

## RESEARCH ARTICLE

# Decoupling of trait and species turnover in fire-prone Mediterranean plant communities

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## Abstract

1. Plant taxa and traits do not necessarily show synchronous responses to ecological disturbance. Based on the observation that taxonomically over-diversified communities might be phenotypically redundant, we speculated that taxonomic and phenotypic community reassembly might be decoupled after fire in Mediterranean ecosystems.
2. We applied a multi-trait approach to describe plant community re-assembly after fire across three 20-year chronosequences based on 117 species and 23 traits, including whole-plant, above-ground and below-ground traits. We quantified the post-fire trajectories of different plant traits by analysing their community-weighted means individually. We estimated the short- and long-term phenotypic diversity of burned plots based on sets of traits. We also tested if trait and species turnover are decoupled across post-fire trajectories. Finally, we calculated phenotypic redundancy, and assessed if above- and below-ground traits have contrasted responses during post-fire community reassembly.
3. Individually, 16 out of 23 traits were affected by fire in the short term. Plant phenotypic diversity (stdMPD) decreased immediately after fire, driven by changes in whole- and above-ground traits. Both whole- and above-ground stdMPD in burned plots described positive trajectories across the chronosequences tending to converge with long-unburned plots, whereas below-ground stdMPD remained unaltered through time.
4. Taxonomic and phenotypic beta diversity showed decoupled trajectories due to a larger species than trait replacement across time since fire. Finally, overall phenotypic redundancy of the studied plant communities described a regressive trajectory, similarly to above-ground traits, whereas root traits kept a steady phenotypic redundancy through time.
5. *Synthesis.* We provide evidence that above- and below-ground traits describe different recovery trajectories after fire, with significant effects on the phenotypic redundancy of plant communities. Our results encourage the use of multi-trait approaches to understand how the plant reassembly operates after disturbance, in order to refine ecological theory. This strategy might improve the efficacy of restoration programs through a functional approach to species selection.

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## KEYWORDS

Beta diversity, functional trait, Mediterranean vegetation, plant economics spectrum, post-fire regeneration, root trait, specific leaf area, specific root length

## 1 | INTRODUCTION

Fire is a key factor explaining plant diversity in many terrestrial biodiversity hotspots (Bond et al., 2005; Kelly et al., 2020). It strongly modifies plant community composition and structure, thus affecting ecosystem functioning (Keeley & Keeley, 1981; Pausas et al., 1999; Pérez-Valera et al., 2018). Fire-prone Mediterranean plant communities have a long history of evolutionary adaptation to fire (Pausas & Keeley, 2014). Their post-fire regeneration in different ecosystems (woodlands, shrublands, grasslands) has been widely studied from a classical taxonomic perspective (see e.g. Keeley & Keeley, 1981; Pausas et al., 1999). Currently, trait-based approaches try to infer functional community patterns and link them to key ecological processes behind community assembly and ecosystem stability (Anacker et al., 2011; Clarke et al., 2015; Fyllas et al., 2020; Pausas & Verdú, 2008; Tsakalos et al., 2019). From these studies, we know that post-fire community reassembly is usually driven by shifts in the relative abundance of species rather than their total substitution (Fournier et al., 2020). Though fire induces a short-term decrease of plant community cover and biomass, taxonomic diversity tends to remain unaffected (González-De Vega et al., 2016; Gosper et al., 2012; Lloret & Vilà, 2003; Pérez-Valera et al., 2018). While surface fires allow a rapid vegetation recovery in woodlands and shrublands, crown fires have harmful effects on the post-fire regeneration of non-serotinous pine woodlands compared to *Pinus halepensis* or *Quercus* woodlands, due to their different regenerative strategies (Pausas et al., 2008). Nevertheless, as fire severity and/or frequency increase, both community composition and structure are severely affected (Clarke et al., 2015; González-De Vega et al., 2016). Under such fire regimes, plant communities become phylogenetically and phenotypically clustered, that is to say, they are composed by species more closely related than expected by chance (Pausas & Verdú, 2008). This observation responds to the overrepresentation of evolutionarily related species, which bear similar suites of traits conferring fire resistance.

