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RESEARCH ARTICLE

Multidimensional diversity recovery following invasive species removal: Roles of colonization, extinction and abundance shifts

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Abstract

1. Biological invasion is a global ecological challenge, threatening biodiversity and ecosystem functionality. While invasive species removal is a widely used strategy for restoring communities, its effects on the recovery of diversity, particularly through the dynamics of species colonization, extinction and shifts in abundance distribution, remain poorly understood.
2. By conducting a three-year field experiment, we assessed the recovery of taxonomic, phylogenetic and functional diversity of non-invasive communities under different intensities of invasive species removal. We further examined how species colonization, extinction and shifts in species abundance distributions contribute to these multidimensional diversity changes.
3. Our results showed that the removal of invasive species increased taxonomic, phylogenetic and functional diversity of non-invasive communities. Notably, abundance-weighted diversity measures showed stronger recovery compared to incidence-based metrics. The removal of invaders promoted new colonization, reduced local extinction and increased the evenness of resident species over time. While the removal did not systematically alter the phylogenetic or functional patterns of species colonization and extinction, it enhanced the dominance of distantly related and functionally dissimilar species and substantially increased abundance-weighted phylogenetic and functional diversity.
4. *Synthesis*. Our findings highlight the critical, yet often overlooked, role of shifts in species abundance distributions in driving the recovery of phylogenetic and functional diversity after invader removal. By integrating colonization–extinction dynamics with shifts in abundance distributions, our study provides a comprehensive framework for understanding community dynamics and restoration outcomes following invasive species management.

KEYWORDS
alien plant, biodiversity, biological invasion, functional trait, phylogenetic diversity, restoration, species abundance distribution

1 | INTRODUCTION

Biological invasion is a global environmental crisis, leading to significant ecological disruptions and economic losses worldwide (Diagne et al., 2021; Kumar Rai & Singh, 2019; Mack et al., 2000; Paini et al., 2016; Pyšek & Richardson, 2010). Invasive species threaten native communities by altering their composition, structure, and functionalities, often outcompeting native species and reshaping the community dynamics (Powell et al., 2011; Pyšek et al., 2020). Understanding the mechanisms by which invasive species impact native communities remains challenging, particularly when disentangling the direct effects of invaders from other confounding factors (Guido & Pillar, 2017; Linders et al., 2019; Simberloff et al., 2013).

Experimental removal of invasive species has emerged as a helpful tool for providing clearer causal inferences by isolating the impacts of invaders. These experiments not only help isolate the specific effects of invasive species on non-invasive communities, but also offer crucial insights into ecological restoration efforts (Flory & Clay, 2009; Guido & Pillar, 2014). However, most removal experiments often focus on eliminating a single invasive species, thereby overlooking the co-invasion of multiple alien species and the varying dominance levels among them (Kettenring & Adams, 2011). This narrow focus limits the applicability of findings to real-world management strategies, where co-invasions are common, and partial removal of invaders is often more practical and enforceable (Prior et al., 2018; Vredenburg, 2004). Testing different removal intensities, such as removing dominant versus non-dominant invaders, is essential for a better understanding of invasion impacts and to inform effective control strategies. Moreover, most studies have focused solely on taxonomic diversity, overlooking phylogenetic and functional dimensions. Phylogenetic and functional diversity provide complementary information that captures the evolutionary histories and ecological traits of species, respectively, and are increasingly recognized as critical to understanding community assembly and ecosystem functioning (Cadotte et al., 2009; Kraft et al., 2015; McGill et al., 2006; Webb et al., 2002). Therefore, incorporating multidimensional diversity would provide a more comprehensive view of how natural communities respond to invader removal and is essential for informing effective restoration strategies.

Species colonization and extinction are fundamental processes that shape the diversity and composition of communities over time (Li et al., 2015; Wardle et al., 2011). Recent studies have shown that removing invasive species often promotes colonization, as the removal of invaders alleviates competition for space and resources, allowing non-invasive species to recolonize and persist, thereby enhancing taxonomic biodiversity (Crimmins & Mcpherson, 2008; Palacio-Lopez et al., 2024; Saito & Tsuyuzaki, 2012; Ward et al., 2024). However, it remains largely unknown how species colonization and extinction after invader removal would affect phylogenetic and functional diversity (Andreu & Vilà, 2011; Erskine-Ogden & Rejmánek, 2005). In particular, it remains unclear whether invader removal would promote the colonization of phylogenetically and functionally similar or dissimilar non-invasive species, or whether such species are more likely to avoid extinction after invader removal. For instance, if newly colonizing species are phylogenetically distant and functionally dissimilar from resident species and from each other, we would expect an increase in both phylogenetic and functional diversity (Figure 1a). Conversely, if colonizers are phylogenetically and functionally similar, the increase in phylogenetic and functional diversity would be less pronounced (Figure 1b). Similarly, if the removal of invasive species reduces the extinction of phylogenetically distant and functionally unique species, we would expect a more pronounced increase in both phylogenetic and functional diversity (Figure 1c, Feng & van Kleunen, 2016; Yang et al., 2018; Zhang et al., 2021; Zhu et al., 2020). Despite these insights, the specific effects of colonization and extinction on the phylogenetic and functional diversity of non-invasive communities following invasive species removal remain largely unexplored.

