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Multi-taxon biodiversity responses to the 2019–2020 Australian megafires

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Abstract

Conditions conducive to fires are becoming increasingly common and widespread under climate change. Recent fire events across the globe have occurred over unprecedented scales, affecting a diverse array of species and habitats. Understanding biodiversity responses to such fires is critical for conservation. Quantifying post-fire recovery is problematic across taxa, from insects to plants to vertebrates, especially at large geographic scales. Novel datasets can address this challenge. We use presence-only citizen science data from iNaturalist, collected before and after the 2019–2020 megafires in burnt and unburnt regions of eastern Australia, to quantify the effect of post-fire diversity responses, up to 18 months post-fire. The geographic, temporal, and taxonomic sampling of this dataset was large, but sampling effort and species discoverability were unevenly spread. We used rarefaction and prediction (iNEXT) with which we controlled sampling completeness among treatments, to estimate diversity indices (Hill numbers: $q = 0–2$) among nine broad taxon groupings and seven habitats, including 3885 species. We estimated an increase in species diversity up to 18 months after the 2019–2020 Australian megafires in regions which were burnt, compared to before the fires in burnt and unburnt regions. Diversity estimates in dry sclerophyll forest matched and likely drove this overall increase post-fire, while no taxon groupings showed clear increases inconsistent with both control treatments post-fire. Compared to unburnt regions, overall diversity across all taxon groupings and habitats greatly decreased in areas exposed to extreme fire severity. Post-fire life histories are complex and species detectability is an important consideration in all post-fire sampling. We demonstrate how fire characteristics, distinct taxa, and habitat influence biodiversity, as seen in local-scale datasets. Further integration of large-scale datasets with small-scale studies will lead to a more robust understanding of fire recovery.

KEYWORDS
citizen science, climate change, conservation, diversity, ecosystem, fire regime, Hill numbers, recovery

1 | INTRODUCTION

Fire is an important landscape-scale disturbance, broadly shaped by climate and anthropogenic activity, and a key driver of ecological processes (Balch et al., 2017; Bowman et al., 2009). Conditions conducive to fire are exacerbated by anthropogenic climate change and are becoming increasingly common and widespread (Abatzoglou et al., 2019; Jolly et al., 2015), driving shifts in fire regimes globally (Keeley & Syphard, 2016; Parks et al., 2016). As a result, fire frequency, intensity, size, and fire season duration (collectively all elements of the "fire regime") are increasing in many regions of the world (Fonseca et al., 2017; Jolly et al., 2015; van Mantgem et al., 2013). This shift is exemplified by fires in 2019–2020 in Australia, Californian, and the Arctic Circle (Abram et al., 2021; Descals et al., 2022; Pickrell & Pennisi, 2020), as well as recent fires throughout the Mediterranean and North America (Canosa, 2023; Sullivan & Tondo, 2023). As fire regimes change, we must be able to monitor and manage the consequences for biodiversity (He et al., 2019; Heim et al., 2022; Nimmo et al., 2021), from the individual and species level to populations and communities.

The effects of fire on biodiversity are complex, and our current understanding is built from studies on one to a few taxa, usually across limited spatial extents (but see He et al., 2019; Heim et al., 2022). Many species in fire-prone environments have traits that can promote population persistence, allowing some individuals to withstand or avoid fires, stimulate regeneration of a new cohort, and/or move away from the fire and then return (Thurman et al., 2020). Plant life histories of fire-cued germination, flowering, resprouting, and seed dispersal have led to a dependence on fires for continued dispersal, gene flow, persistence, and recruitment in fire-prone ecosystems (e.g., Dunker et al., 2019; Lamont et al., 1991; Nolan et al., 2021; Pausas & Keeley, 2014). Survival, avoidance, or recruitment related to fires subsequently allows a wide range of species to capitalize on the changed post-fire landscape (e.g., increased resource availability and decreased competition). For example, granivorous birds can exploit increased pine seed availability soon after fires in Corsican pine forests (Thibault & Prodon, 2006), and bees show increases in both abundance and species richness post-fire, likely attributable to several behavioral traits (e.g., burrowing) and their ability to exploit resource availability post-fire (Mason et al., 2021). Variation in elements of the fire regime will also differentially affect species, either directly or indirectly through subsequent shifts in vegetation communities (e.g., Fontaine & Kennedy, 2012; Le Breton et al., 2022; Mason et al., 2021; Ooi et al., 2014). As such, species responses will vary subject to different fire regime elements, and multi-taxon comparisons of post-fire responses are necessary to understand overall effects on biodiversity (e.g., Heim et al., 2022).

Collecting data on many species immediately after large-scale fires is logistically challenging for a number of reasons, including restricted funding for and availability of professional expertise to match the scale of these events (Kirchhoff et al., 2021) driving a lack of available data to appropriately quantify biodiversity responses (Saunders et al., 2021; Ward et al., 2020). For some taxon groupings (e.g., invertebrates), data collection is particularly rare, due to myriad political, scientific, and social factors which inhibit knowledge and research (Saunders et al., 2021). Citizen science efforts—where data are collected by many amateur observers who can often be experts in specific taxa, habitats, or regions, and are in the field more than professionals (Viola et al., 2022)—can solve many, although not all, of these challenges. For example, multi-taxon species incidence data from before and after fires were collected accurately, rapidly (important given the fast rate of many species fire responses), and at a spatial extent matching the 2019–2020 Australian megafires by large numbers of amateur observers (Kirchhoff et al., 2021). Critically, these observations across diverse taxon groupings and habitats cover a broad temporal and spatial scale for which systematic monitoring data do not exist.

Citizen science sampling effort is very rarely systematic, presenting a potential barrier to their use in analyses of diversity. Recent advances in rarefaction methods can help by controlling for sampling completeness using extrapolation of Hill numbers (q) which represent estimates of diversity indices such as species richness ($q=0$; the number of species in the sample), Shannon diversity ($q=1$; effective number of common species in the assemblage as all individuals are equally weighted), and Simpson diversity ($q=2$; effective number of dominant species in the assemblage, discounting non-dominant species; Chao et al., 2014; Chao & Jost, 2012; Hsieh et al., 2016). Sampling completeness is the proportion of all individuals in an assemblage belonging to species in the sample and controlling for this metric removes systematic biases otherwise present in equal n-based standardization approaches which can fail to accurately characterize communities with high species richness compared to those with lower richness (Chao et al., 2014; Chao & Jost, 2012). Using this approach for iNaturalist data, we can control sampling completeness among treatments. This enables estimation of Hill numbers which allow for investigation of ecological outcomes where standardized datasets do not exist.