Plant species have three broad functional strategies to cope with fire. On one hand, some plants have developed 'evader' adaptations to avoid the fire effect, such as thick barks or self-pruning ability (Romero & Ganteaume, 2020). Others have a resource conservative strategy, which is based on the evolutionary development of above- and below-ground anatomical traits, such as lignotubers, epicormic buds, rhizomes or other storage roots that confer resprouting ability (Pausas & Keeley, 2014). Finally, there is the acquisitive strategy, which is based on the ability to rapidly establish a new community after fire through traits such as seed physical dormancy, flammability, heat- and smoke-mediated germination ability (related to seed dormancy) or nitrophilous habits to cope with transitory nitrogen

peaks in burnt soils (Pausas et al., 2017; Pausas & Keeley, 2014; Wan et al., 2001). Although these strategies have followed different evolutionary routes (Pausas & Verdú, 2005), some facultative species are able to exhibit some of these traits under intermediate aridity and fire intensity levels (Pausas et al., 2017). At the species level, seeders and resprouters differ in a series of above- and below-ground traits, the latter showing delayed maturity, lower resistance to xylem cavitation, larger root:shoot ratios, higher levels of root carbohydrates and lower specific root length (Jacobsen et al., 2007; Paula & Pausas, 2011; Schwilk & Ackerly, 2005). At the community level, species diversity and plant cover of seeders increase after fire and then gradually decrease, whereas resprouters are resilient to fire and become dominant after several decades in the absence of a new burning event. In fire-prone Mediterranean areas, this pattern is common to subhumid and dry broad-leaved woody and shrubby communities (Fournier et al., 2020; Parra & Moreno, 2018), whereas some pines with serotinous cones as those shaped by *Pinus halepensis* can persist as the dominant vegetation in the absence of new fires. All the pre-fire characteristics of the vegetation, fire severity and the post-fire management are fundamental to understand the medium and long-term recovery trajectory of these burned areas (González-De Vega et al., 2016).

Quantifying plant traits at the community level is a useful approach to depict phenotypic trajectories across environmental gradients (Bjorkman et al., 2018; Craine et al., 2001; Shen et al., 2019). This approach needs to avoid short-term monitoring to identify general patterns of community assembly (McGill et al., 2006). Moreover, studies based on a low number of traits can lead to large levels of unexplained variation if key traits are not included. Published studies work with six traits on average (reviewed by Van der Plas et al., 2020), which are typically above-ground traits. Life form, plant size, seed size, as well as morphological and physiological leaf traits are frequently used since they shape the LHS (leaf-height-seed) strategy (Díaz et al., 2016; Laughlin et al., 2010). Nevertheless, below-ground traits are key drivers of ecological functions, playing a role in soil retention and exploration, water and nutrient acquisition, and involvement in ecological interactions between plant, microbial and faunal communities (Bardgett et al., 2014; De Baets et al., 2007; Navarro-Cano et al., 2019). Below-ground traits are also essential to discern between the functional strategies that plants show to cope with fire, as explained above. The plant economics spectrum (PES) theory tries to capture all these ecological roles by integrating stem, leaf and root traits, in order to understand plant ecological strategies as response syndromes to disturbances and drivers of ecosystem functions (Reich, 2014). Thus, quantifying above- and below-ground traits concurrently is the most holistic approach to analyse community-level responses to environmental gradients, although such responses depend on the specific trait

selection (Delpiano et al., 2020; Kramer-Walter et al., 2016). In fire-prone ecosystems we still do not know if the turnover of species and traits are coupled during post-fire community reassembly, and beyond, whether a synchrony exists in the reassembly of above- and below-ground traits.

Based on the assumption that some species might be functionally redundant within taxonomically over-diversified plant communities due to phenotypic overlap (Fonseca & Ganade, 2001; Rosenfeld, 2002), we hypothesised that taxonomic and phenotypic community reassembly might be decoupled after fire in Mediterranean ecosystems (Figure 1). We particularly expected that species turnover might be larger than trait turnover in post-fire trajectories. Moreover, we assumed that below-ground traits are the main determinants of plant community resilience to fire, as fire-prone communities show below-ground adaptations to cope with this disturbance (Paula & Pausas, 2011; Pausas & Keeley, 2014). Thus, we expected that below-ground traits might show the smallest turnover compared to above-ground and whole-plant traits at the community level. To test these hypotheses, we studied three 20-year post-fire chronosequences in semiarid to dry Mediterranean areas in Spain. Our previous studies in these chronosequences indicated that fire did not alter plant richness, whereas it reduced plant phylogenetic diversity—due to the promotion of evolutionarily related fire-prone species—which progressively recovered after two decades (Pérez-Valera et al., 2018). Here, we constructed a trait database for 117 species and 23 traits, including whole-plant, above-ground and below-ground traits. We aimed to: (i) quantify the post-fire trajectories of the community-weighted means of 23 traits analysed individually along the chronosequences, (ii) calculate the phenotypic diversity of burned and long-unburned plots based on whole-plant, above- and below-ground traits, (iii) test if trait reassembly simply reflects a taxonomic rearrangement or, alternatively, trait and species turnover are decoupled across post-fire trajectories and (iv) assess if above- and below-ground traits have a different relevance