Beyond colonization and extinction, shifts in the abundance of resident species also play a pivotal role in community recovery following invasive species removal. Recent research suggests that shifts in species abundance might be the dominant factor driving biodiversity changes over time, often outweighing the contributions of colonization or extinction (Jandt et al., 2022). However, it remains unclear whether dominant non-invasive species benefit disproportionately and become more dominant after invader removal, or whether abundance becomes more evenly distributed among species; the latter may indicate a more successful ecosystem restoration (Sasaki & Lauenroth, 2011). Further, understanding phylogenetic and functional abundance distributions, specifically whether ecologically similar or dissimilar species become more abundant after invader removal, would provide deeper insights into community assembly processes (Allan et al., 2013; Hardy, 2008; Li et al., 2015). For instance, if abundance distributions become phylogenetically and functionally overdispersed, where distantly related and functionally distinct species dominate, this could enhance phylogenetic and functional diversity over time (Figure 1e, Allan et al., 2013; Li et al., 2015). Conversely, an increase in the dominance of closely related or functionally similar species may constrain long-term recovery of phylogenetic and functional diversity (Figure 1f, Zhu et al., 2019). If abundance shift is the primary mechanism underlying recovery, we would expect abundance-weighted metrics to respond more strongly to invasive species removal than incidence-based measures. Therefore, simultaneously examining both incidence-based and abundance-weighted measures of phylogenetic and functional diversity is essential for better capturing the responses of multidimensional diversity to removal interventions. To date, to our knowledge, no studies have directly examined how invasive species removal shapes phylogenetic and functional abundance distributions, leaving a knowledge gap in the understanding of community dynamics and improving restoration strategies.

To address this knowledge gap, we conducted a three-year experiment in a subtropical old field, with four invader removal treatment levels: no removal, removal of non-dominant invaders, removal of dominant invaders and removal of all invaders. This experimental design allowed us to directly assess how different intensities of invasive species removal affect taxonomic, phylogenetic and functional

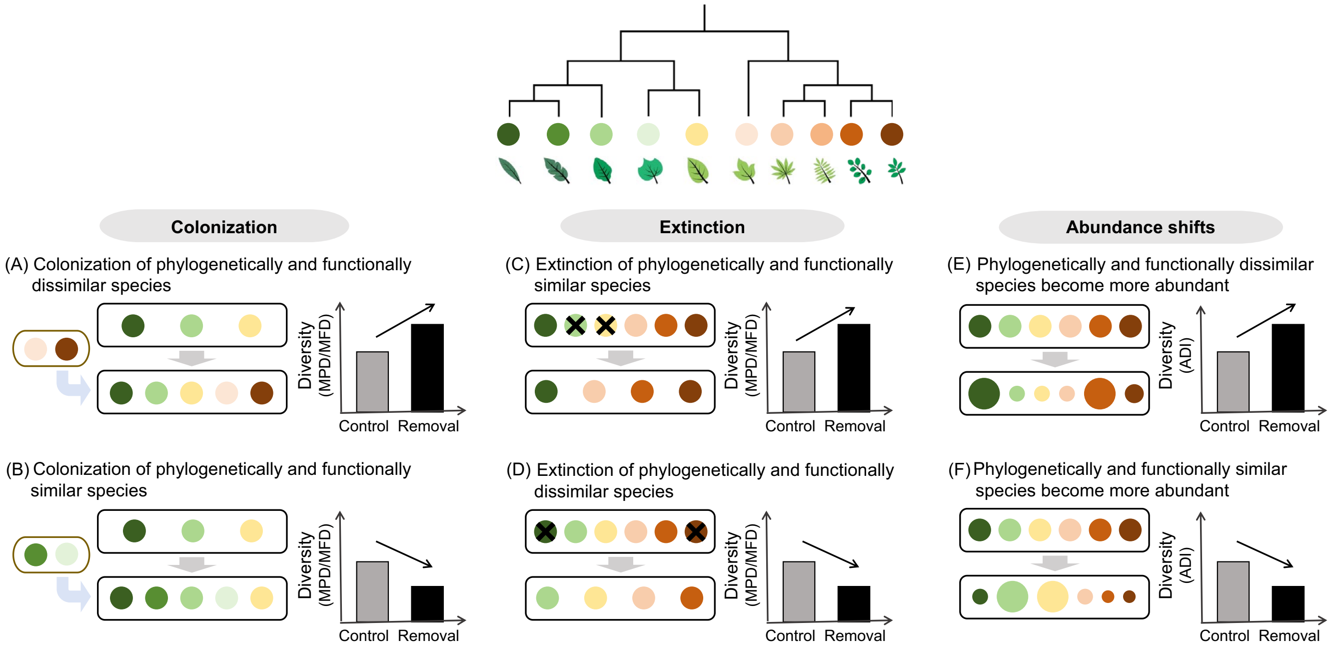

FIGURE 1 Conceptual framework illustrating how species colonization, local extinction, and abundance shifts may influence multidimensional diversity recovery following invasive species removal. (a,b) Colonization by phylogenetically and functionally dissimilar species increases phylogenetic and functional diversity, whereas colonization by similar species decreases them. (c,d) Extinction of similar species increases phylogenetic and functional diversity, while extinction of dissimilar species decreases them. Phylogenetic and functional diversity in panels (a–d) are measured as mean pairwise phylogenetic distance (MPD) and mean pairwise functional distance (MFD). (e,f) Abundance shifts affect abundance-based phylogenetic and functional diversity. Increases in the abundance of dissimilar species enhance phylogenetic and functional diversity, while increased dominance by similar species decreases them. In panels e and f, diversity is quantified using phylogenetic and functional abundance dispersion indices (ADI).

diversity of non-invasive communities over time. Further, by tracking species colonization, extinction and shifts in abundance over the 3 years, we aimed to elucidate the relative contributions of these processes to biodiversity changes and community recovery. We hypothesized that species colonization, extinction and abundance shifts would jointly shape multidimensional diversity recovery, with abundance shifts contributing most strongly at the onset of recovery. Additionally, we predicted that phylogenetically and functionally dissimilar species would become more abundant after invader removal, which would lead to a stronger increase in abundance-weighted diversity metrics compared to incidence-based measures. Together, these insights aim to provide insights into the mechanisms driving diversity changes and offer practical guidance for ecological restoration in the context of biological invasions.

2 | MATERIALS AND METHODS

2.1 | Experimental design and plant community survey

Our study area is located in a subtropical old field in Santang Village, Ningbo, Zhejiang Province, China (29°47′ N, 121°48′ E). The area experiences a warm and humid subtropical monsoon climate, with an average annual temperature of 16.2°C and precipitation of 1374.7 mm. This site is naturally invaded by several invasive species, with *Solidago canadensis* L. being the most dominant one, accounting for more than 80% of the total cover of all invasive species. This study site thus provides an ideal system for studying invasive species removal at a local scale, as it represents a typical old field that has been continuously colonized by various invasive plants.