In the 2019–2020 Australian megafires, the scale and severity of the fires triggered conservation actions and post-fire environmental management interventions in attempts to save species presumed to be at risk (Gallagher et al., 2021, 2022; Legge et al., 2022). However, limited data were available to direct such actions in an informed way. Habitats which are typically exposed to fires are likely to be relatively resilient, at least within the bounds of fire severity and frequencies to which they have adapted (Nolan et al., 2021). Others however, such as Gondwanan rainforests, rarely or never experience fire, and successful regeneration of component species or whole vegetation communities is less certain (Le Breton et al., 2022; Lee et al., 2022), which could potentially lead to habitat transformations (Tepley et al., 2018). The longer term post-fire trends of ecological communities from either of these scenarios (i.e., fire-adapted habitats burnt at thresholds beyond their historic regimes or burnt fire-sensitive habitats) remain poorly understood in the face of large-scale megafire events (Godfree et al., 2021; Rowley et al., 2020; Saunders et al., 2021).

Our objective was to determine biodiversity responses and recovery (i.e., species richness, Shannon diversity, and Simpson diversity) to the eastern Australian megafires of 2019–2020 at a similar scale to these fires, and across multiple taxon groupings. We used citizen science observations from iNaturalist from before and after the 2019–2020 fires to explore biodiversity responses to these fires across nine broad taxon groupings and seven habitats (Figure 1). We collectively used all taxon groupings and habitats to assess how: (a) diversity estimates compared pre- and post-fire in burnt and unburnt regions; (b) pre- and post-fire diversity estimates compared among distinct fire severity classes; and (c) post-fire diversity estimates changed with time-since-fire between burnt and unburnt regions up to 18 months post-fire. We then investigated how pre- and post-fire diversity estimates in burnt and unburnt regions differed among the nine broad taxon groupings and seven habitats.

2 | METHODS

2.1 | Data

iNaturalist (California Academy of Sciences: http://www.inaturalist.org/) is a global citizen science platform, currently hosting approximately 155 million observations (presence-only incidence records) of more than 430,000 species. Observations in iNaturalist are contributed by volunteers, largely via digital media (e.g., photographs and sound recordings), and identified to the finest taxonomic level possible by volunteers (see Kirchhoff et al., 2021). In response to the 2019–2020 megafires, a subproject named the *Environment Recovery Project* was created on iNaturalist (https://www.inaturalist.org/projects/environment-recovery-project-australian-bushfires) to target citizen science effort toward documenting recovery in burnt regions. This allowed for rapid post-fire
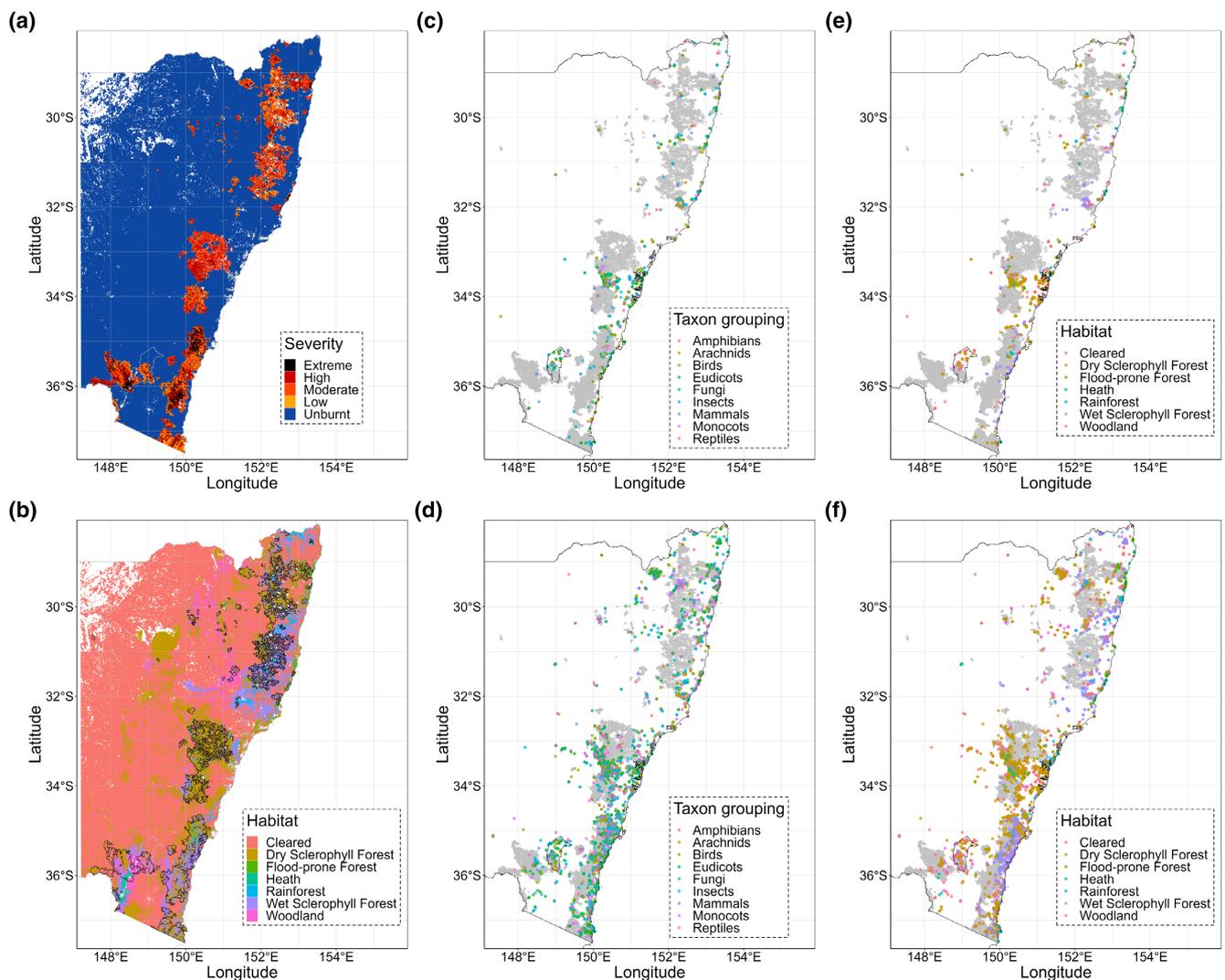

FIGURE 1 Extent of the study area in New South Wales and the Australian Capital Territory (gray with darker gray borders), showing at 1000-m² resolution (a) the extent of the unburnt and burnt sampling regions colored by fire severity levels and (b) this same extent overlaid with seven broad habitats. Distribution of iNaturalist observations colored by taxon groupings—(c, d)—and habitat—(e, f)—which were used in our analyses for the nine before fire periods (c, e) and single after fire period (d, f), over the fire footprint (gray).

data accumulation (Kirchhoff et al., 2021) while addressing the lack of available post-fire biodiversity data (Ward et al., 2020). Through the Atlas of Living Australia (https://www.ala.org.au/), all iNaturalist observations from New South Wales (NSW) and the Australian Capital Territory (ACT) flagged as "Research Grade" were downloaded up to December 2022, including species for which geolocation information automatically obscured on iNaturalist (e.g., threatened species) but can be made available for relevant research (although some records are manually obscured by observers for which geolocation information cannot be obtained). Our analysis included records from two broad periods, before (from January 1, 2017 to October 1, 2019) and up to 548 days after the 2019–2020 fires (November 1, 2019 to 23rd July 23, 2021, see below for more detail).