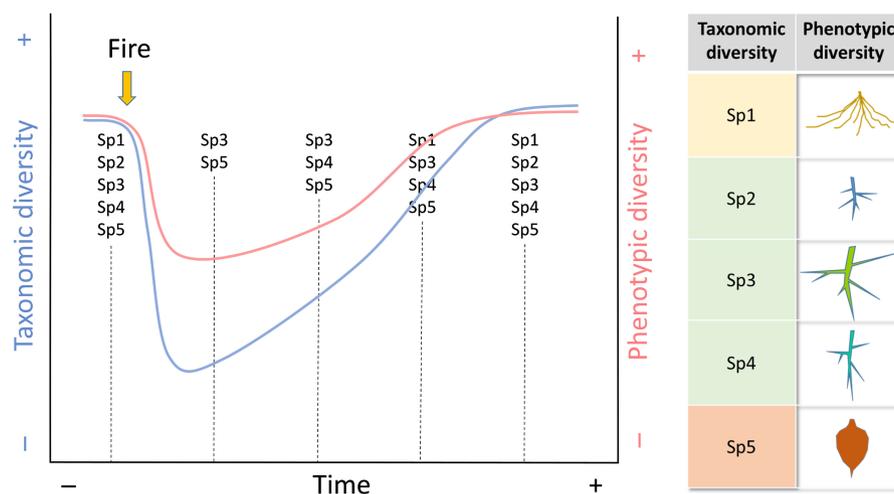
during post-fire community reassembly. Our results may help understand the functional basis of plant reassembly trajectories after fire, as a keystone on which both ecological theory and restoration programmes may be armed.

## 2 | MATERIALS AND METHODS

### 2.1 | Fire chronosequences

We studied post-fire plant reassembly trajectories in three 20-year fire chronosequences distributed across different mountain ranges in the North, Centre and South of Valencia (E Spain; Figure S1; Pérez-Valera et al., 2018). The region has a Mediterranean climate with a mean annual precipitation of  $557 \pm 28$  mm and a mean annual temperature of  $14.6 \pm 0.2^\circ\text{C}$ , with hot and dry summers and a rainy season in autumn. Chronosequences were located approximately 85 km apart. The region is dominated by calcareous lithologies. Organic carbon concentration in topsoils (0–5 cm) range from  $71 \pm 4$  g kg<sup>-1</sup> in burned areas to  $138 \pm 18$  g kg<sup>-1</sup> in long-unburned areas, and pH from  $8.0 \pm 0.02$  to  $7.6 \pm 0.08$ , respectively (Pérez-Valera et al., 2018).

Each chronosequence included eight to nine sites that had experienced a single wildfire event within a 20–19- and 16 year period (North, Centre and South chronosequences, respectively), and had no record of previous fires according to the Regional Government databases. Within each site, we established two paired plots (burned vs. long-unburned) located on average at (mean  $\pm$  SE)  $435 \pm 49$  m apart, to avoid fire edge effects but keeping similar conditions between plots in terms of lithology, soil, aspect and slope. Burned plots were those exposed to a single wildfire and long-unburned plots were those with no fire records. Detailed information on each plot is given in Pérez-Valera et al. (2018) as a supplementary table. A distribution map of the studied sites with the plots (burned and long-unburned) and the year of the last fire is shown in Figure S1. We checked the available historical



**FIGURE 1** Outline of the hypothesised taxonomic and phenotypic decoupling of plant community reassembly after disturbance (a fire here). Functional redundancy of root systems in the example yields a larger species than root type turnover, which contributes to the plant community resilience to fire. In the table (right), sp2, sp3 and sp4 share a similar root system compared to sp1 and sp5.

aerial photographs in order to exclude plots with different vegetation before the fire between burned and long-unburned selected plots within a site. Overall, we established 50 sampling plots (25 sites  $\times$  2 plots) in S-SW oriented slopes with  $<36^\circ$  where regenerated vegetation is dominant due to a long-standing history of fires, human deforestation and marginal cultivation. Current vegetation is dominated by typical Mediterranean fire-prone shrublands (*Cistus* sp., *Erica* sp., *Ulex parviflorus*, *Salvia rosmarinus*) and mixed *Pinus halepensis*–*Quercus coccifera* forests including *Juniperus* sp., *Rhamnus* sp. and *Pistacia lentiscus* (Pérez-Valera et al., 2018; Santana et al., 2018).

