental variables such as quantitative time since fire, fire frequency, habitat measures and categorical TEC.

4. Results

4.1. Fire History

Reliable fire histories were available from the late 1990s across the study area (Figure 2), with both wildfires and prescribed (hazard reduction) burns indicated. Assessment of historical fire intensity or severity was not possible. Across all plots, at the time of the field surveys, the time elapsed since the most recent fire ranged from less than 1 to 25 years, averaging 8.6 years (±7.2 y SD), and fire frequency ranged from zero to four fires over the past 25 years. The average time since fire was significantly shorter in Scribbly Gum Woodland (SGW) (7.7 ± 6.8 y) than in Ironbark Forest (IF) (10.3 ± 7.5 y; $p = 0.01$), and fire frequency was significantly higher in SGW than IF (2.0 ± 1.1 versus 1.6 ± 1.2; $p = 0.03$) (Table 1). Fire frequency was negatively correlated with time since fire across the plots (r = 0.60; $p < 0.001$) (Table 2).

4.2. Canopy Structure, Habitat Values and Biodiversity in Two Communities

Metrics of canopy structure differed between the forest and woodland communities (Figure 3). Canopy height averaged 13.1 ± 4.3 m in IF versus 9.2 ± 2.1 m in SGW ($p < 0.01$; Table 1). Differences were not found in canopy density as estimated from lidar or LAI from photographs (overall average LAI 1.26 m^2 m^{-2} ± 0.66; Table 1). Leaf litter cover was higher in IF than SGW (73% vs. 62%; $p = 0.01$), but bare earth and microbiotic crust cover were similar between the two communities (Table 1). IF had significantly more coarse woody debris on the forest floor, whereas SGW had significantly more hollow-bearing trees, hollows and large trees (>50 cm diameter) (Table 1). Total plant cover was marginally higher in SGW than in IF (59% vs. 50%; $p = 0.07$), because of higher cover in shrub and herbaceous layers, whereas tree cover was higher in IF than in SGW (27% vs. 22%; $p = 0.01$; Table 1).

Detailed botanical surveys revealed a very diverse study area, with 355 vascular plant species across 148 plots (NSW BioNet repository; see Supplementary Materials for a species list). The average richness (S; total number of species including natives and exotics) per plot was 39.5, with 96 species only recorded once, while 14 species were recorded in more than half of all plots. We found significant differences between the ecological communities in S with an average of 41 species in SGW and 31 in IF plots ($p < 0.01$; Table 1). Species evenness (E) was also higher in the SGW (0.61 vs. 0.47; $p < 0.01$; Table 1). Greater biodiversity in SGW was explained by significantly higher species richness of trees, shrubs and forbs. However, the number of listed threatened species was similar between TECs, with about 1–2 found in each plot. Mistletoe cover, although generally low everywhere, was significantly higher

in IF than SGW (Table 1). The cover values of obligate seeders and resprouters were similar between TECs, whereas the richness of obligate seeders and resprouters were both greater in SGW than IF; the proportion of species with canopy-stored seed was higher in SGW than in IF (Table 1).

Table 1. Fire history of the last 25 years, vegetation structure, habitat values and biodiversity metrics of Scribbly Gum Woodland (SGW) and Ironbark Forest (IF) near Sydney, Australia. Shown are mean ± standard deviation (SD) across plots within each Threatened Ecological Community. Exotic species are included in all richness and cover values and evaluated separately below. Significant difference (p value < 0.05) between the two communities indicated in **bold** and marginal significance indicated in *italics*; T-tests were used where data met normality requirements and Mann–Whitney Rank Sum tests were used if not (indicated by ^).