2.2 | Fire data

Spatial fire severity data were downloaded from the NSW Department of Planning, Industry and Environment Fire Extent and Severity Mapping (FESM; DPIE, 2020; Gibson et al., 2020). Using semi-automated machine learning and imagery from Sentinel 2, this dataset of fire severity provided the most accurate available map of the 2019–2020 megafires in NSW and the ACT, at a 10-m spatial resolution (DPIE, 2020). We used five of the six severity categories provided by DPIE (2020; unburnt, and low, moderate, high, and extreme severity), and excluded the reserved class which experimentally defined burnt grassland (Figure 1). Areas not listed as one of the burnt categories were categorized as unburnt. Low severity in FESM is defined as burnt understory with unburnt canopy, where >10% understory was burnt, and >90% of the canopy was green (DPIE, 2020). Moderate severity is defined as partial canopy scorch where 20%–90% canopy was scorched (DPIE, 2020). High severity is defined as complete canopy scorch with or without partial canopy consumption, where >90% canopy was scorched and <50% canopy was consumed (DPIE, 2020). Extreme severity is defined as complete canopy consumption where >50% canopy biomass was consumed (DPIE, 2020). The date of fire (the date when the fire-front burnt within a given grid cell) was determined from satellite-derived hotspot data (https://hotspots.dea.ga.gov.au/), for which hotspots are defined by high levels of infrared radiation and thus were relatively accurate for detecting the date on which fires first occurred.

2.3 | Vegetation data

Habitats were assigned using a vegetation map at 200m spatial resolution for vegetation classes across NSW and the ACT (DPIE, 2012). These vegetation classes were condensed into 10 habitats: cleared, dry sclerophyll forest, flood-prone forest, freshwater wetland, grassland, heath, marine and estuary, rainforest, wet sclerophyll forest, and woodland. Three of these—grassland,

freshwater wetland, and marine and estuary—were subsequently removed due to low sample sizes (see below), resulting in a total of seven habitats used for our analyses (Appendix S1).

2.4 | Data aggregations

Vegetation (200m spatial resolution) and FESM data (10m spatial resolution) were scaled up to 1000m spatial resolution matching the hotspot data and combined into one shapefile using ArcMap (Esri, 2019; Figure 1). This shapefile included a fire severity value (the mode of all the 10m resolution severity values within the 1000m grid cell; see Section 2.2), a habitat (using the majority method to determine the dominant vegetation type in the 1000m grid cell; see Section 2.3), and a date of fire-front (see Section 2.2) per 1000m grid cell. The same number of grid cells in the burnt region assigned to each vegetation class (from which habitat was derived; see Section 2.3) was then randomly selected from areas which were not burnt by the 2019–2020 fires in NSW and the ACT. When burnt or unburnt regions had unequal grid cell numbers per vegetation class, grid cells were randomly removed from the treatment with the higher value, to ensure equal spatial and vegetation class coverage between treatments. Fire severity, fire date, and habitat values were then extracted for each research-grade iNaturalist observation with ≤1000m accuracy (such that observations would only be a maximum of one grid cell offset), resulting in a dataset of species observations at 1000m resolution, with associated fire severity, fire date, and habitat.

iNaturalist records were grouped into 37 broad taxon groupings (e.g., amphibians, birds, bryophytes, eudicots, fungi, green algae, insects, ray-finned fish, etc.). Of the 37 taxon groupings and 10 habitats, only those with ≥90 observations in burnt regions in the 18months after fires were included for further analysis. This resulted in nine broad taxon groupings (amphibians, arachnids, birds, eudicots, fungi, insects, mammals, monocots, and reptiles) and seven habitats (cleared, dry sclerophyll forest, flood-prone forest, heath, rainforest, wet sclerophyll forest, and woodland) which were used for final analyses (Figure 1).

3 | ANALYSIS

3.1 | Estimating biodiversity

We analyzed trends in biodiversity using the first three Hill numbers (q): $q = 0$ (species richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity; Hsieh et al., 2016). This was done using a rarefaction and extrapolation approach to account for differential sampling between units, thus allowing for more direct comparisons. Analyses were done using the "iNEXT" package in R (Hsieh et al., 2016; R Core Team, 2020). We used the $estimateD()$ function in iNEXT to calculate estimates for each Hill number ($q = 0$–2) and plotted these with a 95% confidence interval to compare among factors for

all tests. Statistical significance at 5% can be inferred where confidence intervals do not overlap, although overlapping intervals do not preclude statistical significance (Chao et al., 2014). As such, we infer the strength of differences between treatments by categorizing results by: "no overlap," "partial overlap," and "near-complete/complete overlap" of 95% confidence intervals (CI). Applying rarefaction and prediction through "iNEXT" enabled us to control for uneven sampling effort among samples (by controlling sampling completeness), and to apply Hill numbers >0 to incidence data, such as those derived from iNaturalist (Chao et al., 2014; Hsieh et al., 2016).

3.2 | Standardizing sampling periods

The period from which iNaturalist data were extracted for this analysis was restricted to between 2017 and mid-2021; however, unlike in previous attempts to use iNaturalist data as time-series (e.g., Forister et al., 2021), this alone did not appropriately account for increased sampling effort after the fires. To do this, we created temporally equal sampling periods for each grid cell from which to extract iNaturalist observations for the before–after fire and burnt–unburnt treatments. This was done in burnt areas by extracting all species records up to 548 days (18 months) from the date the fire-front passed through a given grid cell in the post-fire ("after") period. For the pre-fire ("before") sampling, 1029 days was subtracted from the date of fire-front for each cell (such that the earliest simulated date of fire-front was January 1, 2017), and for each of the eight subsequent pre-fire sampling period (nine in total), the date of fire-front was brought forward 46 days (1.5 months). While there was overlap among the nine pre-fire periods, we did not treat these as independent, rather using them as an indication of pre-fire variation to compare to post-fire estimates of biodiversity. The latest starting date for the pre-fire periods was January 3, 2018, to ensure the pre- and post- fire sampling periods did not overlap. The number of unburnt and burnt grid cells per vegetation class was equal, so the date of fire-front in post-fire unburnt cells was randomly assigned to cells of matching vegetation classes from the burnt cells to extract iNaturalist records using the same approach as for burnt areas. The above approach was also used to group six 3-month (91-day) time periods using only the data after the fires (discarding data 547 or 548 days after the fires so groups were even), to compare diversity estimates for blocks of time since fire between burnt and unburnt regions. For fire severity comparisons, only iNaturalist records up to 18-month post-fire (not before; due to very low (<1%) sampling completeness when "before" sampling was included) within the footprint of each severity level were used (i.e., sampling for low fire severity was restricted to grid cells subject to low fire severity during the 2019–2020 megafires).

