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Remotely Sensed Fire Heterogeneity and Biomass Recovery Predicts Empirical Biodiversity Responses

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ABSTRACT

Aim: To compare field-based evidence of plant and animal responses to fire with remotely sensed signals of fire heterogeneity and post-fire biomass recovery.

Location: South-eastern Australia; New South Wales.

Time Period: 2019–2022.

Major Taxa Studied: A total of 982 species of plants and animals, in eight taxonomic groups: amphibians, birds, fish, insects, mammals, molluscs, plants and reptiles.

Methods: We collated 545,223 plant and animal response records from 47 field surveys of 4613 sites that focussed on areas burnt in 2019–2020. For each site, we calculated remotely sensed signals of fire heterogeneity and post-fire biomass recovery, including the delayed recovery index. Meta-regression analyses were conducted separately for species that declined after fire (negative effect sizes) and species that increased after fire (positive effect sizes) for each buffer size (250m, 500m, 1km, 1.5km, 2km and 2.5km radius).

Results: We found that species exposed to homogenous high-severity fire (i.e., low fire heterogeneity) were more likely to exhibit decreased abundance/occurrence or inhibited recovery. Areas with delayed recovery of biomass also had significant negative on-ground responses, with lower abundance or occurrence in areas where biomass recovery was slower.

Main Conclusions: The fire heterogeneity index and the delayed recovery index are suitable for inclusion in monitoring and reporting systems for tracking relative measures over time, particularly when field survey data is not available at the landscape scales required to support reporting and management decisions. Locations with remotely sensed signals of delayed recovery should be prioritised for protection against further disturbances that may interfere with the recovery process. Research attention must next focus on how cumulative fire heterogeneity patterns of successive fires affect the post-fire recovery dynamics to further inform the application of remote sensing indicators as management tools for biodiversity conservation.

1 | Introduction

Wildfire size and severity are increasing in many parts of the world, largely due to higher temperatures and more intense droughts caused by anthropogenic climate change (Abatzoglou and Williams 2016; Ellis et al. 2022). Extreme fire behaviour is resulting in larger areas burning at high severity (Clarke et al. 2014; Cunningham et al. 2024; Di Virgilio et al. 2019; Lydersen et al. 2017). Extensive fires with little unburnt area increase the size of plant and animal declines resulting from fire (Driscoll et al. 2024). The increasing frequency and severity of drought and fire further compound the impacts of fire on biodiversity (Driscoll et al. 2024). Effects can include delays in post-fire recovery (Anderson et al. 2025; Ermitao et al. 2024; Keith et al. 2022) or changes in community composition and ecosystem conversion or collapse (Keith et al. 2023). Monitoring ecosystem health and function is therefore essential for developing predictive capacity for ecosystem dynamics and responses. Such monitoring can be widely achieved using remote sensing (Gibson et al. 2022; Gitas et al. 2012; Lentile et al. 2009; Pérez-Cabello et al. 2021). However, linking remote sensing datasets to on-ground species responses is rarely possible due to the small scale and variable methods of individual field projects.

Large areas of high-severity fire are generally considered harmful to biodiversity (e.g., Holz et al. 2015; Law et al. 2022), although some species benefit, or even depend on high-severity burns (e.g., Fontaine et al. 2009; Jones et al. 2020). However, the importance of differing spatial patterns of fire severity for maintaining or threatening biodiversity is poorly understood (Jones and Tingley 2021). When fire severity is low there are typically unburnt patches within the perimeter of the fire. These unburnt refugia can mitigate the negative effects of wildfire on species' populations by providing habitat to shelter from fire and from which to recolonise burned areas (Robinson et al. 2013; Shaw et al. 2021; Steenvoorden et al. 2019). Unburnt patches may also provide 'stepping-stones' for species to move to other suitable areas (Nimmo et al. 2019). On the other hand, extensive high-severity burn patches—with less edge and more interior area (i.e., homogenous high-severity fire)—have been associated with severe declines in biodiversity, for example in avian species of the Sierra Nevada (Steel et al. 2021) and mammal species in northern Australia (Einoder et al. 2023). However, other studies have found no effect of extensive high-severity fire on animal abundance (Diffendorfer et al. 2012), suggesting that responses depend on scale and species biology (Michel et al. 2023; Nimmo et al. 2021). Consequently, the scale at which fire heterogeneity is mapped is likely to influence our inference and predictions about biodiversity responses but too little research is available to predict what the appropriate scale would be.

Standardised methods to quantify and compare fire heterogeneity between fires—calculated at varying scales—may improve our understanding of how fire heterogeneity influences post-fire biodiversity recovery (Jones and Tingley 2021). One of the more robust methods, using a distance-to-patch-edge concept, was developed by Collins et al. (2017). Originally termed "stand-replacing decay coefficient", this fire heterogeneity index (FHI) has clear ecological relevance. For example, in north American conifer forests, tree regeneration following stand-replacing fire is dependent on seed dispersal from surviving trees either outside the burn area or in unburnt patches. Assessment of the proportion of burnt area more than 120m from the burnt patch edge (the seed dispersal limit of mixed conifer trees) represents the area that will likely have limited or delayed post-fire recovery for an extended period of time (Collins et al. 2017; Stevens et al. 2017). The FHI avoids limitations commonly seen in other studies of landscape patterns of fire, such as not controlling for the size, shape complexity and interspersion of patches (Chapman et al. 2020; Talucci et al. 2022). Although developed for north America conifer forests, this measure of fire heterogeneity is likely to have ecological relevance for other ecosystems and regions, wherever distance to patch edge may influence the post-fire recovery of species' populations.

Globally, land managers increasingly rely on remote sensing technology for regional decisions about allocation of post-fire recovery efforts and resources (ASA 2020; Southwell et al. 2020; Toombs et al. 2018). However, the relationship between change in biomass and post-fire changes in biodiversity varies across taxa and depends on factors such as previous fire frequency, recovery of other habitat elements, competition, and predation (Chalmandrier et al. 2013; Haslem et al. 2012; Keeley et al. 2005; Rainsford et al. 2020). Furthermore, remotely sensed signals of biomass and canopy cover may not have sufficient resolution at the fine scale or for the near-surface vegetation characteristics many fauna species respond to (Senior et al. 2022). Only where overall vegetation cover determines resource and microhabitat availability will species' recovery be closely related to biomass recovery (Arnan et al. 2006; Diffendorfer et al. 2012; Monamy and Fox 2000). These uncertainties highlight the need to determine whether early post-fire monitoring of biomass recovery via remote sensing can be used to indicate generalised ecological recovery.

Between September 2019 and March 2020, Australia experienced the most extreme fire season on record, with the area of forest burnt being more than 10-fold the average area burned annually in eucalypt forests (Boer et al. 2020; Collins, Bradstock, et al. 2021; Nolan et al. 2020). These wildfires instigated a significant response from land managers and researchers from non-government, government, and academic institutions to understand the precursors, immediate impacts, and recovery potential across the vast fire ground. Hundreds of millions of dollars were invested into extensive field-based ecological monitoring and post-fire recovery actions (Legge et al. 2021). Land managers in government are now focusing on improving monitoring and reporting systems to better prepare for increasingly extreme fire seasons in Australia (DCCEEW 2024). There is a strong desire for measurable and reportable fire metrics that facilitate the management and maintenance of ecosystem structure and function.