We referenced the most recent datasets to classify alien, invasive, and native species in the study area (Hao & Ma, 2023; Lin et al., 2022). In the study site, our survey identified a total of 58 plant species, of which eight were classified as invasive species. The other 50 species, including 47 native species and 3 non-invasive alien species, were treated as non-invasive in our analysis. Prior to the experiment, all plots were uniformly abandoned in 2019, thoroughly ploughed and levelled, which minimized variation in initial biotic and abiotic conditions. We then set up four treatments: Control (no plant removal), R1 (removal of all non-dominant invasive species except *S. canadensis*), R2 (removal of the dominant invasive species *S. canadensis*), and R3 (removal of all invasive species) (Table S1). Each 1 m × 1 m plot was considered as a community, with 12 replicates for each treatment, resulting in a total of 48 plots (Figure S1). Plots were randomly assigned and separated by 0.5 m wide passages. For the removal treatments, invasive species were removed four times per year (April, June, August and November) from 2020 to 2022. Most invasive species with shallow roots were manually uprooted. For tall or prostrate species whose root systems could not be extracted without disturbing soils (e.g. *S. canadensis*, *Alternanthera philoxeroides*), we clipped above-ground tissues. The quarterly schedule effectively suppressed re-sprouting and maintained low invader cover while minimizing soil disturbance and collateral damage. We conducted annual surveys of species within the plots during the peak growing season in August from 2020 to 2022. To maintain consistency during the surveys, we used a 1 m × 1 m frame divided into 25 grids (20 cm × 20 cm each). We placed this frame above the canopy, identified all species, and recorded their coverage within each grid (Figure S2). The data from all 25 grids were then aggregated, and the proportion of the plot area occupied by each species was calculated as a proxy for species abundance.

2.2 | Phylogeny and functional traits

We constructed a phylogenetic tree for all 58 species observed during the three surveys using the megatree approach. First, we compiled a species list from field survey data and verified names against the Species2000 database (http://www.sp2000.org.cn/). We then used the V.PhyloMaker2 package (Jin & Qian, 2022) in R to construct the phylogenetic tree, constrained by the established phylogeny of vascular plants (Qian & Jin, 2015; Zanne et al., 2013). We applied the *phylo.maker* function with Scenario 3 to extract phylogenetic branches from GBOTB.extended.TPL.tre (Smith & Brown, 2018; Figure S3).

We collected five key functional traits, including plant height, leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf thickness (LT). These traits represent key axes of plant ecological strategies and are closely related to light acquisition, resource use efficiency and competitive ability (Díaz et al., 2015; Kunstler et al., 2015; Lasky et al., 2013). These traits are also widely applied in invasion ecology to differentiate native from invasive species and to assess invader impacts on community assembly and ecosystem functioning (Funk et al., 2008; Li et al., 2021; Tecco et al., 2010; van Kleunen et al., 2010). Plant height was measured on ten randomly selected individuals per species in our study site. For the other four traits, we sampled ten individuals per species and collected five mature, healthy leaves from each individual. We then measured leaf fresh weight, leaf area (using ImageJ after scanning), leaf thickness (with a thickness meter at three points) and leaf dry weight (after drying leaves at 75°C for 48 h) for each leaf. SLA was calculated as leaf area per unit dry mass (SLA = leaf area (cm^2)/leaf dry weight (g)), and LDMC as dry mass per unit fresh mass (LDMC = leaf dry weight (g)/leaf fresh weight (g)). We obtained these functional traits for 53 species, and the mean values per species were used in subsequent analyses. For the remaining five species, the number of mature individuals occurring in our experimental plots was less than three (i.e. *Rubus parvifolius* L., *Litsea pungens* Hemsl., *Orychophragmus violaceus* (L.) O. E. Schulz, *Ardisia japonica* (Thunb.) Blume, *Aster tataricus* L. f.), traits data were sourced from the TRY database (Kattge et al., 2019).

2.3 | Taxonomic, phylogenetic and functional diversity

To evaluate the impact of invasive plant removal on the taxonomic diversity of non-invasive communities, we calculated Hill Numbers under different removal treatments (Hill, 1973). The formula is:

$$^{q}D = \left(\sum_{i=1}^{S} p_i^{q}\right)^{1/(1-q)}$$

where S is the number of non-invasive species in the plot, p_i is the abundance of the ith species, and q is a non-negative parameter that adjusts the weight given to species based on their abundance. When $q = 0$, diversity represents species richness as an incidence-based measure, considering only the number of species without accounting for their abundances. In contrast, when $q = 2$, diversity is an abundance-based measure that emphasizes dominant species, reducing the influence of rare species and effectively representing the inverse of Simpson's concentration. We calculated Hill Numbers for $q = 0$ and $q = 2$ using the *hill_taxa* function from the R package *hillR* (Li, 2018).

Phylogenetic diversity of non-invasive communities was quantified using the mean pairwise phylogenetic distance (MPD), which calculates the average phylogenetic distance between all possible pairs of species in a given community. MPD provides insights into the phylogenetic relatedness among species while minimizing the influence of species richness (Webb et al., 2002, 2008). For functional diversity, we calculated the mean pairwise functional distance (MFD) by constructing a Gower distance matrix using the standardized trait values (mean = 0, SD = 1) of the five traits (Webb et al., 2002). Both incidence-based and abundance-based measures were employed to capture species presence and dominance. Abundance-weighted measures, including abundance-weighted MPD (MPDab) and abundance-weighted MFD (MFDab), were weighted by species coverage. All metrics were computed using the *picante* package (Kembel et al., 2010) in R 4.1.1 (R Core Team, 2021).