## 2.2 | Plant community sampling

Sampling was carried out in spring 2014. Sampling permission for fieldwork was not necessary. In each plot we sampled plant cover and species composition along three 25 m parallel transects (50 plots  $\times$  3 transects per plot = 150 transects). Transects within each plot followed the direction of the slope and were located 10 m apart. We used the line-intercept sampling method (Butler & McDonald, 1983; Canfield, 1941) by which plant cover is estimated by measuring the horizontal length of the interception of each plant along the transect. The relative plant cover of each species, a measure of relative abundance, was estimated from the species intercepted length expressed over the 25 m total length of transect. The overall plant cover per transect was estimated by adding the intercept lengths of all the species expressed over the total length of transect.

## 2.3 | Plant trait database

We created a database of 23 traits for the 117 species found in the three chronosequences. We included three groups of traits, which are described in Table S1: (i) four whole-plant traits (bud height, sclerophylly, xerophily and resprouting ability), (ii) 10 above-ground traits (plant height, flowering time and span, leaf size, area, weight, thickness, specific leaf area, seed size and dispersal distance) and (iii) nine below-ground traits (root length, depth, laterality, root depth:laterality ratio, root weight, specific root length, root C and N concentration and the root CN ratio). Table S1 gives the description of how traits were measured and their ecological meaning. Briefly, we obtained whole-plant traits and the dispersal distance from own local observations and the literature. Average values of above- and below-ground traits were obtained from five adult plants per species that were randomly selected across the three chronosequences (a total of 585 plants sampled), fully dug up, collected and transported to the laboratory. Above- and below-ground parts of the plants were manually separated and measured. Leaf organic C and N concentrations were estimated from 1 g of fresh ground leaves per plant using a TruSpec Analyser (FLASH EA 1112 Series, LECO Corporation, MI, USA). Organic C was quantified after a 55°C acidic (HCl) treatment. Data are expressed on an oven-dried (65°C) weight basis. Our phenotypic trait matrix (117  $\times$  23) is given in Table S2.

## 2.4 | Plant diversity metrics

The community weighted mean (CWM) of each trait in each transect was calculated as the sum of the average trait value per species weighed by the relative abundance of each species in the same transect, following the equation by Garnier et al. (2004).

The standardised mean phenotypic distance (stdMPD) was used as a measure of plant phenotypic diversity and was quantified as the abundance-weighted mean phenotypic distance between all pairs of plant species in each transect using the *ses.mpd* function with the *taxa.labels* null model in the *picante* package for R 4.2.0 (Kembel et al., 2010; R Core Team, 2020). Pairwise phenotypic distances were calculated based on the Gower distance (Gower, 1971) using the *gawdis* function and the 'optimized' argument in the *gawdis* package for R (de Bello et al., 2021). This function produces multi-trait dissimilarity with uniform contributions for all traits.

Taxonomic and phenotypic beta diversity were used to compare species and trait turnover across burned and long-unburned transects. We used the approach by Cardoso et al. (2014), which allows separating beta diversity into its replacement (species substitutions, calculated as twice the minimum number of species exclusive to a community in a pairwise comparison) and richness components (species gains and losses). We used the *beta* function in the *BAT* package for R (Cardoso et al., 2015) based on the *gawdis* distance as above. Finally, we calculated the phenotypic diversity in burned and long-unburned communities using the *uniqueness* function in the *adiv* package for R (Pavoine, 2021). Redundancy is the complement of uniqueness, which is defined as the average phenotypic dissimilarity of a species from the whole community divided by the maximum dissimilarity (i.e. considering all species being equally and maximally dissimilar) (Ricotta et al., 2016).

All stdMPD, phenotypic beta diversity and redundancy were calculated separately for whole plant, above- and below-ground traits.