Recent advances in remote sensing of fire offer accessibility to data on fire extent and severity, fire heterogeneity, and post-fire biomass recovery in south-eastern Australia (DPE 2021, 2023; Gibson et al. 2020; Gibson et al. 2023; Gibson et al. 2022). The unprecedented scale of the Australian 2019–20 fires and the extraordinary corresponding field survey effort present an important opportunity for the first large-scale field verification of remote sensing data in relation to biodiversity responses to fire. We examined remote sensing signals of the fire heterogeneity index (following Collins et al. 2017) and post-fire biomass recovery (following Gibson et al. 2022), in relation to 545,223 taxon response records from 47 projects, which comprised 982 species or higher level groupings of plants and animals, in eight broad taxonomic groups. We examined species responses separately for those species that increased and for those that decreased in abundance or occurrence after fire. We tested the following predictions at 250 m, 500 m, 1 km, 1.5 km, 2 km and 2.5 km radii around site locations:

1. Compared to high fire heterogeneity, low fire heterogeneity (i.e., homogenous high-severity fire) will be associated with larger negative effects for those species that declined in abundance post-fire due to higher mortality and greater reductions in resources and habitat. Positive effects could become either larger or smaller. Smaller positive effects could occur if low fire heterogeneity is associated with reduced resources for species that normally increase in abundance post-fire. Larger positive effects could occur if, for example, low fire heterogeneity reduced competition or if predation decreases due to larger negative effects for species that declined.
2. Higher rates of post-fire biomass increase will be associated with larger positive effects (and smaller negative effects) on plant and animal responses, assuming the signal of biomass increase is associated with greater resource and habitat availability for many species.
3. A higher proportion of delayed recovery of vegetation cover will be associated with larger negative responses. Smaller positive responses could occur if the delayed recovery signal is associated with reduced resources and habitat requirements for species that increase in abundance post-fire. However, larger positive effects could occur if positive effects are more strongly influenced by reduced competition or prolonged open-habitat structure.

2 | Materials and Methods

2.1 | Species Response Field Data

We collated 545,223 plant and animal response records from 47 field surveys of 4613 sites that focussed on areas burnt in 2019–20 within New South Wales (Figure 1), with data collected from February 2020 to May 2021. The data represent a wide range of ecosystems, including alpine and subalpine woodlands and heathlands, dry and wet sclerophyll forests and rainforests. These ecosystems experience a range of fire regimes, from rare to no fire in rainforest, to tolerable fire intervals from 15–60 years in wet sclerophyll forest, and 8–50 years in dry sclerophyll forests (Kenny et al. 2004; NSW Rural Fire Service 2022). Nine ecosystem types were highly exposed ($\geq 50\%$ of distribution) to high frequency fires as a result of the 2019–2020 fires, including primarily wet eucalypt forest types, one dry eucalypt forest type, and one subalpine woodland. The 2019–2020 fires also caused 26 ecosystem types to become highly exposed to future risks of frequent fires should fire recur within their respective fire interval thresholds (Keith et al. 2022). These data are a subset of the nation-wide dataset used in Driscoll et al. (2024). The surveys each had at least three burnt and unburnt sites (e.g., survey points, plots, or transects), or three sites with before-after data; at least three non-zero records across all sites (at the species/taxon level); and reported either an estimate or index of abundance, or occurrence. The direction of the response was

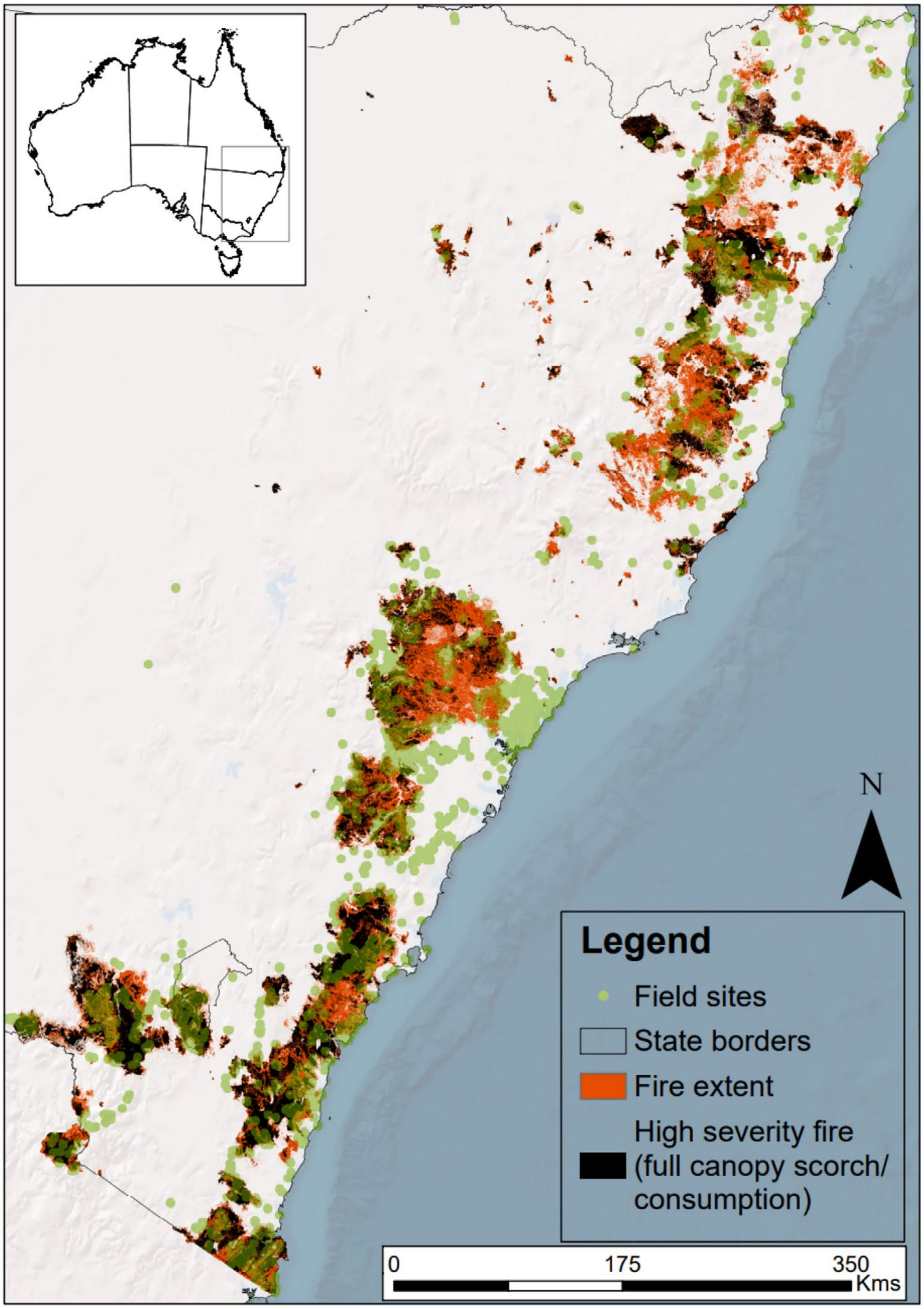

FIGURE 1 | Field site locations in relation to the fire extent of the 2019–2020 fire season in south-eastern Australia. High severity (full canopy scorch/consumption) is indicated in black. Extent and severity mapping derived from NSW Fire Extent and Severity Mapping (DPE 2021; Gibson et al. 2020).

categorised as either a decrease after fire or an increase after fire, based on the mean effect size (see *Statistical Analysis*).