2.4 | Species colonization and extinction

To assess the contributions of species colonization and extinction to changes in taxonomic, phylogenetic and functional diversity following invasive plant removal, we classified non-invasive species in each plot into three components based on the data of the first survey (2020) and the final survey (2022): colonists (C), which were absent in the plot in 2020 but present in 2022; locally extinct species (E), which were present in 2020 but absent in 2022; and resident species (R), which were present in both 2020 and 2022 (Figure S4).

To assess whether the colonists and local extinctions were more or less similar to residents than expected by random assembly, we calculated the standardized effect size (SES) of βMPD and βMFD using a null model approach (Li et al., 2015; Rao et al., 2023). Specifically, βMPD and βMFD quantified the phylogenetic and functional dissimilarities between residents and either colonists or locally extinct species in each plot over the 3-year period. SES values were computed as: (observed value − mean expected value)/SD (expected value), where expected values were generated from 999 random communities created by the null model. For colonists, we used a null model that kept the residents unchanged, maintained the number of colonists, but randomly assigned colonist identities from the colonization pool, which included all non-invasive species except those classified as extinctions and residents in the plot. Negative SES.βMPD and SES.βMFD values indicate that colonists are more phylogenetically related or functionally similar to residents than expected by chance, while positive values suggest the opposite. For local extinctions, we applied a null model that preserved the number of extinctions unchanged, with extinct species randomly selected from those species present in the community of the plot in 2020 (Li et al., 2015; Rao et al., 2023). Negative SES.βMPD and SES.βMFD values imply that species more closely related or functionally similar to residents had a higher chance of going locally extinct, while positive values indicate the contrary. Together, these models assume that all non-resident species have equal potential to colonize and that all resident species have equal likelihood of local extinction, providing an ecologically meaningful null expectation for assembly processes (Li et al., 2015; Rao et al., 2023). These analyses were conducted using the *comdist* function in the R package *Phylocom* (Webb et al., 2008).

The changes in phylogenetic and functional diversity after invasive plant removal are influenced not only by the dissimilarities of colonists and extinctions to the residents, but also by the internal dissimilarities within colonists, local extinctions, and residents. To account for this, we also calculated the SES.MPD and SES.MFD of the subset of colonists, local extinctions and residents in the plots. We calculated SES.MPD and SES.MFD for colonists and local extinctions themselves using the identical null models mentioned above. For residents, we use a null model that kept the number of residents unchanged, with resident species randomly selected from a non-invasive species pool. Negative SES.MPD and SES.MFD indicate that the members of each component—colonists, local extinctions, and residents—are more phylogenetically closely related or more functionally similar than expected by chance, while positive values suggest the opposite.

2.5 | Shifts in abundance distributions of resident species

The removal of invasive species can impact not only the colonization and extinction dynamics of non-invasive species but also their abundance distributions. To evaluate these changes, we calculated Pielou's evenness and abundance dispersion indices (ADI) at both phylogenetic and functional levels. Pielou's evenness for residents was calculated using the average species coverage in 2020 and 2022 as an abundance metric. We also calculated Pielou's evenness for all non-invasive species within each treatment based on yearly coverage data, presenting the three-year average. This evenness index ranges from 0 to 1, with higher values indicating a more even distribution of species abundances (Pielou, 1966).

We quantified phylogenetic and functional ADI for resident species in 2020 and 2022 separately, using coverage data from each respective year, and reported the average ADI for each treatment across both years. Similar to Pielou's evenness, we also calculated the ADI for all non-invasive species. The ADI was derived by comparing incidence-based mean pairwise distances with abundance-weighted mean pairwise distances, following the methods of Allan et al. and Hardy (Allan et al., 2013; Hardy, 2008). To facilitate interpretation, we transformed the ADI values by multiplying them by −1, as suggested by Allan et al. (2013). Consequently, positive ADI values in our study indicate overdispersed abundance distributions, where abundant species are more phylogenetically and functionally dissimilar than average, while negative values indicate clustered distributions, where abundant species are more closely related and functionally similar.

2.6 | Statistical analysis

We used linear mixed-effects models (LMMs) to analyse the effects of different removal treatments on community taxonomic diversity (Hill numbers for $q = 0$ and 2), phylogenetic diversity (incidence and abundance-based MPD), and functional diversity (incidence and abundance-based MFD), with the treatment as a fixed effect and year as a random effect. Generalized linear models (GLMs) with a Poisson distribution were applied to compare the number of colonizing and extinct species among treatments, while GLMs with a Gaussian distribution were used for evenness, SES.βMPD, SES.βMFD and abundance-weighted dispersion indices. Tukey's HSD tests were used for post hoc comparisons. One-sample t-tests were used to compare SES.βMPD and SES.βMFD of colonists and local extinctions to residents against zero under different treatments. In addition to our primary analyses of non-invasive communities (natives plus non-invasive aliens), we conducted parallel analyses on native species alone. These are reported in the Supporting Information and yielded consistent results, providing further support for the robustness of our conclusions. All statistical analyses were conducted using R 4.1.1 (R Core Team, 2021). LMMs and GLMs were constructed using the *lme4* package (Bates et al., 2015), and marginal R^2 values were calculated using the *r.squaredGLMM* function in *MuMIn* (Bartoń, 2023). Tukey's HSD were performed using the *emmeans* package (Lenth, 2023).

3 | RESULTS

3.1 | Taxonomic, phylogenetic, and functional diversity under different removal treatments

Invader removal generally increased taxonomic, phylogenetic, and functional diversity. Incidence-based taxonomic diversity ($q=0$) significantly increased with removal, whereas incidence-based phylogenetic and functional diversity did not show much change across all removal treatments (Figure 2a–c). In contrast, abundance-based measures revealed a significant increase in taxonomic, phylogenetic, and functional diversity following invasive species removal (Figure 2d–f). The strongest increases were observed in the full removal treatment (R3), where all invasive species were removed. These trends were consistent across individual years (Figure S5) and when analyses were restricted to native communities (Figure S6).