3.3 | Standardizing sampling effort

Sampling effort was standardized by creating two checks for comparison with post-fire burnt region diversity ("before" and unburnt

region estimates), as well as controlling for sampling completeness using iNEXT. Our sampling approach resulted in fewer post-fire records across both burnt and unburnt regions than before, but more records in unburnt regions than burnt regions both before and after the fires (burnt-before: 527; unburnt-before: 703; burnt-after: 5151; unburnt-after: 10857). This provided a double check to increase confidence that results were not driven by sampling effort. Most importantly, however, as Hill number estimates (diversity estimates) increase with sampling effort and therefore sample completeness (Chao et al., 2014; Chao & Jost, 2012), we used iNEXT to standardize sampling completeness within our comparisons to directly control for uneven sampling effort among treatments (Hsieh et al., 2016). Comparisons at the maximum common level of sample completeness among treatments for species richness were derived using rarefaction and prediction up to twice the reference sample size (n) of the least sampled factor (Chao et al., 2014). As extrapolation for $q > 0$ introduces little to no bias, estimates for Shannon and Simpson diversity were extrapolated to 100% sampling completeness where possible, and 90% when estimations at 100% failed (Chao et al., 2014). Our data represented species incidences, so the abundance values in Shannon and Simpson diversity indices used relative frequency of a given species within the reference sample, using the `datatype="incidence_freq"` argument in "iNEXT" (Chao et al., 2014; Hsieh et al., 2016). See Appendix S2 for further details on our standardization approach.

3.4 | Data summary

The final dataset included 3885 species from 23,568 iNaturalist observations, with 7560 before and 16,008 after the fires, and 5678 observations from burnt regions and 17,890 observations in the unburnt region. A total of nine taxon groupings: amphibians ($n_{burnt\ after} = 137$), arachnids ($n_{burnt\ after} = 98$), birds ($n_{burnt\ after} = 771$), eudicots ($n_{burnt\ after} = 1925$), fungi ($n_{burnt\ after} = 101$), insects ($n_{burnt\ after} = 995$), mammals ($n_{burnt\ after} = 149$), monocots ($n_{burnt\ after} = 757$), and reptiles ($n_{burnt\ after} = 218$); and seven habitats: cleared ($n_{burnt\ after} = 1099$), dry sclerophyll forest ($n_{burnt\ after} = 2435$), flood-prone forest ($n_{burnt\ after} = 169$), heath ($n_{burnt\ after} = 253$), rainforest ($n_{burnt\ after} = 127$), wet sclerophyll forest ($n_{burnt\ after} = 936$), and woodland ($n_{burnt\ after} = 132$); were used in our analysis. For severity analyses, iNaturalist observations up to 18-months post-fire were used from unburnt regions ($n = 10,857$) and those subject to the four fire severity categories: low ($n = 1203$), moderate ($n = 1308$), high ($n = 2135$), and extreme severity ($n = 505$). The six periods used for our analysis of time-since-fire were 0–3 months ($n_{burnt} = 692$, $n_{unburnt} = 2321$), 3–6 months ($n_{burnt} = 659$, $n_{unburnt} = 2546$), 6–9 months ($n_{burnt} = 840$, $n_{unburnt} = 1348$), 9–12 months ($n_{burnt} = 1100$, $n_{unburnt} = 1582$), 12–15 months ($n_{burnt} = 1032$, $n_{unburnt} = 1840$), 15–18 months ($n_{burnt} = 811$, $n_{unburnt} = 1162$). Using iNEXT to analyze these data when all taxon groupings were grouped together, we compared: (a) post-fire diversity estimates to the range of confidence intervals from the

nine pre-fire estimates between burnt and unburnt regions; (b) post-fire diversity estimates among distinct fire severity classes and unburnt regions; and (c) post-fire diversity estimates between burnt and unburnt regions with time-since-fire among six 3-month (91-day) periods of 0–3, 3–6, 6–9, 9–12, 12–15, and 15–18 months post-fire. We also compared post-fire diversity estimates to the range of confidence intervals from the nine pre-fire estimates between burnt and unburnt regions among the nine broad taxon groupings and seven habitats.