Community	SGW	IF	*p* Value
Fire history metrics			
Time since fire	7.7 ± 6.8	10.3 ± 7.5	**0.01**
Fire frequency	2.0 ± 1.1	1.6 ± 1.2	**0.03**
Structural and Habitat Properties			
Canopy height (m)	9.2 ± 2.1	13.1 ± 4.3	**0.00**
Canopy density	4.2 ± 1.7	4.8 ± 2.2	0.14
Leaf area index (m^2 m^{-2})	1.2 ± 0.7	1.3 ± 0.6	0.32
Litter cover (%) ^	62.2 ± 21.9	72.7 ± 23.3	**0.01**
Bare earth cover (%) ^	15.0 ± 16.4	12.7 ± 14.2	0.37
Microbiotic crust cover (%) ^	3.3 ± 4.7	3.3 ± 4.4	0.98
Woody debris (m) ^	28.3 ± 25.3	40.2 ± 4.4	**0.01**
Hollow bearing trees ^	1.7 ± 2.2	0.5 ± 1.1	**0.00**
Total hollow count ^	3.7 ± 6.9	1.0 ± 2.3	**0.00**
Large trees (>50 cm) ^	1.2 ± 1.2	0.7 ± 0.9	**0.01**
Total cover (%) ^	58.6 ± 28.1	49.8 ± 21.2	*0.07*
Tree cover (%) ^	22.3 ± 11.6	27.1 ± 11.3	**0.01**
Shrub cover (%) ^	21.2 ± 18.9	14.7 ± 17.3	**0.00**
Vine cover (%) ^	0.2 ± 0.1	0.2 ± 0.2	0.57
Mistletoe cover (%) ^	0.0 ± 0.01	0.03 ± 0.11	**0.01**
Forb cover (%) ^	2.0 ± 1.8	1.5 ± 2.4	**0.00**
Grass cover (%) ^	3.6 ± 8.9	1.5 ± 2.3	0.14
Sedge and rush cover (%) ^	8.0 ± 10.9	4.5 ± 8.1	**0.00**
Fern cover (%) ^	0.2 ± 0.8	0.09 ± 0.2	0.35
Total herbaceous ground cover (%) ^	14.2 ± 14.8	7.8 ± 9.5	**0.00**
Biodiversity Properties			
Species richness (S)	41.1 ± 9.3	31.4 ± 9.4	**0.00**
Evenness (E)	0.6 ± 0.1	0.5 ± 0.1	**0.00**
Tree species richness ^	3.2 ± 1.0	2.2 ± 1.1	**0.00**
Shrub species richness	18.1 ± 4.8	10.8 ± 4.2	**0.00**
Forb species richness ^	9.6 ± 5.3	7.8 ± 4.9	**0.03**
Grass species richness ^	5.3 ± 3.2	5.7 ± 2.5	0.45
Sedge and rush species richness ^	4.6 ± 1.8	4.3 ± 1.7	0.20
Herbaceous groundcover species richness	20.5 ± 8.0	18.8 ± 7.8	0.23
Threatened species richness ^	1.3 ± 1.1	1.5 ± 0.8	0.19
Exotic species richness ^	0.9 ± 2.0	1.2 ± 0.3	0.22
Exotic weed cover (%) ^	0.2 ± 0.8	2.3 ± 1.1	0.17
Obligate seeder richness ^	7.9 ± 3.1	6.7 ± 3.1	**0.02**
Obligate seeder cover ^	3.5 ± 4.0	4.0 ± 7.4	0.13
Resprouter richness	30.5 ± 7.8	22.7 ± 7.7	**0.00**
Resprouter cover ^	53.8 ± 26.9	45.2 ± 18.7	0.10
Species with canopy seed (%)	7.2 ± 1.9	4.1 ± 1.8	**0.00**
Species with soil seed (%) ^	22.9 ± 6.6	17.2 ± 6.0	0.87

Table 2. Spearman rank order correlation coefficients (r) for relationships between vegetation structure, habitat and biodiversity metrics with time since fire (TSF) and fire frequency (FF), for all plots and individual TECs, Scribbly Gum Woodland (SGW) and Ironbark Forest (IF). ***Bold/italic*** indicates *p* < 0.05; **bold** indicates *p* < 0.001.