3 | Satellite Imagery

All remote sensing products used in this study were derived from freely available Sentinel 2 satellite imagery (10 m pixel size). Imagery was downloaded as level 1C products (ortho-rectified, top-of-atmosphere reflectance) respectively for the pre- and post-fire periods for each study fire. Sentinel 2 SWIR bands (11 and 12) were pan-sharpened from 20 m to 10 m resolution using the Theil-Sen Estimator, a robust regression technique (Sen 1968). The images were processed to represent standardised surface reflectance with a nadir view angle and incidence angle of 45° (Flood et al. 2013), which corrects for variations due to atmospheric conditions, topographic variations and the bi-directional reflectance distribution function (Farr et al. 2007; Gallant and Read 2009), minimising the differences between scenes caused by different sun and view angles. Fractional cover products, used in fire extent and severity modelling, were generated for each Sentinel 2 image, which calculates for each pixel, the proportion of photosynthetic (green) vegetation, non-photosynthetic ('non-green', dead or senescent vegetation), and bare ground cover (Guerschman et al. 2015). Pre and post-fire imagery was taken close to the fire start and end dates, generally within 2–4 weeks. The post-fire recovery products were based on the NBR2 index, with imagery taken within February or March 2020 for time step 1, and within February or March 2021 for time step 2. This closely aligns with the post-fire field survey period used in this study.

3.1 | Fire Heterogeneity Index

The fire heterogeneity index (FHI; previously termed the stand-replacing decay coefficient, SDC, following Collins et al. 2017) is based on the high-severity patches and reflects their degree of isolation from low severity or unburnt patches. High severity is defined as full canopy scorch +/− canopy consumption, classified as high and extreme severity following Gibson et al. (2020). This is analogous to the total 'stand-replacing' patch area of Collins et al. (2017). Specifically, the FHI is a parameter which describes the rate of decay in remaining area of high severity as sequentially larger interior buffer distances are subtracted from the initial area of high severity. The extent of interior buffering is progressively increased and the proportion of patch area remaining after subtracting the buffer is calculated until the internal buffer distance is equal to the maximum distance to edge within the largest patch within the sample area (Figure 2). The relationship between the proportion of the patch area remaining and the internal buffer sizes is approximated by a modified logistic function (Equation 1):

$$P = \frac{1}{10\hat{}(FHI \times Dist)} \tag{1}$$

where P is the proportion of the total initial high-severity area, $Dist$ is the internal buffer distance (m), and FHI is the parameter that describes the shape of the relationship, which we refer to as the fire heterogeneity index (Collins et al. 2017). The fire heterogeneity index ranges between 0 and 1, smaller values describe a less heterogeneous, more homogenous landscape with fewer patches of larger sizes and larger values describe a more heterogeneous landscape with more high-severity patches of smaller size. The FHI distinguishes among configurations of patch shape from elongated to round that otherwise display similar patch area metrics. Rounder shapes or simpler patch edges have larger overall distances to forest edge and thus have flatter FHI curves (slower 'decay') compared to elongated patches or patches with more complex edges with steeper FHI curves (rapid 'decay' [Collins et al. 2017]).

Calculation of the fire heterogeneity index for field survey sites involved several steps. First, within sample areas around each site with radii of 250 m, 500 m, 1 km, 1.5 km, 2 km and 2.5 km, we intersected and clipped the NSW Fire Extent and Severity Mapping data for 2019–2020 wildfires (DPE 2021; Gibson et al. 2020). For each site, and each buffer size, the high (plus extreme) fire severity area was converted to a vector format; the initial high-severity area was calculated, then the vector was iterated through increasing internal buffers by 10 m increments. The area remaining was calculated at each iteration until the internal buffer distance was equal to the maximum distance to the edge within the largest patch, or until a maximum of 25 iterations was reached. The FHI was then fit following Equation (1). The FHI was calculated for buffer distances for each site for radii of 250 m, 500 m, 1 km, 1.5 km, 2 km and 2.5kms and divided into categories using quantile values (Table 1 and Figure 2).

3.2 | Post-Fire Biomass Recovery

Observational monitoring of post-fire biomass recovery has been applied in NSW using satellite-based technology for the three years since the extreme Australian bushfire season of 2019–2020 (DPE 2023). The method uses the concept that a disturbed system state will show high rates of system change, while undisturbed or recovered system states are characterised by near-zero rates of change (Gibson et al. 2022; Hodgson et al. 2015). This reflects the typical pattern of diminishing rates of spectral change in post-fire recovery trajectories. The burnt area initially shows large post-fire changes in vegetation cover until it eventually returns to a stable state, synchronising with surrounding unburnt areas (Gibson et al. 2022). The method compares the difference in the Normalised Burn Ratio-2 (NBR2, a short-wave infrared spectral index) based on Sentinel 2 imagery (10 m pixel size) between the target recovery year relative to 1 year previous, for any time since fire. This method overcomes limitations of assessing vegetation cover relative to a pre-fire baseline to estimate the relative increase or decrease in vegetative cover in the post-fire environment.

Data from the NSW Post-fire Biomass Recovery Monitoring system following the 2019–2020 fires (DPE 2023) was extracted for various buffer distances around the central coordinates for each unique site location. The mean biomass recovery values for 1 year post-fire were calculated for buffer distances for each of the 4613 sites for radii of 250 m, 500 m, 1 km, 1.5 km, 2 km and 2.5kms. A binary classification of delayed recovery was developed based on post-fire biomass recovery signals corresponding with field measurements at 63 field sites in dry sclerophyll forests in the Blue Mountains and South Coast of New South Wales. Elevated fuel cover, fuel connectivity, and mean maximum height were significantly lower at sites burnt at high or extreme severity with two sequential shortintervals ($<$ 10 years) compared to long intervals ($>$ 10 years). There was significantly lower post-fire biomass recovery at high-severity sites with short fire intervals for years 1 and 2 post-fire (DPE 2023), corresponding with the reduced vigour in vegetative recovery, likely due to exhausted soil seedbank or bud bank reserves (Gordon et al. 2024). The thresholds for the binary classification of the delayed recovery index were high or extreme severity, plus a post-fire biomass recovery index value of $<$ 400 in year 1 and $<$ 100 in year 2. The delayed recovery index was calculated as the percent cover for each buffer distance. The collation of all data at survey sites was scripted in Python 3.10.2 for automation and processing efficiency (see data availability).