4 | RESULTS

4.1 | Overall trends

Grouping all taxon groupings and habitats, diversity estimates ($q \geq 0$) were greater up to 18 months after fires than the nine periods from before fires in the regions burnt by the 2019–2020 megafires (no 95% CI overlap; Figure 2a). This was also the case for regions which were unburnt except for Simpson diversity before and after the fires (complete
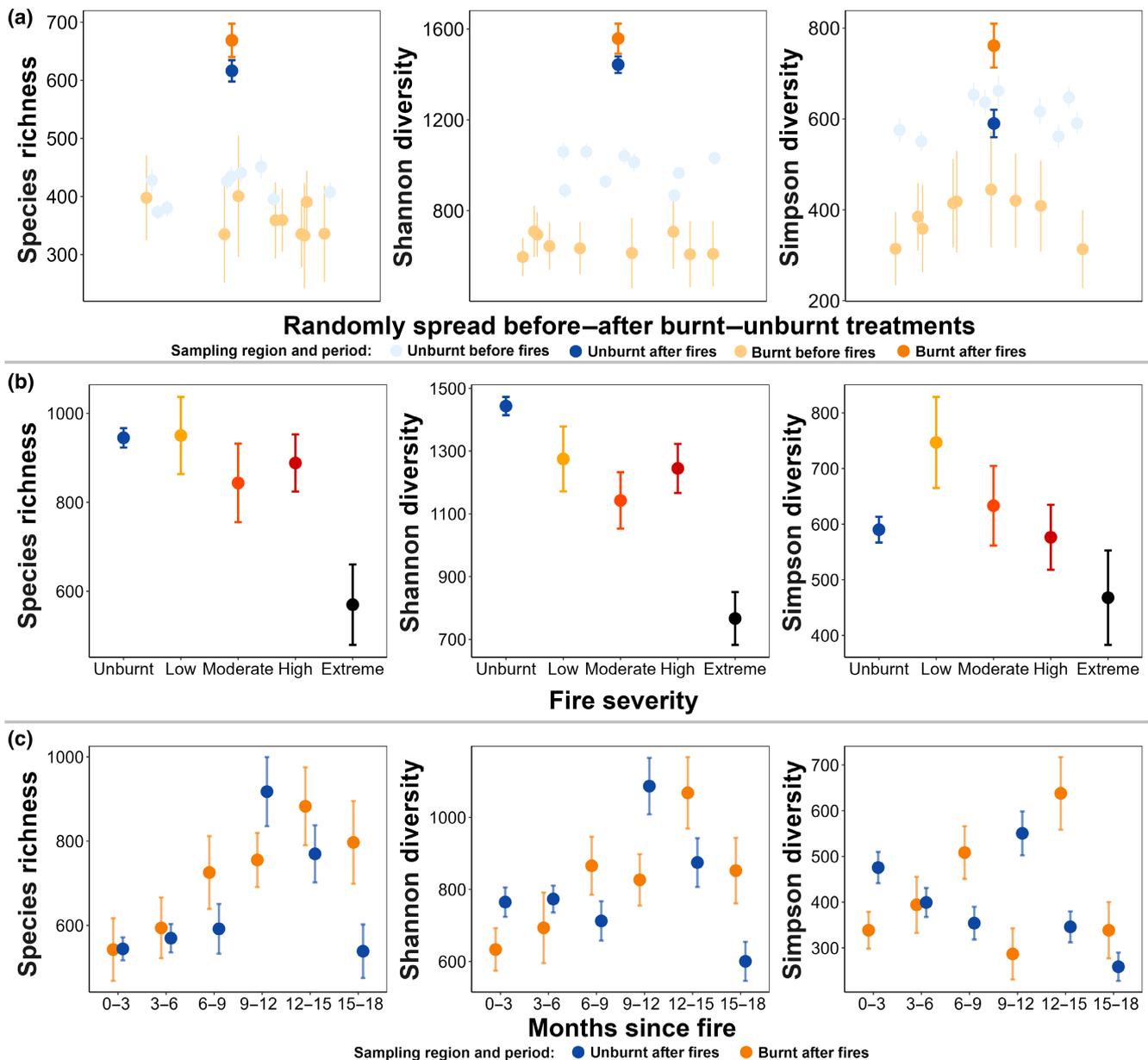

FIGURE 2 Estimates of Hill numbers $q=0$ (species richness), $q=1$ (Shannon diversity), and $q=2$ (Simpson diversity) with 95% confidence intervals (error bars) using rarefaction and prediction of iNaturalist observations (using the "iNEXT" package) grouped across nine taxon groupings and seven habitats. Sampling completeness (SC) was 100% for $q>0$, and double the reference sample for $q=0$ (per Chao et al., 2014). Estimates shown from: (a) unburnt (blue) and burnt regions (orange), before (nine 18-month periods; faded colors) and after (one 18-month sampling period; non-faded colors) the 2019–2020 megafires (SC$_{(q=0)}$=52.9%); (b) areas exposed to low, moderate, high, and extreme fire severity up to 18 months after the 2019–2020 megafires, and unburnt regions (SC$_{(q=0)}$=65.4%); and (c) up to 18 months after the 2019–2020 megafires in 3-month periods between unburnt (blue) and burnt (orange) regions (SC$_{(q=0)}$=70.3%).

95% CI overlap; Figure 2a). There was no 95% CI overlap between be- fore- and after-fire estimates. After the fires, estimates for the burnt re- gion were greater than those for the unburnt region, (no overlap in 95% CI) and before the fires, unburnt region estimates tended or were higher than burnt region estimates (partial or no 95% CI overlap; Figure 2a).

Compared to unburnt regions, diversity estimates when grouped across all taxon groupings and habitats remained similar (complete 95% CI overlap for species richness), decreased (Shannon diversity: no 95% CI overlap), or increased (Simpson diversity: no 95% CI overlap) after low severity fires (Figure 2b). Diversity estimates after moderate and high severity fires tended lower (species richness: partial 95% CI overlap), were lower (Shannon diversity: no 95% CI overlap), or re- mained similar to unburnt estimates (complete or near-complete 95% CI overlap). After extreme severity fires, all diversity estimates were lower than all other treatments (no 95% CI overlap; Figure 2b). There was partial to complete 95% CI overlap in some diversity estimates among all severity levels including unburnt, except extreme severity (except for low severity Simpson diversity estimates which showed no overlap with unburnt and high severity estimates; Figure 2b).

Grouped across all taxon groupings and habitats, diversity esti- mates generally increased with time since fire in burnt areas, while this trend was less clear in unburnt regions (Figure 2c). Compared to unburnt regions, diversity estimates were greater in burnt regions at 6–9, 12–15, and 15–18 months post-fire (no 95% CI overlap, except Simpson diversity at 15–18 months with partial 95% CI overlap) and similar at 3–6 months post-fire (complete 95% CI overlap except Shannon diversity which tended lower with partial 95% CI overlap; Figure 2c). Estimates were lower at 0–3 months for Shannon and Simp- son diversity but not species richness (complete 95% CI overlap) and were lower at 9–12 months post-fire (no 95% CI overlap; Figure 2c).