	All plots	All plots	SGW	SGW	IF	IF
	TSF	FF	TSF	FF	TSF	FF
Fire frequency	**−0.601**	NA	**−0.472**	NA	**−0.806**	NA
Structural and Habitat Properties						
Canopy height (m)	*0.264*	−0.160	0.158	−0.009	0.014	0.117
Canopy density	**0.436**	**−0.661**	*0.250*	**−0.653**	**0.777**	**−0.660**
Leaf area index (m^2 m^{-2})	**0.335**	**−0.428**	*0.285*	**−0.432**	**0.365**	*−0.370*
Leaf litter (%)	**0.592**	**−0.469**	**0.562**	**−0.390**	**0.531**	**−0.479**
Bare earth (%)	**−0.653**	**0.407**	**−0.646**	*0.294*	**−0.674**	**0.615**
Microbiotic soil crust (%)	**0.421**	*−0.227*	**0.394**	−0.182	**0.515**	*−0.309*
Woody debris (m)	*0.164*	*−0.187*	*0.207*	*−0.227*	−0.132	0.036
Hollow bearing trees	0.048	−0.140	0.193	*−0.220*	0.044	−0.218
Total hollow count	0.009	−0.132	0.126	*−0.209*	0.034	−0.214
Large trees (>50 cm)	0.029	−0.116	0.171	*−0.270*	−0.167	0.108
Total cover (%)	0.083	−0.106	0.193	*−0.267*	−0.050	0.065
Tree cover (%)	*0.246*	*−0.191*	0.152	−0.172	*0.288*	−0.162
Shrub cover (%)	−0.095	*0.236*	0.153	0.005	*−0.405*	**0.477**
Mistletoe cover (%)	**0.305**	**−0.315**	0.102	−0.108	**0.497**	**−0.512**
Forb cover (%)	0.045	−0.140	0.131	*−0.240*	0.041	−0.158
Grass cover (%)	*0.171*	−0.121	0.133	−0.094	*0.418*	−0.287
Sedge and rush cover (%)	*−0.198*	−0.012	−0.117	−0.047	−0.156	−0.118
Fern cover (%)	0.070	*−0.213*	0.007	−0.163	0.187	−0.250
Herbaceous ground cover (%)	−0.026	*−0.169*	0.051	*−0.221*	0.015	*−0.280*
Biodiversity Properties						
Species richness (S)	−0.132	*0.222*	0.001	*0.318*	−0.081	−0.163
Evenness (E)	0.005	0.070	0.184	−0.026	0.049	0.018
Tree richness	0.027	−0.152	0.106	*−0.234*	0.149	*−0.348*
Shrub richness	*−0.217*	**0.394**	0.087	**0.341**	**−0.531**	*0.366*
Forb richness	0.028	−0.041	0.036	0.063	0.127	*−0.291*
Grass richness	0.147	−0.034	0.046	0.207	*0.349*	*−0.420*
Sedge and rush richness	**−0.289**	*0.257*	**−0.347**	**0.419**	−0.116	−0.1.00
Herbaceous ground cover richness	0.025	−0.023	−0.009	0.156	0.187	*−0.380*
Threatened species richness	0.124	0.005	*0.229*	−0.135	−0.263	*0.330*
Exotic species richness	0.027	*−0.164*	−0.141	0.001	*0.314*	*−0.387*
Exotic species cover (%)	0.027	−0.137	−0.137	0.015	*0.280*	*−0.316*
Obligate seeder richness	0.120	0.049	*0.319*	−0.016	−0.155	0.013
Obligate seeder cover (%)	*0.176*	−0.078	**0.353**	*−0.233*	−0.065	0.095
Resprouter richness	−0.134	*0.207*	−0.015	*0.282*	−0.062	−0.176
Resprouter cover (%)	0.071	−0.097	0.159	*−0.242*	−0.021	0.035
Species with canopy seed (%)	−0.115	0.125	−0.002	−0.031	−0.068	0.099
Species with soil seed (%)	−0.070	0.131	0.119	−0.097	**−0.469**	**0.491**

4.3. Responses of Ecosystem Structure and Biodiversity to Fire

Rapid recovery of ecosystem structure was observed in both communities. A graphical example of succession is shown in Figure 4. Canopy density and LAI increased linearly (r = 0.54; *p* < 0.01; Figure 5). The litter cover increased non-linearly over time since fire up to about 7 years, while the bare ground fraction decreased up to about 10 years (Figure 6) consistently in both TECs (*p* values all < 0.05). Microbiotic soil crust increased with time since fire and total herbaceous ground cover decreased with increasing fire frequency consistently across both TECs (Table 2). Habitat values of woody debris and numbers of hollow-bearing trees, hollows and large trees (>50-cm diameter) all decreased significantly with increasing fire frequency in SGW, but not in IF (Table 2). With increased fire frequencies in SGW, total cover decreased significantly, most notably in forbs and herbaceous ground cover (Table 2). In IF, shrub cover increased significantly with fire frequency and decreased

with time since fire, while tree, mistletoe and grass cover all increased with time since fire (Table 2). Other structural properties were not correlated with fire metrics.
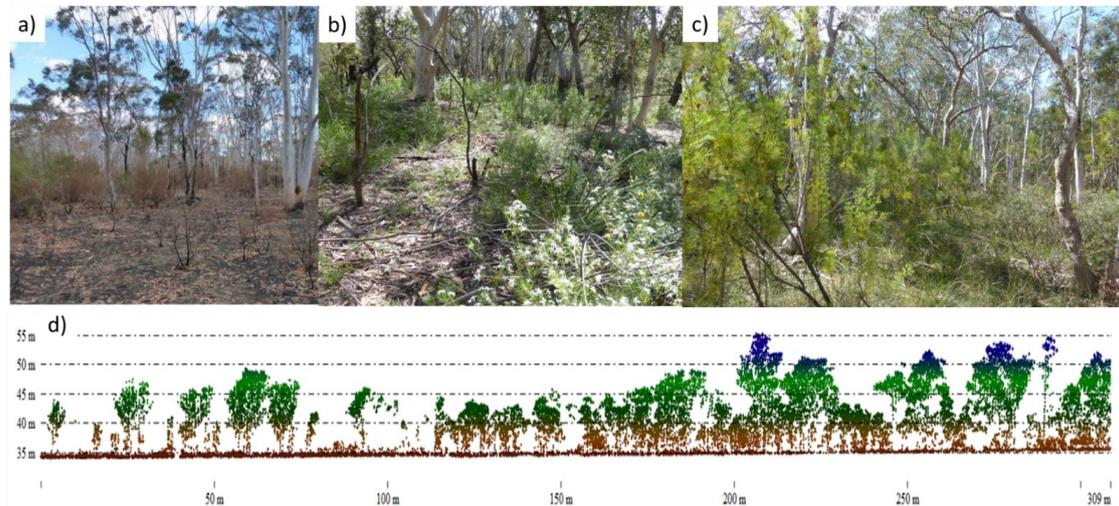