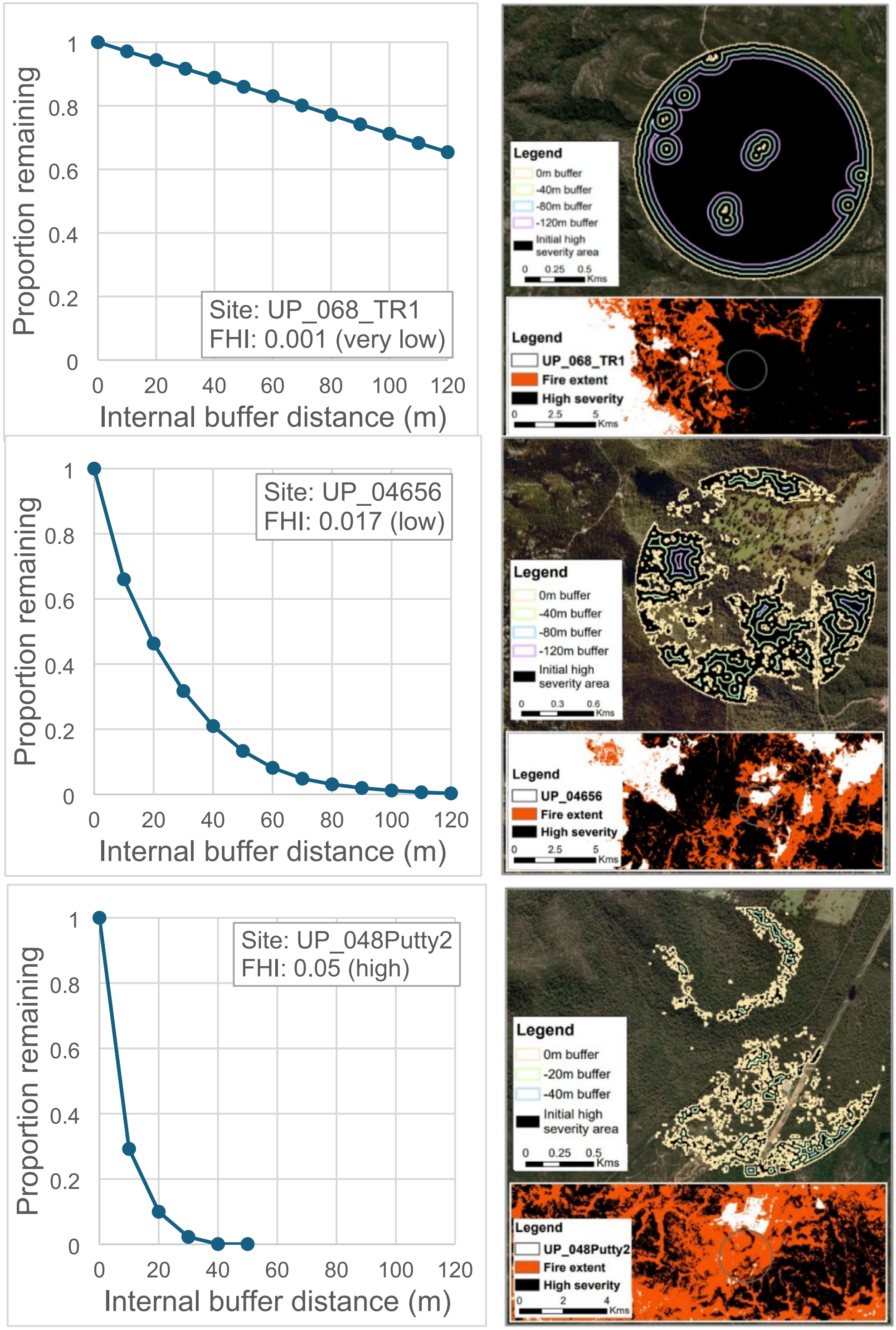

FIGURE 2 | Example sites with 1 km buffers, demonstrating the logistic function and corresponding visual representation for high (top panels), low (middle panels) and very low (bottom panels) FHI (fire heterogeneity index) values. The fire heterogeneity index (FHI) is fit based on the relationship between the remaining area of high severity (*y*-axis) and the sequentially larger interior buffer distances (*x*-axis).

3.3 | Statistical Analyses

Mean effect sizes were calculated using the standardised mean change for before-after study designs, which accommodates the expected non-independence of repeated measures of the same sites (Morris and DeShon 2002), and the standardised mean difference for control-impact designs (Morris and DeShon 2002; Viechtbauer 2010; Viechtbauer 2024). Two before-after-control-impact designs were converted to control-impact designs by subtracting before data from after data then analysed as control-impact designs. Given that before-after designs are confounded by changed climatic conditions, they were excluded from the analysis (Driscoll et al. 2024). Before calculating effect sizes, sites were excluded within projects if they were beyond the expected range of the focal species or were from an ecosystem the species never occurred in (see Driscoll et al. 2024

TABLE 1 | Category definitions for the spatial covariates.

Covariate	Levels	Category definitions
Fire severity	Unburnt; Low; High	Unburnt = unburnt surface with green canopy Low severity (combines low and moderate severity) = burnt understory, unburnt canopy or, partial canopy scorch High severity (combines high and extreme severity) = burnt understory and full canopy scorch or consumption
Fire heterogeneity index	1, 2, 3, 4	1 = very low: < 0.0093 2 = low: 0.0093–0.0180 3 = moderate: 0.0181–0.0340 4 = high: 0.0340–0.3519
Fire heterogeneity index (interaction term)	1,2	1 = hLow: < 0.0181 2 = hHigh: > 0.0180
Post-fire biomass recovery	1, 2, 3, 4	1 = very low: < 114.70 2 = low: 114.71–218.35 3 = moderate: 218.36–366.68 4 = high: 366.69–3086.68
Post-fire biomass recovery (interaction term)	1,2	1 = rLow: < 218.36 2 = rHigh: > 218.35
Delayed recovery index	1, 2, 3	1 = nil: 0 2 = low: 10%–20% 3 = high: > 20%

for details). Difference in abundance between unburnt and burnt sites (control-impact) was the dominant measure of response, with occurrence (presence/absence) comprising 7.5% of the dataset (Table S1).

Mean effect sizes were calculated for categories of each response variable (Driscoll et al. 2024). For calculating effect sizes, sites within projects were selected based on quantiles of (1) fire heterogeneity, (2) post-fire biomass recovery and (3) delayed recovery (each replicated at each buffer size, Table 1). For post-fire biomass recovery, we further subdivided sites within projects by fire severity, enabling us to calculate effect sizes for each level of biomass recovery at sites burnt at high or low severity. Similarly, we calculated effect sizes for each level of biomass recovery at sites burnt at high or low heterogeneity. This array of effect sizes enabled us to test for differences between categories of covariates and, for biomass recovery, interactions with fire severity and fire heterogeneity using meta-analysis.

Meta-regression analyses were conducted separately for species that declined after fire (negative effect sizes) and species that increased after fire (positive effect sizes), for each buffer size (250 m, 500 m, 1 km, 1.5 km, 2 km and 2.5 km radius). Species are expected to have opposite responses to fire through a range of mechanisms, making it more appropriate to examine positive and negative responses separately rather than the typical meta-analysis approach of considering just the overall mean effect (Driscoll et al. 2024).