3.2 | Species colonization, extinction and the abundance distribution of resident species

Over the three-year experiment, the removal of invasive species significantly affected colonization, extinction and the abundance distribution of resident species (Figure 3). The control treatment had the fewest colonists and the highest number of extinctions, the removal of non-dominant and all invaders significantly increased colonization, and the removal of non-dominant invaders significantly reduced species loss (Figure 3a,b). These findings suggest that removing invaders

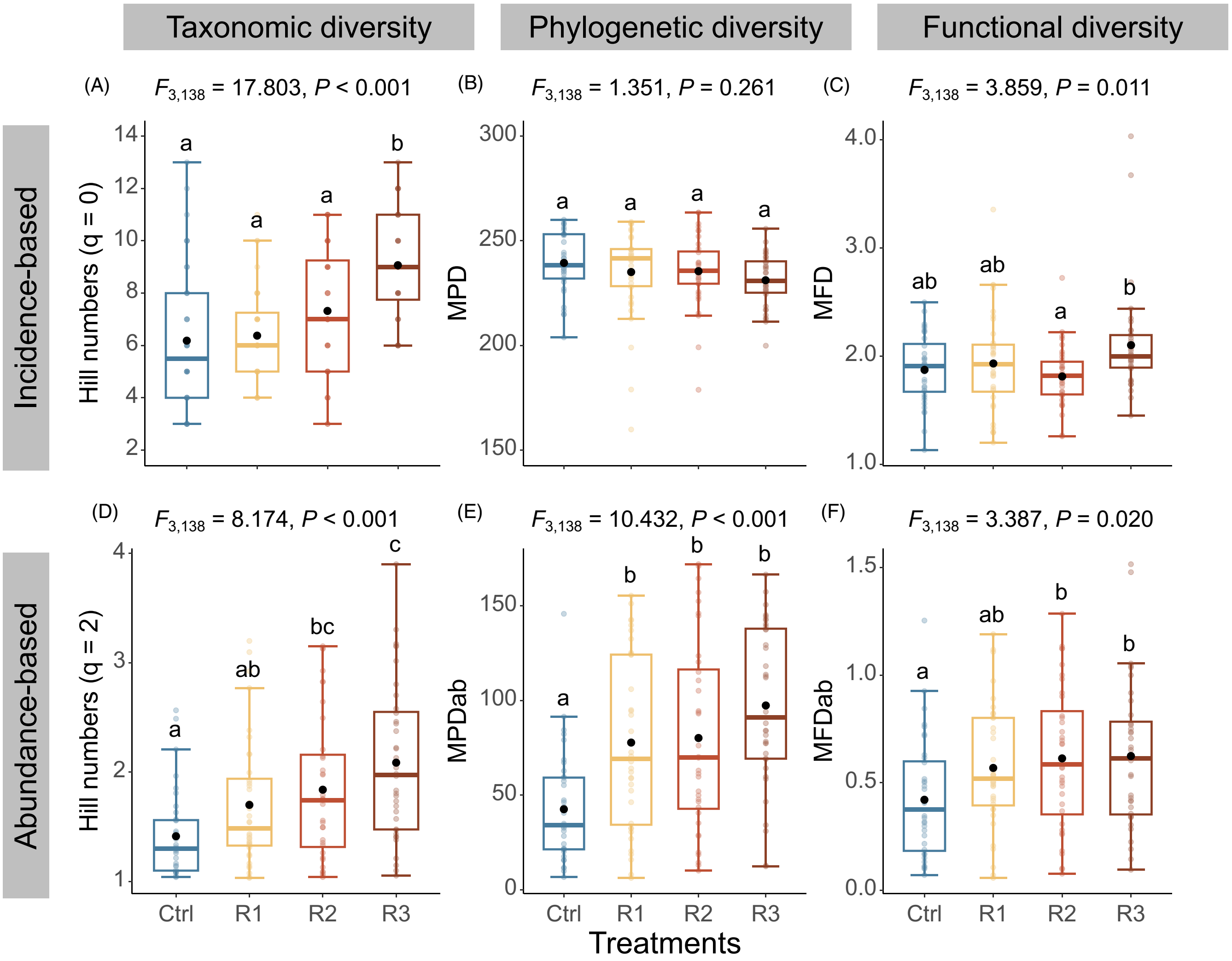

FIGURE 2 Taxonomic (a,d), phylogenetic (b,e), and functional diversity (c,f) of non-invasive communities under different removal treatments. The diversity metrics presented include taxonomic diversity (Hill numbers for $q=0$ and $q=2$), mean pairwise phylogenetic distance (MPD and MPDab for incidence- and abundance-based measures), and mean pairwise functional distance (MFD and MFDab for incidence- and abundance-based measures). The *x*-axis represents the four treatments: Ctrl (No removal), R1 (Removal of non-dominant invaders), R2 (Removal of dominant invaders), and R3 (Removal of all invaders). Coloured points represent individual plot diversity values for each year, while black dots/boxplots represent overall means and distributions (median ± interquartile range). Different lowercase letters indicate significant differences among treatments (Linear mixed-effects models with Tukey's HSD, $p<0.05$).