Figure 4. Examples of Scribbly Gum Woodland recovery from fire: (**a**) six weeks after fire; (**b**) one year after fire; (**c**) 14 years after fire; (**d**) lidar-derived canopy profile transect through SGW one year since fire (left) to eight years since fire (right) (*y*-axis scale indicates height above sea level).
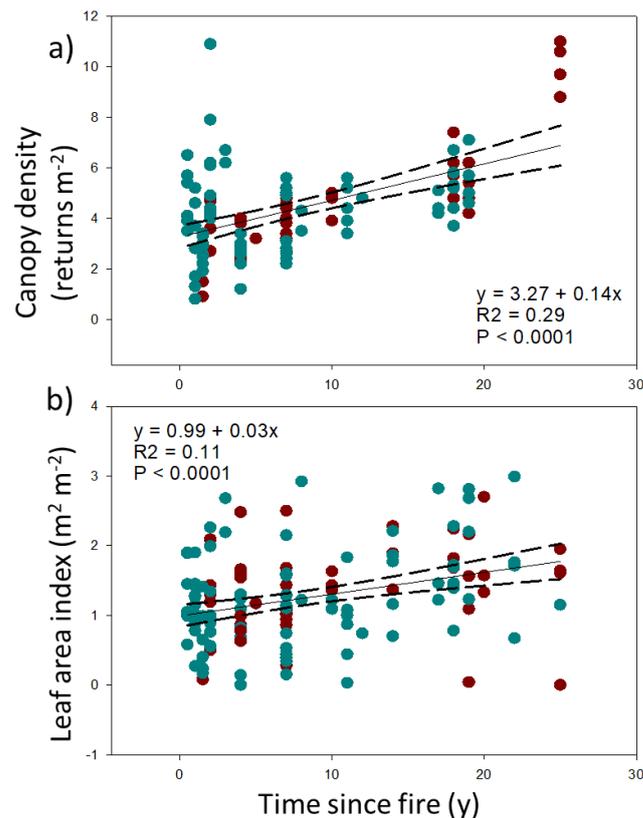
Figure 5. (**a**) Canopy density estimated from lidar surveys and (**b**) leaf area index both increased linearly over time since fire across the study area. These metrics met assumptions of normality and equal variance (Table 1); no interactions were found with Threatened Ecological Communities. Maroon, Ironbark Forest; Teal, Scribbly Gum Woodland.
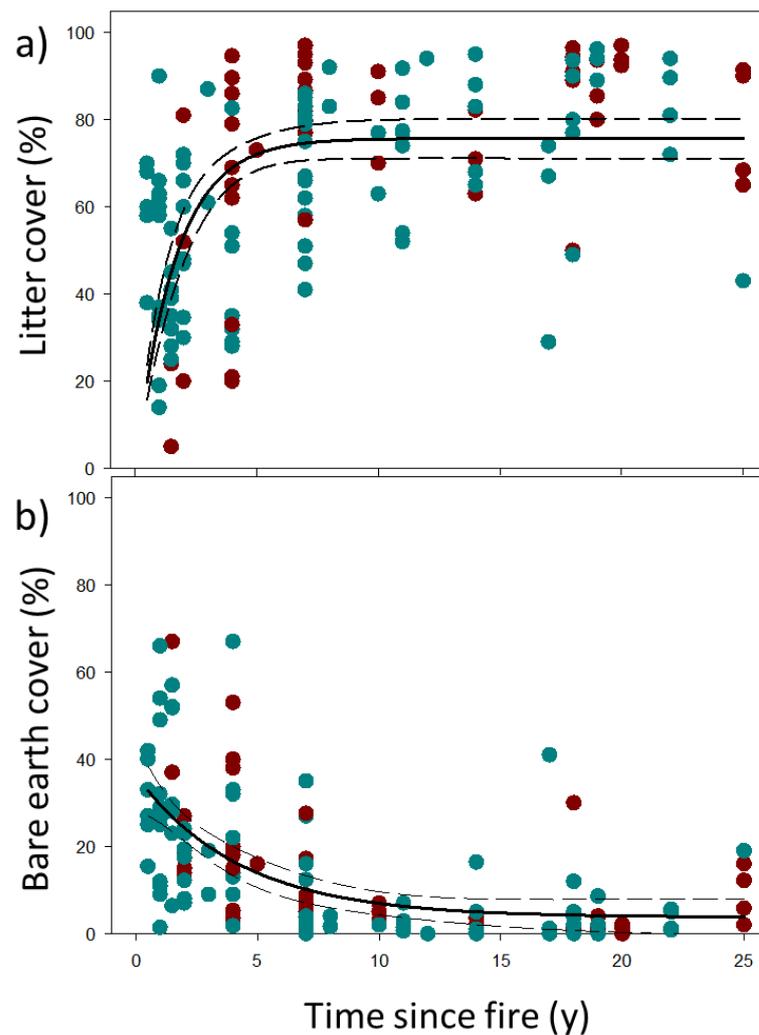
Figure 6. Litter cover increased (**a**) and bare earth decreased (**b**) nonlinearly after fire. No interactions were found between threatened ecological community type and time since fire. Symbols are the same as in Figure 5.