In our meta-analyses, the appropriate subset of effect sizes was the response variable, and in separate models we fit: (1) fire heterogeneity class; (2) post-fire biomass recovery class; (3) the interaction of post-fire biomass recovery class with fire heterogeneity class; (4) the interaction of post-fire biomass recovery class with fire severity class and (5) delayed recovery class. Each model included three random effects: broad taxon (plants, insects, snails, amphibians, birds, mammals, reptiles), project identity and taxon (species, morphospecies or higher taxonomic groups where species-level classification was not available).

Our models were fitted with the rma.mv function of the metafor (Viechtbauer 2010) R (R Core Team 2024) package with options: test = "t"; dfs = "contain"; method = "REML" (Pappalardo et al. 2020). We set control = list(optimizer = "optim", optmethod = "Nelder–Mead") which enabled models to converge and used robust variance estimation (Pustejovsky and Tipton 2022) with project as the cluster to further account for non-independence within projects. Where data were divided into different severity classes, we used the vcalc function of metafor to create a variance–covariance matrix that accounted for using the unburnt sites twice in each analysis (effect sizes calculated as abundance/occurrence at high or low severity burnt sites minus abundance/occurrence at unburnt sites within the project). The full species list with corresponding effect type and response type is provided in (Table S1), along with a comparison of the ratio of negative effects to positive effects across broad taxon (Figure S2).

4 | Results

4.1 | Species Response Types

Overall, birds dominated the number of records in the dataset (n = 13,727 records), followed by insects (n = 7722) and plants (n = 5083; Table S1). In some cases, multiple records for the same species report both positive and negative effects. This is presumed to be due to different conditions and spatial covariates

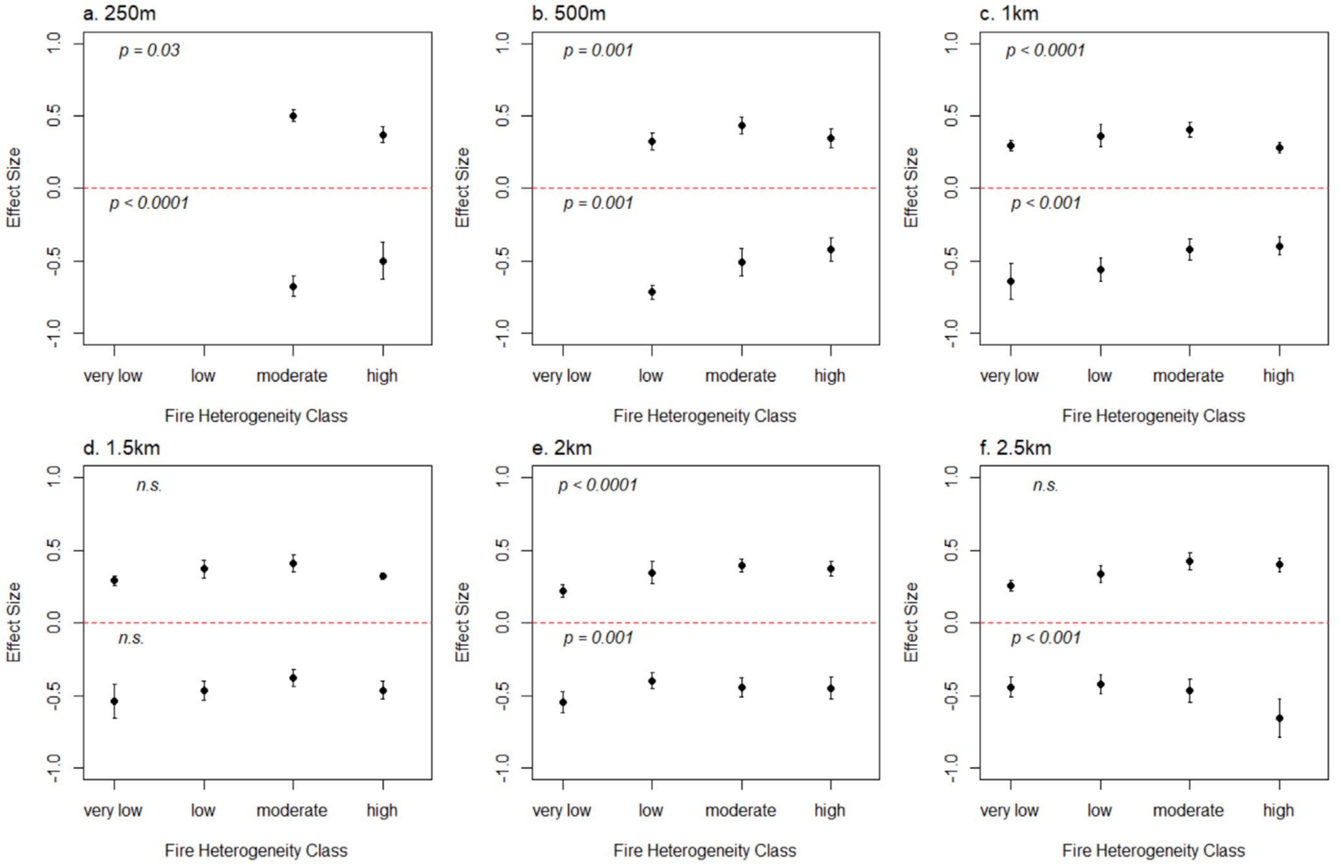

FIGURE 3 | Effect of fire heterogeneity on effect size for the taxa that increased after fire (i.e., effect sizes are positive above the red dotted line) and for the taxa that declined after fire (i.e., effect sizes are negative, below the red dotted line) across scales from (a) 250 m radius, (b) 500 m radius, (c) 1 km radius, (d) 1.5 km radius, (e) 2 km radius, and (f) 2.5 km radius.

associated with the different locations of the records. Although this could also be due to different methods of assessment for the same species (e.g., control-impact vs. before-after). Bird, fish, mollusc and plant taxon groups all had 1.5–2 times more negative than positive effects, while insects and reptiles had more species that had positive effects (Figure S2).

4.2 | Effects of Fire Heterogeneity

Our results generally supported the hypothesis that low fire heterogeneity (homogenous high-severity fire) is associated with larger negative effects (or smaller positive effects) in plant and animal responses, compared to high fire heterogeneity. For species that were negatively affected by fire (Table S1), there were larger declines with more homogenous high-severity fire at most spatial scales. The negative effect sizes were smaller with increasing fire heterogeneity. This relationship was consistent at the 250 m, 500 m and 1 k radius scales (Figure 3a–c). At 2 km radius, the very low fire heterogeneity class had significantly larger negative effect sizes, but there was no difference between the other classes (Figure 3e). At 2.5 km radius, there was no difference between classes except for larger negative effect sizes in the high heterogeneity class (Figure 3f).

For species that increased after fire (Table S1), at most spatial scales there were larger positive effect sizes at moderate levels of fire heterogeneity. Both very low and high fire heterogeneity had similar mean effect sizes. This was consistent at the 250 m, 500 m, and 1 k radius scales (Figure 3a–c). At 2 km radius, the very low fire heterogeneity class had significantly smaller positive effect sizes, compared to the other heterogeneity classes (Figure 3e).