4.2 | Taxon groupings and habitat trends

Grouped across all habitats, diversity estimates after the fires in burnt regions compared to unburnt regions were higher for rep- tiles (no 95% CI overlap); tended higher in amphibians, arachnids, eudicots (Shannon diversity only), and monocots (partial 95% CI overlap, except for amphibian and arachnid Shannon diversity which had complete 95% CI overlap); tended lower for mammals and eudicots (partial 95% CI overlap, except eudicot Shannon diversity); and were lower for birds, fungi, and insects (no 95% CI overlap, except complete overlap in fungi Shannon diversity; Figure 3a; Appendix S3). When compared to diversity estimates
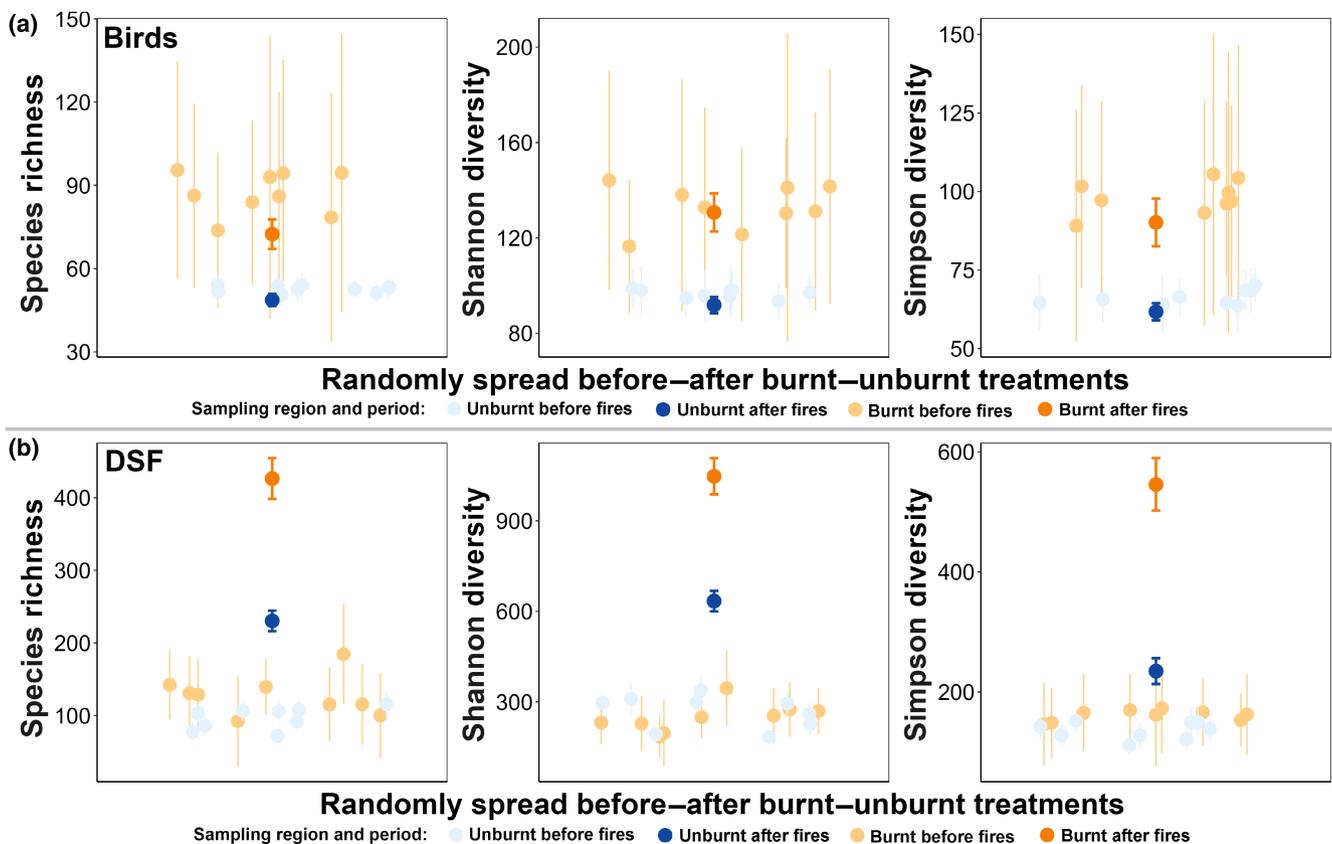

FIGURE 3 Example estimates of Hill numbers $q = 0$ (species richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity) with 95% confidence intervals (error bars) using rarefaction and prediction of iNaturalist observations (using the "iNEXT" package). Sampling completeness (SC) was 100% for $q > 0$ in these examples (see Appendix S3 for exceptions for some groupings), and double the reference sample for $q = 0$ (per Chao et al., 2014). Estimates were grouped (a) across habitats for taxon-specific estimates (birds shown here; $SC_{(q=0)} = 61.9\%$); and (b) across taxon groupings for habitat estimates (dry sclerophyll forest shown here; $SC_{(q=0)} = 49.7\%$). Estimates shown from: unburnt (blue) and burnt regions (orange), before (nine 18-month periods; faded colors) and after (one 18-month sampling period; non-faded colors) the 2019–2020 megafires. Figures from all analyses taxon groupings and habitats can be found in Appendix S3.

before the fires in the burnt regions, estimates increased after the fires for eudicots (Simpson diversity only), insects (except species richness), and reptiles (Shannon diversity only; no 95% CI overlap), and tended higher in eudicots (Shannon diversity only) and mammals (Shannon and Simpson diversity; partial 95% CI overlap; Figure 3a; Appendix S3). After the fires in unburnt regions, diversity estimates were higher than before the fires for insects (no 95% CI overlap, except for Simpson diversity) and tended higher in amphibians, mammals, monocots, and reptiles (partial 95% CI overlap; except amphibian Simpson diversity and mammal and monocot Shannon diversity estimates; Figure 3a; Appendix S3). Before the fires, diversity estimates were lower in burnt than unburnt regions for insects (no 95% CI overlap), tended lower for eudicot and mammal Simpson diversity (partial 95% CI overlap), and tended higher for amphibians and arachnids (species richness for both, and arachnid Simpson diversity; partial 95% CI overlap; Figure 3a; Appendix S3). All other estimates for taxon groupings remained similar among the four treatment comparisons (complete 95% CI overlap; Figure 3a; Appendix S3).

Grouped across all taxon groupings, diversity estimates for burnt regions compared to unburnt regions after the fires were higher in dry sclerophyll forest, flood-prone forest, and rainforest (no 95% CI overlap except rainforest Shannon and Simpson diversity); tended higher in rainforest, wet sclerophyll forest, and woodland (partial 95% CI overlap in Shannon diversity, as well as rainforest Simpson diversity); tended lower in heath and woodland (partial 95% CI overlap, except woodland richness and Shannon diversity); and were lower in cleared regions (no 95% CI overlap, except richness; Figure 3b; Appendix S3). In burnt regions, diversity estimates increased after the fires compared to before in cleared regions (Shannon diversity), dry sclerophyll forest, flood-prone forest (Shannon diversity), heath, rainforest, and woodland (no 95% CI overlap, except for Simpson diversity in heath, rainforest, and woodland) and tended higher for Simpson diversity in cleared regions, heath, rainforest, and woodland and species richness in flood-prone forest (partial 95% CI overlap; Figure 3b; Appendix S3). In unburnt regions, diversity estimates increased after the fires compared to before in cleared, dry sclerophyll forest, wet sclerophyll forest, and woodland (no 95% CI overlap) and tended lower in flood-prone forest (partial 95% CI overlap; Figure 3b; Appendix S3). Before the fires, diversity estimates for burnt and unburnt regions were higher in cleared regions for Simpson diversity (no 95% CI overlap) and tended higher for Shannon diversity (partial 95% CI overlap; Figure 3b; Appendix S3). All other estimates for habitats remained similar among the four treatment comparisons (complete 95% CI overlap; Figure 3b; Appendix S3).