We found fewer correlations of fire frequency or time since fire with biodiversity metrics than with structural properties in both communities. In contrast to our hypothesis, species richness (S) increased significantly with fire frequency across all plots ($r = 0.23$, $p < 0.01$), which was driven mainly by the response in SGW ($r = 0.34$, $p < 0.01$) (Figure 7). The increased S with increasing fire frequency was mainly driven by increased shrub species richness, which offset decreased tree species richness in both TECs (Table 2). In SGW, the cover of obligate seeders and resprouters both decreased with fire frequency, while obligate seeder richness increased with time since fire and resprouter richness increased with fire frequency (Table 2). In IF, exotic species richness and cover increased with time since fire and decreased with increasing fire frequency (Table 2).

Multivariate analysis suggested that species composition within the two TECs was not strongly affected by fire, although the two communities did differ in their fire responses. Applying a nonparametric ordination to the species matrix against environmental variables was statistically significant, with the proportion of variance represented by the first two axes totaling 74% (Figure 8). The grouping variable plant community type was strong with plots clustering into IF and SGW. An association was found between longer time since fire and IF, while higher fire frequencies were associated with the SGW (Figure 8).
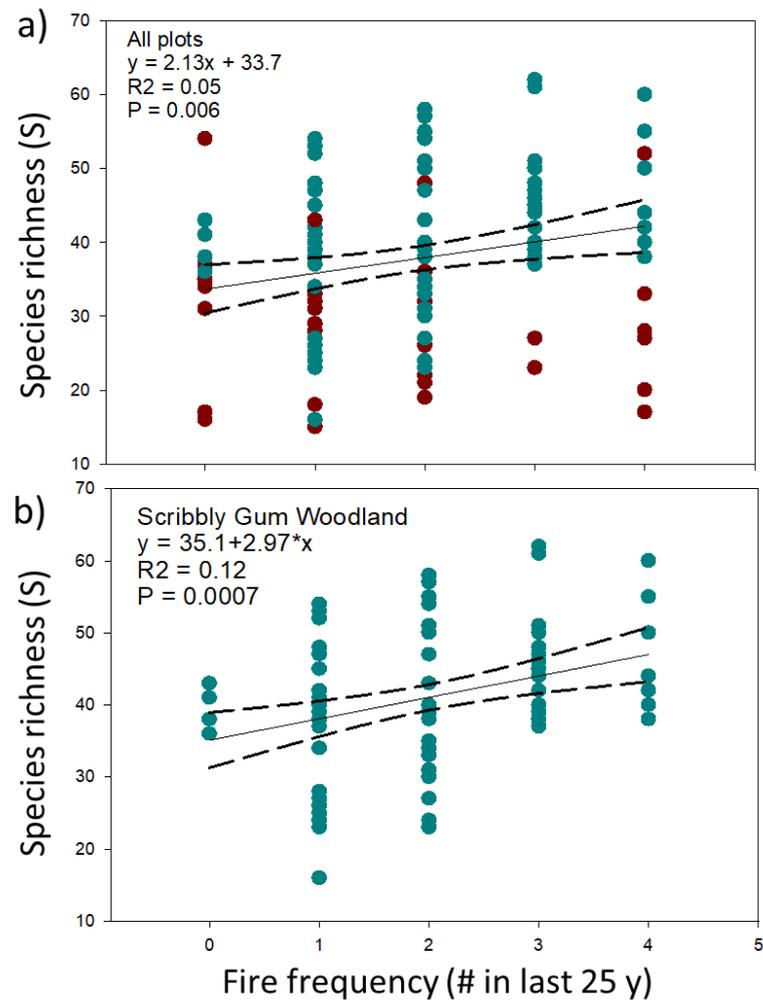
Figure 7. Species richness (S) increases with fire frequency (**a**) across all plots and (**b**) especially within SGW. Assumptions of normality and equal variance were met. Symbols are the same as in Figure 5.
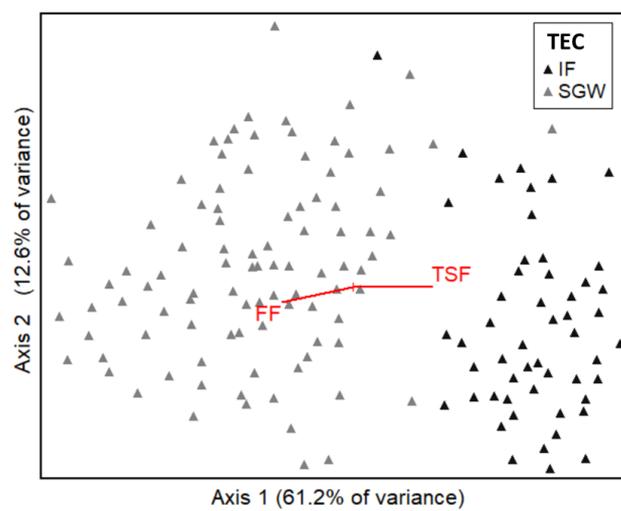