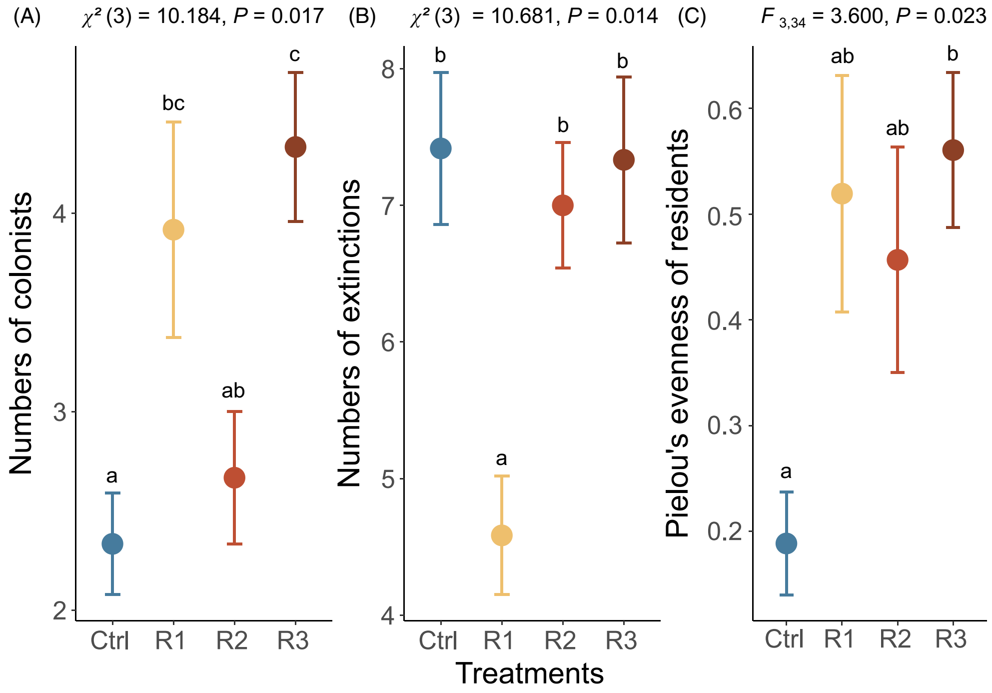

FIGURE 3 Numbers of colonists (a) and extinctions (b), and the evenness of resident species (c) under different removal treatments. The *x*-axis represents the treatments as defined in Figure 2. Points indicate the mean values across all replicates for each treatment, with error bars showing the standard errors. Results are based on generalized linear models with a Poisson distribution (a,b) and a Gaussian distribution (c). Different lowercase letters indicate significant differences among treatments (Tukey's HSD, $p < 0.05$).

enhanced taxonomic diversity by simultaneously promoting colonization and reducing extinction of non-invasive species, with the extent of these effects varying among treatments. Additionally, removal significantly increased evenness of the residents compared to the control treatment, indicating that invader removal fostered a more even distribution of abundance among resident species (Figure 3c). These patterns were consistent when evenness was calculated across all non-invasive species instead of resident species (Figure S7) and when analyses were restricted to native communities (Figure S8). Thus, the removal of invasive species facilitated new colonization, decreased local extinction and promoted the evenness of species abundance, collectively contributing to an increase in taxonomic diversity.

3.3 | The role of colonization and extinction in phylogenetic and functional diversity changes

Removal treatments had minimal effects on the phylogenetic and functional patterns of species colonization and extinction (Figure 4). The phylogenetic and functional distances between colonists and residents, measured by SES.βMPD and SES.βMFD, did not significantly differ from the null model across most treatments (Figure 4a,c), indicating that new colonists were neither more nor less similar to residents than expected by chance. Furthermore, there were no significant differences among the four treatments, suggesting that removal treatments did not influence the phylogenetic and functional relationships between colonists and residents. For extinction, SES.βMPD and SES.βMFD values were consistently greater than zero across all treatments, suggesting that locally extinct species were generally more distantly related and functionally distinct from residents (Figure 4b,d). However, no significant differences were detected among treatments, suggesting that invader removal did not alter the phylogenetic and functional relationships between extinctions and residents. Although some deviations from the null model were observed for phylogenetic and functional distances within colonists, extinctions and residents for certain treatments, these deviations were not significant between the four treatments (Figure S9). Results were similar when analyses were restricted to native communities (Figure S10).

3.4 | Impact of invasive species removal on phylogenetic and functional abundance distribution

The removal of invasive species significantly affected the phylogenetic and functional abundance distribution of resident species (Figure 5). Under the control treatment, the phylogenetic and functional abundance dispersion indexes were significantly negative, indicating that the dominant species were closely related and functionally similar to each other. After the removal of invasive species, the phylogenetic and functional abundance dispersion indexes increased compared to the control, suggesting that the removal promoted the dominance of more distantly related and functionally dissimilar species. These patterns were consistent whether

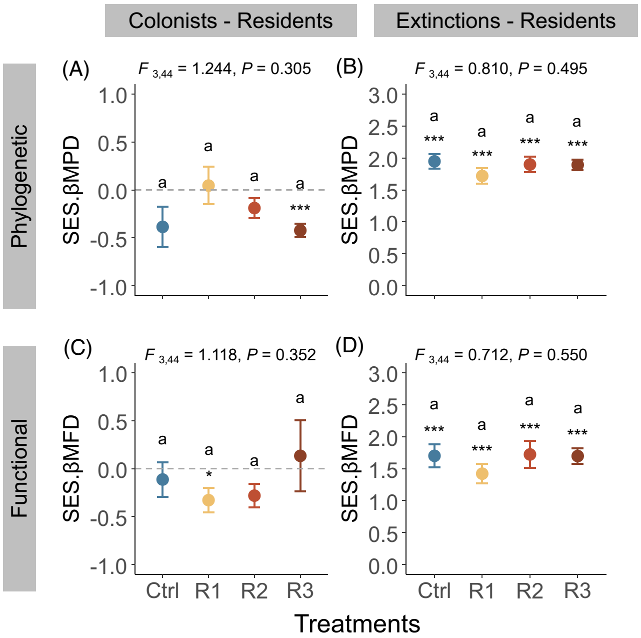

FIGURE 4 Phylogenetic (a,b) and functional (c,d) patterns of colonization and extinction under different removal treatments. Phylogenetic and functional distances of colonists and extinctions to residents were measured as the standardized effect size of mean pairwise phylogenetic distance (SES.βMPD) and mean pairwise functional distance (SES.βMFD). Positive SES values indicate that the colonists or extinctions are more distantly related or functionally dissimilar to the resident species than expected by chance, while negative values suggest the opposite. The *x*-axis represents the treatments as defined in Figure 2. Points represent mean values of all replicates under each treatment; error bars represent standard errors. Asterisks indicate significant deviations from zero based on one-sample t-tests (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Results are based on generalized linear models with a Gaussian distribution. Different lowercase letters indicate significant differences among treatments (Tukey's HSD, $p < 0.05$).

considering only resident species (Figure 5) or all non-invasive species (Figure S11) over the three-year period and were also supported by analyses restricted to native communities (Figure S12).