## 2.5 | Statistical analyses

We tested the existence of short-term effects of fire on community weighted means and plant phenotypic diversity by comparing CWMs and stdMPD between transects that had burned 0–3 years ago and their long-unburned counterpart transects through paired *t*-tests in R. To analyse the post-fire trajectories of CWMs and stdMPD, we used the difference between paired burned and long-unburned transects as the dependent variable and time since fire as the fixed effect variable in Bayesian generalised linear mixed models (GLMM). Spatial autocorrelation was accounted for in the model by incorporating the geographic distance matrix between transects as a random effect variable as in Stone et al. (2011) in the *MCMCglmm* package v2.32 for R (Hadfield, 2010). To test if species and trait turnover are decoupled across post-fire trajectories, we compared taxonomic and phenotypic beta diversity values using paired *t*-tests in R. Finally, we assessed the contributions of whole-plant, above- and below-ground traits on post-fire re-assembly, by repeating

stdMPD, phenotypic beta diversity and redundancy analyses for each set of traits separately.

### 3 | RESULTS

#### 3.1 | Plant traits across species

The distribution of 23 traits across 117 species showed a dominance of skewed distributions towards low values (Figure S2). Most species had life forms with bud heights below or equal to 100 cm, not many species were identified as sclerophyllous (15%), but still xerophyllous species dominated (68%) and there was a balanced presence of resprouting versus non-resprouting species. Above-ground traits indicated that blossoming at early spring was the most common, as well as the predominance of species with small leaves with SLAs  $\leq 10 \text{ mm}^2 \text{ mg}^{-1}$  and small seeds that disperse mainly at short distances, though a second mode of long-distance dispersal was observed. Below-ground traits were all unimodal and clearly skewed towards the expression of low values, root lengths and lateralities being usually shorter than 50 cm. Furthermore, root N concentrations and CN ratio showed peaks at 0.6% and 50, respectively. Root C was the only trait with a long tail of low values and a dominance of values above 35%.

#### 3.2 | Plant traits across communities

Recently burned plant communities (less than 36 months after fire) were shorter, less sclerophyllous and had a larger proportion of resprouters (Figure 2; Table 1). Communities had on average smaller leaves with larger SLAs, as well as shallower roots with larger SRLs and lower CN ratios.

Differences in CWM between burned and long-unburned transects in terms of bud height, sclerophylly, plant height, SRL, root N and root CN ratio significantly decreased with time since fire, describing a recovery trajectory of burned plots towards the values of long-unburned plots over 20 years (Figure 2; Table 1).

#### 3.3 | Fire effects on phenotypic diversity

Plant phenotypic diversity (stdMPD) considering all traits was lower in burned compared to long-unburned transects immediately after fire (paired *t*-test, transects <36 months;  $t_{11} = -4.02$ ,  $p \leq 0.01$ ; Figure 3). This pattern was stronger when stdMPD based on whole-plant ( $t_{11} = -4.08$ ,  $p \leq 0.01$ ) or above-ground traits ( $t_{11} = -6.40$ ,  $p \leq 0.001$ ) were analysed separately. However, stdMPD based on below-ground traits did not respond to fire ( $t_{11} = 1.44$ ,  $p \geq 0.1$ ).

Phenotypic diversity using all traits significantly increased in burned areas across the chronosequences, the difference between stdMPD in burned and long-unburned transects showing a significant and positive regression with time since fire (MCMCgImm

post-mean estimate [95% credible interval] = 0.003 [0.001, 0.006]). Both whole-plant and above-ground traits showed similar trends (whole plant: 0.004 [0.001, 0.006]; above-ground: 0.004 [0.001, 0.006]), stdMPD in burned transects reaching similar values to those in long-unburned transects after 20 years (Figure 3). However, stdMPD based on below-ground traits remained unaffected across the chronosequences, and the difference between burned and unburned transects did not change with time since fire as shown by the credible interval crossing zero (0.001 [-0.001, 0.003]).