Figure 8. Non-metric multidimensional scaling plot of 160 species cover scores by 148 plots showing separation by Threatened Ecological Community (TEC) and a biplot overlay of time-since-fire (TSF) and fire frequency (FF) vectors.

5. Discussion

Canopy structure values (e.g., LAI) recovered quickly after fire in two TECs near Sydney Australia, as expected. Although canopy height increased significantly across all plots (Table 2), this is likely explained by the significantly longer time since fire in the taller IF compared to SGW (Table 1). In IF, succession following fire was associated with increasing tree, mistletoe and grass cover and decreasing shrub cover, demonstrating the importance of long fire-free intervals to the development of robust overstorey canopies and associated habitat and biodiversity. However, habitat quality decreased with increasing fire frequency in SGW, as indicated by significantly lower quantities of woody debris, large and hollow-bearing trees, and total hollows (Table 2); any future increases in fire frequency could negatively impact suitable habitat for arboreal and ground-dwelling animals.

We hypothesized that increased fire frequency would have a negative impact on biodiversity metrics, and indeed, tree species richness decreased in both TECs (Table 2). Conversely, we found that total richness (S) increased in SGW and shrub richness increased in both TECs, indicating the importance of repeated fires in maintaining some aspects of biodiversity in these fire-adapted ecosystems. While limited as a case study in a local area, overall, our detailed biodiversity inventories and lidar-based structure analyses demonstrate remarkable resilience and rapid recovery of vegetation structure and biodiversity in response to fires in this region, despite compound threats of urbanization, potential invasion of exotic species and climate change (Figure 1). However, large uncertainties remain, especially related to mitigation efforts to alleviate potential impacts forecast by multiple climate change scenarios of hotter, drier futures and potentially more frequent fires.

5.1. Vegetation Structure and Habitat Recovery

Our data indicates a linear increase in canopy cover (LAI and canopy density) up to 25 years after fire, suggesting that a longer duration would be needed before the canopy cover levels off at a higher steady state. The average LAI in SGW and IF of between 1 and 1.5 m^2 m^{-2} (Figure 4) was comparable to that of nearby Cumberland Plain Woodland (CPW; another TEC) that had not been burned for at least 35 years, but which had been experiencing canopy decline and a severe mistletoe infestation [56]. However, research in nearby IF that had not burned for 35 years found denser canopies, with understory species composition dominated by shade-tolerant sedges and grasses [57]. The agreement between ground-based LAI and airborne lidar estimates of canopy density (R^2 of 0.11; data not shown) demonstrates the suitability of lidar technology for broader surveys of vegetation recovery from disturbance [25] and simpler and cheaper LAI methods appropriate at smaller scales.

Tree cover increased significantly over the 25-year period, mainly due to the growth of IF, partly supporting our hypothesis that this forest community would recover rapidly owing to its taller and denser canopy structure compared to SGW. The Melaleuca trees in addition to the eucalypts of the IF contributed to the ongoing canopy closure at these extended times since fire. Tree cover, and especially large hollow-bearing trees, provide critical wildlife habitat; in NSW, hollow-dependent vertebrate species include at least 46 mammals, 81 birds, 31 reptiles and 16 frogs [58,59]. Of these, 40 are listed as threatened species in NSW [60]. The distribution and abundance of hollow-bearing trees in NSW has been reduced by extensive clearing of native vegetation during the past two centuries, but regulations now require ecological survey for hollow bearing 'habitat' trees and reasonable attempts must be demonstrated to avoid removing them from the landscape within development proposals [36]. These regulations could be particularly critical in SGW, considering the higher number of habitat trees than in IF, and the compounded negative impacts of increasing fire frequency on the tree-based habitat values (Table 2).