4 | DISCUSSION

Controlling biological invasions and restoring ecosystems degraded by invasive species are critical priorities for global conservation efforts. While invasive species removal is recognized as an important strategy for restoration, the mechanisms through which it influences diversity recovery are still not fully understood. In this study, we conducted a three-year experiment in a subtropical old field to investigate how invasive species removal impacts the recovery of taxonomic, phylogenetic, and functional diversity of non-invasive communities. Our findings reveal that abundance-based diversity measures consistently exhibited stronger recovery than incidence-based metrics, underscoring the importance of considering the shifts of species abundance distributions in assessing community recovery. More importantly, our study provides compelling evidence that increased abundance of distantly related and functionally dissimilar species was likely a key driver of recovery in phylogenetic and functional diversity following invasive species removal. By simultaneously examining species colonization, extinction and abundance shifts, our study offers a comprehensive framework for uncovering the mechanisms underlying diversity recovery and guiding ecological restoration following invasive species removal.

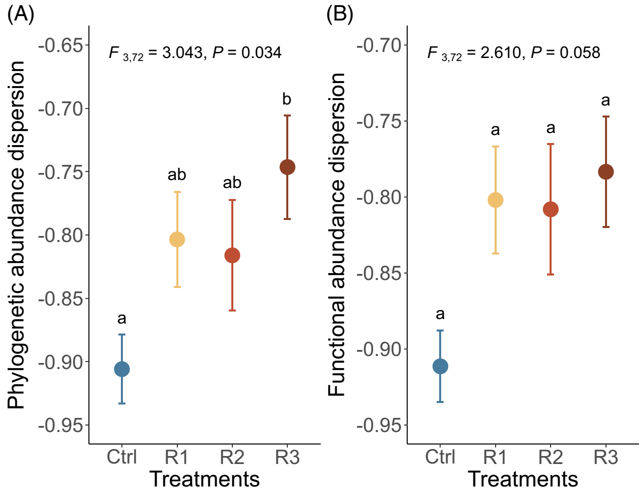

FIGURE 5 Phylogenetic (a) and functional (b) abundance dispersions of resident species under different removal treatments. Positive values indicate that abundant species are more phylogenetically and functionally dissimilar to each other, while negative values indicate the opposite. The *x*-axis represents the treatments as defined in Figure 2. The points represent the mean values of all replicates under each treatment, and error bars represent standard errors. Results are based on generalized linear models with a Gaussian distribution. Different lowercase letters indicate significant differences among treatments (Tukey's HSD, $p < 0.05$).

Understanding the impact of invasive species removal on biodiversity recovery is crucial for advancing invasion ecology. While some studies observed limited or no recovery in taxonomic diversity after invader removal (Harms & Hiebert, 2006; Hejda & Pyšek, 2006), others often demonstrated positive effects on taxonomic diversity (Andreu et al., 2010; Andreu & Vilà, 2011; Erskine-Ogden & Rejmánek, 2005). These studies often attribute diversity gains to increased species colonization, such as the increases in annual herbs or seedlings (Andreu et al., 2010; Saito & Tsuyuzaki, 2012). Our study, which comprehensively assessed the dynamics of species colonization, extinction and abundance shifts, shows that all three processes contribute to taxonomic diversity recovery, though their relative importance varies across removal treatments. Specifically, the removal of non-dominant invasive species primarily promotes colonization and reduces extinction, while the removal of the dominant invader, *S. canadensis*, primarily increases the evenness of the resident species. These findings suggest that different removal strategies can have contrasting effects on the dynamics of species colonization, extinction, and abundance shifts, highlighting the need to consider these processes together to enhance recovery outcomes.

Beyond taxonomic diversity, the effect of invasive species removal on the phylogenetic and functional diversity of non-invasive communities has gained increasing attention. While some studies demonstrate that removing invasive species can enhance phylogenetic and functional diversity (Lishawa et al., 2019; Modiba et al., 2017), few have considered both abundance- and incidence-based metrics together. Our findings highlight that the recovery of abundance-weighted phylogenetic and functional diversity occurred more rapidly than incidence-based metrics. This suggests that, in the short term, shifts in abundance distributions may provide a more sensitive indicator of community recovery than changes in species colonization and extinction. Consequently, abundance-based diversity measures are more effective at capturing dynamic changes in community diversity in the early stages following invasive species removal. These findings highlight the importance of integrating both incidence- and abundance-based metrics to better understand the recovery process.

Species colonization and extinction are key processes shaping phylogenetic and functional diversity, and understanding their patterns is crucial for uncovering community assembly mechanisms. While previous studies have highlighted how these processes drive diversity patterns over succession (Li et al., 2015) and under global change (Yang et al., 2018; Zhu et al., 2020), their response to invasive species removal remains underexplored. Over the three-year experiment, we found removal treatments did not systematically alter the phylogenetic or functional patterns of colonization. Colonists were neither more nor less similar to residents than expected by chance (Figure 4a,c), suggesting that during early recovery, colonization was not strongly constrained by environmental filtering or competitive exclusion. Similarly, extinction patterns were also not significantly affected by removal treatments. Local extinctions primarily involved species that were distantly related and functionally dissimilar to residents across all treatments (Figure 4b,d). This pattern likely reflects strong environmental filtering under early successional conditions, where fluctuating soil moisture and resource availability may exclude pioneer species such as *Digitaria sanguinalis* (L.) Scop., *Setaria pumila* (Poir.) Roem. & Schult., *Fimbristylis littoralis* Gaudich. and *Scleromitrion diffusum* (Willd.) R. J. Wang. These species generally are distantly related and functionally distinct from residents. In summary, while colonization and extinction processes may have more pronounced effects over longer time scales, their response to removal treatments was limited during the short duration of this study.