5 | DISCUSSION

We found no evidence of post-fire declines in diversity across the burnt regions of NSW and the ACT over the 18 months after the 2019–2020 Australian megafires compared to periods before the fires and in unburnt regions among taxon groupings, habitats, and fire severity level (noting burnt region fire severity estimates were only compared to unburnt regions). Rather, we found an overall increase in diversity up to 18 months after the fires as well as increases in diversity estimates in some specific taxon groupings and habitats, although diversity in most groupings did not clearly change after the fires. We attribute these findings to a trio of key factors: the evolutionary and behavioral adaptations of taxon groupings fostering resilience to fire, the post-fire recovery processes, and the increased detectability of certain species post-fire due to heightened activity or attractiveness to observers, such as post-fire flowering (Pyke, 2017). Overall, our study underscores the invaluable contribution of rapidly and continuously collected citizen science data which offers some of the earliest quantitative across-taxa evidence demonstrating biodiversity responses to the 2019–2020 Australian megafires.

5.1 | Adaptations to fire and the impacts of changing fire regimes

Biomes across Australia evolved with fire, with species exhibiting adaptations and behavioral traits which support their resilience to fire disturbance (Bowman et al., 2012). For example, 95% of plant species found in Australian forests (dry and wet), shrublands, and woodlands, and 82% of plants in rainforests, exhibit life histories of persistent seed banks or post-fire resprouting, enabling regeneration after fire (Clarke et al., 2015). Many animals can flee from fire grounds to avoid flames and smoke, including birds, flying insects, mammals, and reptiles (Christensen, 1980; Griffiths & Christian, 1996; Keith, 2012), while others have been observed to shelter from fires (Brennan et al., 2011; Griffiths & Christian, 1996; Keith, 2012; Whelan et al., 1996), which may enable their persistence through fire events. While limited information is currently available on short- to mid-term biodiversity responses to the 2019–2020 megafires, the successful short-term persistence of at least one taxon, amphibians (frogs), has been observed (Rowley et al., 2020). This is likely due to the ability of frogs to seek refuge from the fires (Rowley et al., 2020) and is consistent with our finding of no clear change in frog diversity post-fire in burnt regions compared to before fire or unburnt regions. This does not, however, discount more localized or species-specific impacts of these fires on frogs (e.g., Beranek et al., 2023). Adaptations and behaviors which facilitate fire survival across taxon groupings may reduce immediate mortality and support persistence; potentially alleviating immediate declines in diversity, but this does not necessarily translate to longer term persistence in post-fire landscapes.

Extremely severe fires and associated fire storms may reduce survival if fire severity exceeds that to which species are adapted. Some plant species may not persist at local scales in areas subject to extreme fire, especially where overlapping threats occur such as a history of high fire frequency or severe drought (Auld et al., 2022; Nolan et al., 2021). Overwhelmingly, animals tend to survive the immediate passage of fires; however, a greater

proportion of animals are killed as fire severity increases (Jolly et al., 2022). The 2019–2020 megafires were exceptional in scale, resulting in a proportionately large area which was burnt by more severe fires (Collins et al., 2021).

Our analysis reveals a generally positive correlation between the presence of fire and diversity, a trend likely driven by the emergence or discovery of additional species post-fire. The evidence for this correlation was not clearly driven by a particular taxonomic grouping, although bird and reptile diversity estimates were greater in burnt than unburnt regions after the fires. One habitat, dry sclerophyll forest, had an effect evident across all taxon groupings which matched the overall trend (Figure 3b; Appendix S3), and may be due to the high frequency of post-fire flowering in this ecosystem (Knox & Clarke, 2006). An important anomaly to this general trend is observed when the severity of the fire reaches extreme levels, with no apparent uptick in biodiversity (Figure 2). This is consistent with the effects of a negative effect of severe fire on diversity in other systems (e.g., Steel et al., 2022) and suggests a possible equilibrium wherein the local species extinctions have offset introductions and/or greater detectability. Another complexity could lie in the potential delay in habitat recovery in such heavily affected sites, requiring an extended period for the return of locally extinct species, potentially exceeding the timeframe of our study. Continued collation of citizen science observations will provide long-term data over large scales, which would be suitable for use to investigate these issues, especially when coupled with standardized data collection.

While most regions in our study which burnt are naturally exposed to fire, the changes to fire regimes (e.g., increased fire frequency) and not necessarily the individual event will have the greatest long-term influence on the affected communities (Le Breton et al., 2022; Nolan et al., 2021). Rainforests, for example, naturally but rarely burn patchily and at low intensity during extremely dry periods (Collins et al., 2019; Murphy et al., 2013). However, the higher prevalence of plants incapable of post-fire recruitment, or with limited resprouting capacity after severe fires in rainforests, makes them particularly vulnerable to increasingly frequent and intense fires (Clarke et al., 2015). This can slow recruitment or cause local extinction of species in some functional groups, potentially leading to state shift and habitat change (Clarke et al., 2015; Tepley et al., 2018). As such, while examination of diversity responses to single, large fire events such as the 2019–2020 Australian megafires provides valuable insights into short- to medium-term fire impacts at scale, examination of potential shifts in fire regimes to which such events may contribute is critical for informing long-term on-ground management and conservation actions associated with changing fire regimes under climate change.

5.2 | The effects of recovery processes after fire

Over the 18-month period after the 2019–2020 megafires across the study area, diversity estimates increased after the fires in burnt areas, generally at its lowest in the first 3-month post-fire,

peaking 12–15 months post-fire (Figure 2c). This trend was less clear in unburnt regions, although diversity estimates were greatest 9–12 months post-fire (Figure 2c). Increases in both burnt and unburnt treatments post-fire may have been driven by a boost in growth and productivity as high rainfall in eastern Australia driven by a shift toward La Niña conditions broke a severe drought which contributed to the 2019–2020 megafires (Qin et al., 2022). This shift in conditions was consistent between unburnt and burnt sampling regions in our study, thus would not have caused any bias our results (Appendix S4). Despite this, there was variation between burnt and unburnt diversity estimates, likely driven by a combination of seasonality, local and broader scale environmental conditions, fire ephemeral responses, detectability or attractiveness to observers, and potential shifts in interspecific interactions such as competition, herbivory, and predation (Keith, 2012). For example, fire-stimulated flowering species, including the orchids and fire ephemerals, showed noteworthy blooms in the spring–summer following the fires, which may have contributed to increased detectability and therefore diversity in burnt areas 6–9 months post-fires.