The different fire regimes evident in the two communities (a higher fire frequency in SGW than in IF) are associated with the contrasting vegetation composition and fuel structure of the two communities. SGW has significantly higher cover of shrubs and herbaceous species and marginally higher total plant cover (despite significantly lower tree

cover) compared to IF. This would result in higher ground level fuel loads, greater connectivity, and more flammable vegetation, all increasing the potential for fire activity [61,62]. However, increased fire frequency evidently favored shrub cover only in IF; this indicates that shrub cover was relatively insensitive to fire frequency in SGW, possibly because the more numerous shrubs are quick growing species adapted to the higher fire frequencies of this community. Shrubs are highly flammable, and their increase will likely strengthen feedback between shrub cover and fire frequency [12], such as reported here for IF and by Carmac et al. [63] in Australian alpine vegetation.

Our results are in contrast to Mariani et al. [33] and others [64,65] whose studies in fire-adapted Australian ecosystems point to decreases in shrub cover under high frequency fires and increasing woody encroachment in the long absence of fire. Likewise, nearby grassy CPW shows a decrease in shrub cover under higher fire frequencies and higher shrub cover in long unburnt areas, driven largely by the dominant shrub species *Bursaria spinosa* (a species which both recruits between fires and resprouts from fire) [66]. *Bursaria spinosa* is less common in SGW and IF than in CPW; its low abundance (recorded in only 21 of 148 plots) in SGW and IF may relate to their higher fire frequency or alternatively to the contrasting soils compared to CPW [37]. These nuances suggest that multiple interacting influences, such as differing plant communities and soil types, fire regimes and associated human uses, contribute to uncertainties around how the vegetation structure has changed over the last 200 years since European settlement of the Sydney Basin [34].

Forest floor litter and coarse woody debris are important functional components of forested ecosystems, serving as habitat for numerous invertebrates, a source of nutrients and the foundation of belowground food webs [67]. Litter serves as fuel and is associated with high intensity fires in Australian temperate forests [3,68]. Although litter cover was found to be sensitive to fire, it recovered to a plateau within 10 years for both the communities, which may reflect an equilibrium between litter fall and decomposition. While IF plots had significantly more woody debris overall than SGW, an increased time since fire saw increased dead woody debris in SGW. Our results support research in southwest Australia that long fire intervals (e.g., >50 years) are recommended to maintain its habitat value [67]. Fire frequency has been shown to impact the elemental composition of the litter layer in forests in Eastern Australia, with important implications for soil processes and nutrient dynamics [69,70] and for soil biota [71]. Future studies could evaluate the responses of soil biodiversity, food web structure and soil nutrient cycling associated with the significant changes to forest floor structure observed in this study.

5.2. Biodiversity is Largely Resilient to the Fire Regimes Studied

The Black Summer bushfires of 2019–20 were reported to result in massive losses of biodiversity across eastern and southern Australia [7]. However, in our study of temperate eucalypt communities, overall biodiversity metrics (e.g., S, E) were not adversely affected by the highest levels of fire frequency studied (3–4 fires in 25 years), in opposition to our hypothesis. Apparently, plant species richness in the SGW and IF communities as they are presently observed is so far resilient to the fire regime of the early 21st century. Nevertheless, even resilient communities like these could experience increased frequency of fire such that the time between successive fires is too short for species to reach reproductive maturity [72,73].

Contrary to our expectations, we observed significantly increased threatened species richness with higher fire frequencies in IF; this finding is noteworthy in that these species are all obligate seeding shrubs (e.g., *Pultenaea parviflora*, *Grevillea juniperina* subsp. *juniperina*, *Dillwynia tenuifolia*) and so are considered to be at risk of local extinction under high fire frequency [74]. Threatened species richness increased with time since fire in SGW, along with obligate seeder richness and cover (Table 2). Results from SGW support understanding from southwest Australia (e.g., [75]) that obligate seeders need substantial intervals between fires for successful establishment. The contrasting results between TECs suggest that the threatened, obligate-seeding species of the IF community show rapid re-establishment

post-fire and reach reproductive maturity within the fire return intervals studied [76]. The IF also had a greater proportion of obligate seeders than the SGW (both threatened and non-threatened species) and this possibly reflects the lower fire frequencies occurring in this community compared to SGW. Under climate change and more frequent fire the structure of the communities may become more similar, with shrubs becoming more prominent in IF than currently.