A novel finding of our study is the critical role of shifts in abundance distributions as a mechanism driving the recovery of community diversity following invasive species removal. In particular, we found that the removal of invasive species increased the dominance of distantly related and functionally dissimilar non-invasive species, leading to substantial increases in abundance-weighted phylogenetic and functional diversity (Figure 5, Figures S11 and S12). In plots where invasive species were not removed, closely related species such as *Commelina communis* L. and *Arthraxon hispidus* (Thunb.) Makino dominated. This dominance is likely due to these species sharing similar traits, including high specific leaf area, rapid reproductive rates and relatively short stature, which allows them to cover a large portion of the ground and efficiently capture light resources despite the presence of the invaders. Following the removal of invasive species, the availability of resources increased and interspecific competition weakened. This shift enabled distantly related and functionally dissimilar species, such as *Persicaria lapathifolia* (L.) Delarbre, *Lactuca indica* L., and *Rubus hirsutus* Thunb., to thrive and become dominant. Therefore, our study suggests that shifts in abundance distributions can serve as more sensitive indicators of diversity recovery than colonization and extinction, providing an earlier signal of the impact of invasive species removal on diversity.

While our study offers valuable insights into the early dynamics of multidimensional diversity recovery following invasive species removal, several limitations should be acknowledged to guide future research. First, our experiment was conducted in relatively small plots over a three-year period. Although this design effectively captures short-term responses, it may underestimate colonization and extinction processes that unfold over broader spatial and temporal scales. Continued monitoring is needed to determine whether the observed patterns reflect early successional dynamics or signal more persistent assembly trajectories. Second, interannual climate variation could have influenced community trajectories, particularly for short-lived or environmentally sensitive species. Incorporating climate data and extending the study across broader climatic gradients would improve our understanding of how climate variability shapes recovery dynamics. Third, the stronger recovery observed following complete invader removal suggests a potential role for co-invasion dynamics and associated soil legacies. Invasive species can modify soil microbial communities in ways that suppress native species while benefiting other invaders (Cheng et al., 2025; Zhang et al., 2020). As a result, partial removal of invaders may unintentionally maintain biotic conditions unfavourable to native recovery. Understanding the extent and mechanisms of such belowground interactions will be essential for designing more effective restoration strategies. Together, these considerations highlight the need for future studies to incorporate multi-scale, long-term and mechanistically informed approaches to generalize these findings across diverse ecosystems.

By simultaneously examining species colonization, extinction and shifts in species abundance, our study provides a comprehensive framework to understand the recovery of taxonomic, phylogenetic and functional diversity following invasive species removal. Through a three-year field experiment in a subtropical old field, we demonstrated that increases in phylogenetic and functional diversity were primarily driven by the enhanced dominance of distantly related and functionally dissimilar species, rather than by colonization or extinction processes. From a management perspective, our findings underscore the importance of prioritizing the removal of dominant invaders, as their removal disproportionately facilitates the abundance recovery of phylogenetically and functionally dissimilar species. Moreover, evaluating restoration success should go beyond simple species gains and losses; incorporating changes in species abundance distributions provides a more informative measure of community recovery. While our research offers valuable short-term insights, the generality and applicability of our findings warrant further investigation over longer temporal scales. We encourage future studies to adopt this integrative framework to deepen our understanding of the mechanisms driving community recovery and to refine strategies for effective ecological restoration in invaded ecosystems.

AUTHOR CONTRIBUTIONS

Shao-peng Li developed and framed research questions. Bingwei Lv, Shu-ya Fan, Xiaorong Lu, Yani Meng, Wenbo Yu, Shan Rao, Xiaoye Shi, Yue Li, Yangfan Fei, Yan-song Zhang, Wen-gang Zhang, Qi Yao, Guomeng Zhao, Caiyue Yang, Xiang Li, Jiamin Liu collected the data used in this analysis. Bingwei Lv analysed the data with substantial input from all authors. Bingwei Lv and Shao-peng Li wrote the first draft of the manuscript and all authors contributed to discussing the results and editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare: https://doi.org/10.6084/m9.figshare.30090082 (Lv, 2025).

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SUPPORTING INFORMATION

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

Figure S1. Diagram of experimental treatments.

Figure S2. Visual and schematic representation of the study site and sampling methodology.

Figure S3. The phylogenetic tree for the 58 species observed in the study area.

Figure S4. Schematic diagram of the concepts of colonists, extinctions, and resident species.

Figure S5. Taxonomic, phylogenetic, and functional diversity of non-invasive species under different removal treatments from 2020 to 2022.

Figure S6. Taxonomic, phylogenetic, and functional diversity of native communities under different removal treatments.

Figure S7: Pielou's evenness of all non-invasive species under different removal treatments.

Figure S8. Numbers of colonists and extinctions, and the evenness of resident species in native communities under different removal treatments.

Figure S9. Phylogenetic and functional patterns of colonists, extinctions, and resident species under different removal treatments.

Figure S10. Phylogenetic and functional patterns of colonization and extinction in native communities across treatments.

Figure S11. Phylogenetic and functional abundance dispersions of all non-invasive species under different removal treatments.

Figure S12. Phylogenetic and functional abundance dispersions of resident species in native communities under different removal treatments.

Table S1. Experimental treatments and corresponding removal processes.

Table S2. Results of linear mixed-effect models (LMMs) analyzing removal treatment effects on community diversity metrics.

Table S3. Results of generalized linear models (GLMs) analyzing removal treatments effects on number of colonists, number of extinctions and Pielou's evenness of residents.

Table S4. Results of generalized linear models (GLMs) analyzing removal treatments effects on SES.βMPD and SES.βMFD between colonists/extinctions and residents.

Table S5. Results of generalized linear models (GLMs) analyzing removal treatments effects on phylogenetic and functional abundance dispersions of resident species.

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