Increased detectability of species recorded by citizen scientists, more generally, is a factor which likely influenced our findings regarding post-fire recovery. For example, fire ephemeral plants such as Pink Flannel Flowers (*Actinotus forsythii*) and the Sandy Hollow Commersonia (*Andocalva rosea*) are undetectable before fires (Bell & Copeland, 2004; Paroissien et al., 2020), but germinated, flowered prolifically, and became highly detectable across the firegrounds 12–14 months after the 2019–2020 fires. Similarly, many monocots, such as the species-rich geophytic orchid group, have cryptic habits keeping them relatively undetectable, but have fire-stimulated flowering 5–18 months post-fire (Lamont & Downes, 2011) making them more attractive and identifiable to observers. Both animals and plants in recently burnt regions were also likely more exposed and therefore more detectable to citizen scientists, potentially leading to increased recording of these species due to increased detectability rather than increased presence. Similarly, it is not readily possible to distinguish between rare species, and those which are rarely detected, and how the inclusion or omission of these species in our dataset may have influenced our results. However, while we acknowledge the potential bias of changes in detectability, such biases are likely to also be present in most standardized monitoring (Isaac et al., 2011).

Our results using citizen science data complement findings using standardized data in available literature, which typically have a finer taxonomic and spatial scope. However, prior studies on fire responses of given taxon groupings often paint a complex picture of post-fire responses. For example, our results supported prior findings that reptile diversity can often remain unchanged or increase after fire, but contrary to our findings some diversity indices can also decrease (Hu et al., 2013, 2016; Moseley et al., 2003; Mott et al., 2010). Burnt and unburnt diversity estimates for insects both increased after the fires to a similar degree, despite unburnt estimates from before the fires being substantially greater than burnt region estimates. Determining the influence of the 2019–2020 megafires on insects, as well as making comparison

to prior findings on post-fire responses (which vary among and within insect taxa, influenced by fire characteristics, and spatial and temporal factors; Arnold et al., 2017; Koltz et al., 2018; Palusci et al., 2021) is therefore challenging. Fire-driven, spatial, and temporal influences likely exist across all taxon groupings and habitats we analyzed. Our analysis illustrates the potential of unstandardized data collected through iNaturalist to expand on current understanding of the effects of fire on diversity derived from standardized data.

5.3 | Future directions

We have demonstrated the value of continually collected and targeted citizen science data in providing valuable insights into effects of the 2019–2020 megafires on biodiversity at a large geographic scale. We answered questions using iNaturalist data across multiple taxon groupings, and a broad temporal and spatial scale for which there are no standardized monitoring data. However, the use of these data comes with caveats including the influence of the substantially reduced volume of data from before the 2019–2020 megafires, compared to afterwards. With targeted post-fire sampling (*Environment Recovery Project*; Kirchhoff et al., 2021), there were more records in our dataset after the 2019–2020 megafires, compared to the number of records before the fires. However, there were also more records in unburnt regions than burnt regions. While our findings indicated overall diversity was greater after the 2019–2020 fires, post-fire estimates were substantially greater in burnt than unburnt regions, which suggests uneven sampling effort among treatments was unlikely to have substantially driven these trends. Regardless, using iNEXT, we accounted for this in our analysis approach by controlling for sampling completeness (see Section 2). Furthermore, behavioral, ecological, evolutionary explanations support our findings, as does the fact that, despite increased sampling, only some taxon groupings or habitats showed clear increases in diversity estimates post-fire and/or compared to unburnt treatments. Furthermore, this bias of increased sampling was likely to be systematic across taxon groupings and habitats (the project encouraged general sampling of fire-affected areas instead of targeting specific species or habitats), meaning that comparisons among taxon groupings and/or habitats are likely valid.

The potential bias of urbanization such that diversity estimates may be greater due to human influences on seed dispersal and disturbance was also assessed using VIIRS night-time lights at a 15 arc-second resolution (Elvidge et al., 2017; Appendix S4). There was a slight increase in median VIIRS values in unburnt areas compared to burnt areas, but no difference between before and after the fires (Appendix S4). Our findings indicated burnt areas which were less urban, showed greater diversity estimates post-fire than unburnt areas; thus, this bias was either negligible or outweighed by environmental (e.g., fire) drivers (Appendix S4). We also examined whether shifts in diversity estimates more likely reflected species richness or species abundance distribution shifts by estimating beta diversity within the

iNEXT framework (Chao et al., 2023; see Appendix S4). Estimates were derived from comparisons of pairs of assemblages (see Appendix S4). There was little overall change within assemblage pair beta estimates as the value of q increased across [0,1,2], with two notable results (Appendix S4). Comparison of unburnt regions before and after the fire period showed a flattening of the curve as q increased, which suggests much of the change for this pair can be attributed to abundant species. This was not apparent for the comparison of unburnt and burnt regions post-fire which showed beta estimates decreased with q, although we note that this is in the extrapolated part of the curve. An understanding of the underlying drivers of diversity shifts is important for informed management and is achievable through the use of citizen science data. Such data should continue to form an integral part of the ecological and management toolbox for monitoring, assessing, and responding to large-scale disturbance events, such as the 2019–2020 Australian megafires.

This toolbox could be further improved with the integration of citizen science data and structured monitoring data, to maximize the quantity, rigor, and breadth of information available to support the management of biodiversity. In our case, our analyses and results cover broad biodiversity trends, but the lack of declines detected at this scale cannot be extrapolated to the species or local scale. For example, management and policy implications from further investigations of insect responses to fire would benefit from a focus on lower taxonomic levels (Saunders et al., 2021). To this end, further fire-response research on readily identifiable insect species, from groups including dragonflies, damselflies, and butterflies which are well represented in iNaturalist observations (Mesaglio et al., 2023), would provide finer scale insights more applicable to environmental managers. By integrating the data available through standardized local, species-, or population-specific monitoring and broader scale citizen science data, we will have a greater information base from which to identify how and where to sample minimizing gaps and redundancies post-disturbance.

6 | CONCLUSIONS

In the context of widespread changes to fire-conducive conditions and associated fire regimes globally (Abatzoglou et al., 2019; Jolly et al., 2015; Keeley & Syphard, 2016; Parks et al., 2016), ecologists, managers, and governments need to determine the influence of such changes on biodiversity at a broad scale, to adapt, and appropriately manage ecosystems. We have demonstrated across a fire footprint of over five million hectares, that diversity across taxon groupings and habitats increased up to 18 months after the 2019–2020 Australian megafires. Further examination of the influence of long-term fire regimes is critical to inform long-term trends in diversity.

AUTHOR CONTRIBUTIONS

This study was conceptualized by Corey T. Callaghan, Will K. Cornwell, and Simon B. Z. Gorta, and subsequent data curation, and analyses were led by Simon B. Z. Gorta with support from Fabrice

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.nk98sf7zz. However, these data are not complete, as threatened species data which were made available for this research on request from the Atlas of Living Australia have been excluded, as these are not permitted to be publicly available. This, and information on how to replicate our dataset via download of iNaturalist data, is detailed in Appendix S5.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.