The decreasing cover of resprouters and obligate seeders with increased fire frequency in SGW appears to reflect a loss of species that are considered well preserved and common in the area, such as *Hakea sericea*, *Isopogon anemonifolius*, *Pimelea linifolia*, *Bossiaea* spp., *Acacia* spp., *Daviesia* spp. and *Dillwynia* spp. The proportion of species with soil-stored seed increased with fire frequency and decreased with time since fire in IF, suggesting greater resilience of those species in future fire regimes. These subtle shifts in community composition signal early concern for a scenario of increasing fire frequency under climate change. However, decreased herbaceous ground cover under frequent fires was evident in both communities, and this reduction in fuels may mitigate risk for a few years to come. Nevertheless, cover of post-fire resprouters and obligate seeders within the TECs were found to be similar to published estimates across eucalypt communities more broadly [18]. These adaptive strategies and traits have clearly been successful to date in enabling species persistence through repeated fires within the remaining SGW and IF of the Sydney basin.

We found important patterns in a few keystone groups of plants. For example, mistletoe plays an important role in nutrient cycling [77] and supports fauna such as the threatened painted honeyeater (*Grantiella picta*), a migratory mistletoe specialist whose arrival in the area and departure following breeding occur either side of peak mistletoe fruiting [78]. Mistletoes were absent everywhere except sites with the longest time since fire, because they are killed by fire and are reliant upon recolonization via seeds dispersed from surrounding unburned areas [79]. Our study indicates that re-establishment of obvious mistletoe populations can take up to two decades in this region of southeast Australia [80]. However, presence and population density of the main dispersal agent (Mistletoe bird, *Dicaeum hirundinaceum*) was not assessed in this study but should be considered for future work. It is apparent that more frequent fire under climate change will drive down mistletoe populations in systems already under stress from habitat loss and fragmentation.

Moreover, we found significantly increased exotic (weed) species richness and cover with increasing time since fire in IF, consistent with findings by Watson [52] of significantly higher frequencies of exotic shrubs in long-unburned areas of CPW and significantly fewer exotic herbs and lower weed abundance at high fire frequency sites. While fire responses of individual weed species will vary, fire would appear to be a promising tool against both woody and herbaceous weed encroachment, at least in the Ironbark Forest ecosystem. In contrast, invasions by *Andropogon gayanas* (gamba grass) in tropical Australia, and by *Cenchrus ciliaris* (Buffel grass) in arid zones, have resulted in altered fire fuel properties and increased fire frequencies, which further favors these invaders (termed a 'fire–invasion feedback') [81,82]. Although fire has proven a successful control agent against the invasive, smothering weed *Cryptostegia grandiflora* (rubber vine) in northern Queensland, experimental burning has been shown to detrimentally alter the vegetation structure and habitat for native reptiles [83]. This research highlights a need for careful studies on the broader relevance of adopting fire as a weed control method.

Resilience of peri-urban forests cannot be expected to be maintained indefinitely as rates of climate change and urbanization increase into the future. As the risk of fire ignition from natural and anthropogenic sources increases, fires may become more frequent [5]. However, urbanization is also associated with a loss of connectivity between flammable patches, potentially reducing fire risks if native ecosystems are lost [62], and increasing the difficulty of re-colonization by sensitive species. Adaptive conservation planning strategies should integrate multiple climate change scenarios and uncertainty analysis [84] and strengthen self-limiting feedback cycles that mitigate fire extremes and improve resilience for ecologically robust and sustainable outcomes.

Continuing habitat loss and fragmentation is the predominant threat to the persistence of TECs in the greater Sydney region [48,50]. Small, isolated patches of remnant vegetation are more likely to experience genetic drift, depleting gene pools and effective population sizes, which increases the likelihood of local extinctions. Urbanization will also impact animal populations that pollinate flowers and disperse propagules. A narrow geographical range and disjunct occurrences within fragmented remnants heightens the risk of extinction due to stochastic events, reduced genetic variability, reproductive failure and dispersal boundaries [85,86]. More detailed investigation of species' traits associated with recovery and resilience to fire and other disturbances will improve future adaptive management in the face of accelerating threats to biodiversity [87].

6. Conclusions

Urban forests around the world are facing compound threats to their biodiversity, ecosystem structure and function (Figure 1). Despite these threats, we found relatively few significant, detrimental effects of fire frequency and time since fire on metrics of biodiversity and canopy structure in the flammable bushland near Sydney, Australia, suggesting general resilience to fire regimes of the past 25 years. However, arboreal habitat quality is likely to diminish as climate change increases the frequency and severity of fires to levels our ecosystems have not previously experienced. This case study illustrates that structural and floristic differences between threatened, eucalypt-dominated woodland and forest communities are associated with contrasting fire history patterns and responses, and highlights the importance of locally targeted fire management and regular plot-level monitoring.

We demonstrated the feasibility of lidar as a baseline and reassessment tool of landscape scale canopy structure, while intensive on-ground surveys are required to track recovery of species and functional types. Ongoing assessment and cooperation among managers, landowners and researchers will help ensure that the ecosystem services and biodiversity values of fire-adapted forest fragments can be maintained.

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