4.3 | Effects of Post-Fire Biomass Recovery and Fire Heterogeneity Interaction

Evidence in support of the hypothesis that higher rates of post-fire biomass increase are associated with larger positive effects (and smaller negative effects on species-level responses was mixed). Overall, there was a trend towards larger declines and smaller increases in species responses associated with post-fire biomass increase. For species that declined after fire, there was no difference in species responses between fire heterogeneity classes when post-fire biomass recovery values were high for any buffer size (Figure 5a–f). Contrary to expectation, negative effect sizes were smaller when biomass recovery values were low for both low (Figure 5c,d) and high fire heterogeneity (Figure 4a,f). Furthermore, effect sizes for species that increased after fire were larger with lower post-fire biomass recovery, irrespective of fire heterogeneity levels at buffer radii of 500 m and 1.5 km (Figure 4b,d).

For species that declined after fire, our tests of species responses to the interaction of post-fire biomass recovery with fire severity returned mostly non-significant results. However, where there was a difference between severity classes for a given level of post-fire

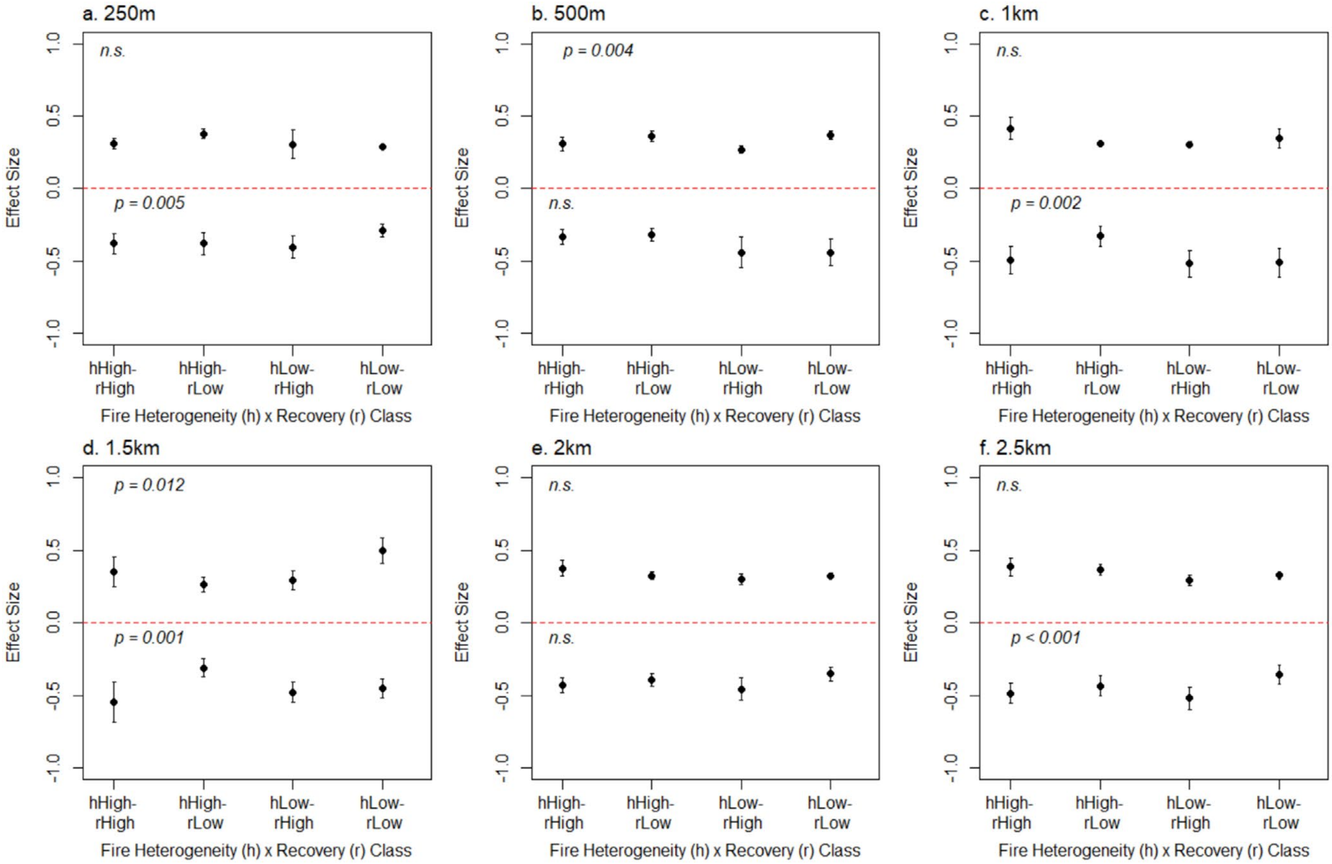

FIGURE 4 | The interaction of fire heterogeneity (h) and post-fire biomass recovery (r) on effect sizes for the taxa that increased after fire (i.e., effect sizes are positive above the red dotted line) and for the taxa that declined after fire (i.e., effect sizes are negative, below the red dotted line), across scales from (a) 250 m radius, (b) 500 m radius, (c) 1 km radius, (d) 1.5 km radius, (e) 2 km radius, and f. 2.5 km radius.

biomass recovery (e.g., at 500 m, 1 km and 2.5 km), there tended to be larger declines in high severity compared to low severity (Figure S3b,c,f). For species that increased after fire, the increase was greater with higher severity and lower post-fire biomass recovery values, consistent across all spatial scales (Figure S4a–f). This indicates that these species do well under a large degree of fire impact (i.e., high severity) as well as where the larger fire impacts are maintained over time (i.e., lower biomass recovery).

4.4 | Effects of Delayed Recovery

For species that declined after fire, there were larger negative effect sizes with delayed recovery (i.e., low and high) at the 250 m radius scale (Figure 5a). At all other scales, delayed recovery did not influence species response. For species that increased after fire, there were smaller positive effect sizes with delayed recovery (i.e., low and high; Figure 5). This was consistent at all spatial scales except for the 250 m radius (Figure 5).

5 | Discussion

5.1 | Effects of Fire Heterogeneity

Our results indicate that fire heterogeneity had a significant influence on broadscale biodiversity responses following the 2019–2020 fires in south-eastern Australia. Low fire heterogeneity (i.e., more homogenous landscape patterns of high-severity fire) was associated with both larger negative effects and smaller positive effects on biodiversity (Figure 3). Our results align with Driscoll et al. (2024) who found that declines after high-severity fire were 114% larger on average when sites had less unburnt vegetation nearby (area unburnt in the 2019–2020 fires within 2.5 km). Our results suggest that high fire heterogeneity (FHI > 0.0340), which represents weaker fire impacts on vegetation and habitat resources, does not create the conditions that support large post-fire increases by plants and animals. However, our results also demonstrate that low fire heterogeneity (i.e., homogenous patterns of high-severity fire) represents difficult conditions for post-fire recovery, even for species that can increase after fire. While many studies have examined the effects of fire severity on species recovery, very few have examined the spatial context of high-severity fire patterns, which we have shown can bring important insights into the expected impact of a fire on species' post-fire trajectories.

Heterogeneous habitats provide a greater array of resources for animals than more homogeneous habitats. Fire heterogeneity increases habitat edge and unburnt refugia, attracts birds and other animals, and has been found to promote coexistence of multiple plant functional types (He et al. 2019; Martin and Sapsis 1992). Reduced fire heterogeneity in the landscape has long been assumed to accompany losses of biodiversity (Bowman et al. 2016; Martin and Sapsis 1992). Our study is the first to quantify the degree of fire heterogeneity that is broadly detrimental to biodiversity (i.e., low and very low heterogeneity, FHI < 0.0180) in south-eastern

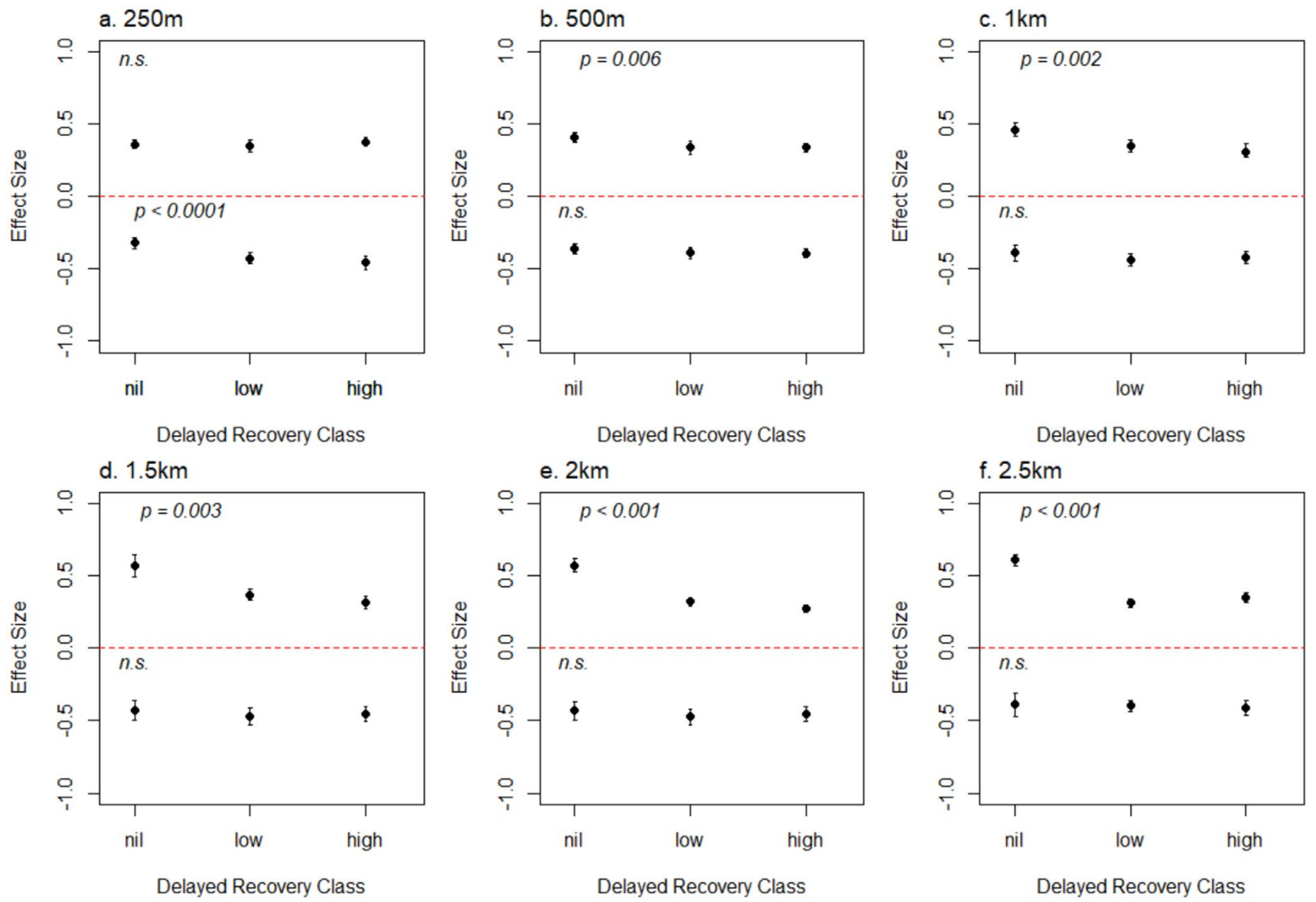

FIGURE 5 | The effect of delayed recovery on effect size for the taxa that increased after fire (i.e., effect sizes are positive above the red dotted line) and for the taxa that declined after fire (i.e., effect sizes are negative, below the red dotted line) across scales from (a) 250 m radius, (b) 500 m radius, (c) 1 km radius, (d) 1.5 km radius, (e) 2 km radius, and (f) 2.5 km radius.

Australian forests. This provides evidence that satellite-derived indices of fire heterogeneity, such as the FHI, are appropriate for applications in monitoring and reporting on the expected broad-scale biodiversity impacts in situations where field survey data of post-fire plant or animal responses are not available.

5.2 | Effects of Post-Fire Biomass Recovery

As predicted, the delayed recovery index was associated with larger negative effects and smaller positive effects on species responses (Figure 5). Bendall et al. (2024) found sites with a remotely sensed signal of delayed recovery had elevated levels of tree mortality and topkill (i.e., completely dead or loss of the majority of live above-ground biomass, with basal resprouting only) based on 350 field sites that were burnt during the 2019–2020 fires in south-eastern Australia. Sites with delayed recovery were more likely to have sparse or no epicormic resprouting on the stems and canopy, with low levels of basal resprouting and low density of seedling regeneration (e.g., see Figure S5). Such environments have relatively low resources and habitat availability, even for species that can increase in abundance in burnt areas due to preferred open habitat with less competition or predation (Jones et al. 2020). As such, remotely sensed estimates of delayed recovery provide a robust measure of locations vulnerable to severe impacts on ecosystem structure and function. This approach is innovative and overcomes many limitations of traditional remote sensing methods of post-fire recovery monitoring that rely on long-term trend detection across timeseries with reference to pre-fire baselines (Gibson et al. 2022). This index would serve well as an early warning system in risk assessments, to prioritise post-fire recovery actions and protect against additional disturbances that may further degrade ecosystem health and resilience.

Remotely sensed signals of increased vegetation cover and greenness in the early years post-fire were expected to be associated with larger positive effects (or smaller negative effects) on species responses. However, our results indicate the opposite, with larger positive and smaller negative species responses associated with low post-fire recovery values (Figure 5). Given that sites burnt homogenously at high severity have changed to a larger degree than low or heterogeneous severity, recovery of biomass is likely to interact with fire heterogeneity and severity. We found species declines tended to be smaller and species increases tended to be larger at sites with lower post-fire biomass recovery values, based on interactions with fire heterogeneity (Figure 4) and severity (Figures S3 and S4). This suggests that large rates of change in vegetation cover following fire (i.e., early seral habitats) may be broadly detrimental to biodiversity responses. Large post-fire responses of vegetation may be associated with vigorous stem and canopy epicormic resprouting as well as dense shrub regeneration in the understory (native and/or invasive species; [Nolan et al. 2021]). Remote sensing signals of increased biomass shortly after fire may be a poor surrogate for habitat structural development, because fast spectral recovery does not necessarily indicate ecosystem recovery (Celebrezze et al. 2024). By contrast, remote sensing signals of delayed recovery may be more indicative of fire impacts on habitat resources. This highlights a significant limitation of remote sensing approaches for monitoring post-fire recovery that rely on increases in vegetation cover and greenness as the primary indicator (Lopes et al. 2024; Qin et al. 2022; Yang et al. 2017), without considering the insights that can be gained by comparing remote sensing to field measures of ecosystem recovery (Celebrezze et al. 2024).

Research into feedback dynamics between fire regimes and ecological processes may provide mechanistic insights into these results (Bowman et al. 2016). Analyses of fire severity, fire frequency, fire heterogeneity, topography, vegetation, and soil types across spatial and temporal scales may be needed to better understand the processes that determine biodiversity responses in fire-prone ecosystems (Rainsford et al. 2020). For example, previous research has shown that high fire severity increases the propensity for subsequent high-severity burns (Collins, Hunter, et al. 2021). Such feedbacks may also be true for landscape patterns of fire heterogeneity, where cumulative patterns of sequential fires may interact to promote increasingly homogenous patterns of high-severity fire, but this is poorly understood and requires further research (Harvey et al. 2023).

5.3 | Effects of Scale

Biodiversity responses to fire impacts are likely to vary between taxa as a function of scale, in part related to dispersal capabilities and habitat requirements (Nimmo et al. 2019). For example, following a patchy prescribed burn, Senior et al. (2022) documented higher reptile species richness at unburnt sites and at sites with more unburnt vegetation in the surrounding area, but did not detect any clear relationships with fine-scale fire patterns for mammal species (Senior et al. 2022). Our study combines species responses from a broad range of taxa to examine generalised patterns at the landscape scale. Despite having analysed over 500,000 records, we did not have the replication available to robustly examine the effects of scale on species responses between different taxa. The varying mobility, dispersal capacity, and habitat requirements of the wide array of species included in this study may have masked patterns related to scale. Further research would be needed to comprehensively examine the effects of scale by species trait syndromes.

Correlation analysis of flora and fauna responses to landscape pattern indices is often impeded by the complicated behaviour of indices to changes in scale (Li and Wu 2004). While our results did vary with scale in some instances, there were some clear consistencies and important insights gained from including scale in our analyses. For species that were negatively affected by fire, the effects of fire heterogeneity on species responses were consistent across scales up to the 1 km radius, with smaller negative responses at moderate and high compared to low heterogeneity (Figure 3). For species that increased after fire, larger positive responses were observed at moderate compared to high heterogeneity (Figure 3). There were no further consistent patterns with increasing scales. However, for species that declined after fire, at the 2.5 km radius scale, the effect was the opposite of that observed up to the 1 km scale, whereby high fire heterogeneity corresponded with larger negative effect sizes (Figure 3f). This may be due to lower contiguous habitat cover, diversity in vegetation types, or habitat/non-habitat at the 2.5 km radius scale. Our results suggest that the 1 km radius may be the threshold where patterns in fire heterogeneity are relevant for estimating broadscale biodiversity responses.

5.4 | Management Implications

With increasing reliance on remote sensing to inform fire and land management policy and practice, understanding the ecological relevance of such indicators is pertinent. Our study provides clear evidence that fire heterogeneity has a significant association with species responses to fire, whereby low heterogeneity (i.e., high homogeneity) was associated with negative consequences to both species that declined after fire (larger negative responses) and species that increased after fire (smaller positive responses). With the increases in more severe fire weather with anthropogenic climate change, homogenous high-severity fires are likely to increase. Beyond the call to action to reduce greenhouse gas emissions globally, fire and land managers should aim to avoid extensive, frequent, homogenous high-severity fires. Increased funding may be required for managers to enact strategic plans to contain wildfires when there is a risk they will burn under extreme conditions (Kreider et al. 2024; Plucinski et al. 2023; Wollstein et al. 2022) to reduce the extent of homogenous high-severity fire. Other actions may include fuel management, fire breaks, and suppression, although more research is required to understand their effectiveness, particularly under extreme fire conditions (Penman et al. 2013; Simpson et al. 2019). Such actions may also help to reduce fire frequency, which has been identified as a major risk to biodiversity conservation (Driscoll et al. 2024; Gallagher et al. 2021).

Given the evidence we present that remotely sensed indices of fire heterogeneity and delayed recovery have significant associations with broadscale biodiversity responses to fire, these indices are suitable for including in monitoring systems alongside a suite of measurable and reportable fire metrics to facilitate the management and maintenance of ecosystem structure and function (DCCEEW 2024; Haslem et al. 2024). These remotely sensed indices would be appropriate for tracking relative measures over time, particularly when field survey data is not available at the landscape scales required to support reporting and management decisions. Our study combines post-fire responses of multiple taxa to examine generalised patterns of configurational, rather than compositional, heterogeneity (Fahrig et al. 2011). Management to maintain heterogeneous fire regimes needs to be tailored at the local scale to suit particular environments and taxa, and consider the potentially conflicting fire regime and habitat needs of local species, especially where there are threatened species that have specialist habitat requirements (Martin and Sapsis 1992; Taylor et al. 2011).

Further research is needed to quantify cumulative effects of successive fires with respect to maintenance or shifts in landscape patterns of fire severity, heterogeneity, and post-fire biomass recovery dynamics, to inform the application of remote sensing products as management tools and reporting metrics to maintain and measure biodiversity conservation in the long term.

5.5 | Conclusions

Our study provides evidence that locations with remotely sensed signals of delayed recovery were associated with worse biodiversity outcomes than locations without the delayed recovery signal. Given corresponding evidence of elevated levels of tree mortality and topkill at sites with the delayed recovery signal, further short-interval disturbances are likely to exacerbate the declines in ecosystem structure and function. Locations with remotely sensed signals of delayed recovery should be prioritised for protection against further disturbances that may interfere with the recovery process, including short-interval fire and forestry operations. Our findings also suggest that remote sensing signals of post-fire biomass increase alone are a poor indicator of habitat structural recovery and therefore biodiversity responses. Changes in vegetation community structure and composition towards more flammable and fire-prone systems may be driving rapid and vigorous vegetative regrowth in the early post-fire environment.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The remote sensing datasets for severity and post-fire biomass recovery are publicly available on the SEED data portal (https://datasets.seed.nsw.gov.au/dataset/nsw-post-fire-biomass-recovery-monitoring-by-remote-sensing and https://datasets.seed.nsw.gov.au/dataset/fire-extent-and-severity-mapping-fesm). The effect size datasets and R code are available from Dryad: Digital object identifier: https://doi.org/10.5061/dryad.34tmpg4vp. Reviewer URL: http://datadryad.org/stash/share/Rq6wFHZBoC-Ln6GthKpo3fhfw4M-6D4nAl0EyPWPHyY.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.