#### 3.4 | Taxonomic and phenotypic beta diversity across chronosequences

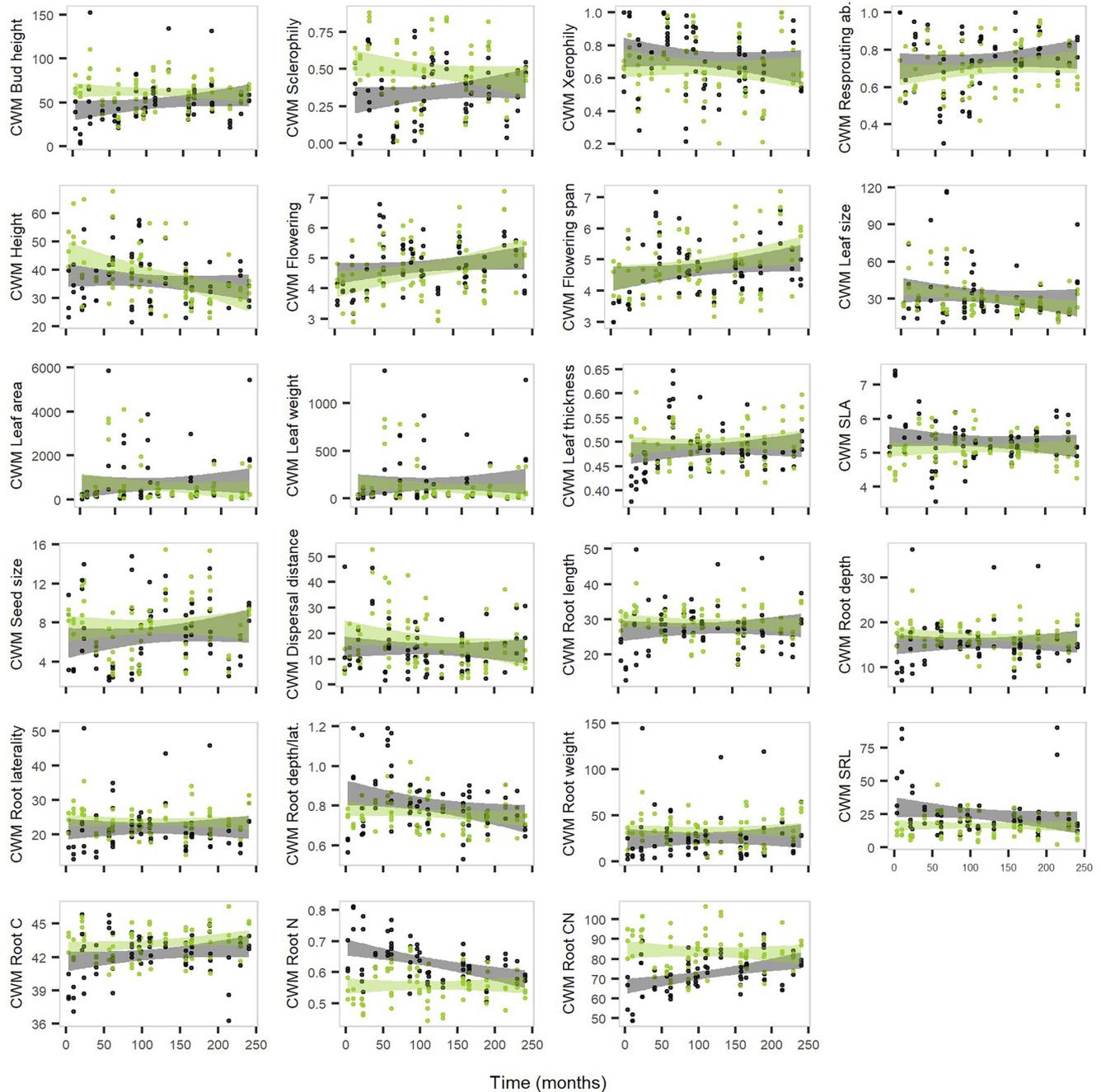
The post-fire trajectories of taxonomic and phenotypic beta diversity, taking all traits, followed similar patterns. Maximum dissimilarity in community composition between recently burned transects and long-unburned transects was observed immediately after fire both considering species and traits (Figure 4a). Dissimilarity between burned and unburned transects declined progressively with time since fire, at different rates for species and traits. Beta diversity values were lowest ca. 160 months after fire, when both taxonomic and phenotypic curves reached a plateau. Overall, taxonomic beta diversity was larger than phenotypic beta diversity, as indicated by larger dissimilarity values in species than traits (paired *t*-test;  $t_{71} = 17.89$ ,  $p < 0.001$ ). Differences between taxonomic and phenotypic beta diversity were mostly due to a larger replacement of species than traits ( $t_{71} = 20.26$ ,  $p < 0.001$ ; Figure 4b), despite a (small but significantly) lower gain of species than traits ( $t_{71} = -12.44$ ,  $p < 0.001$ ; Figure 4c).

These patterns held when whole-plant, above- or below-ground traits were analysed separately (Figure S3). Nevertheless, mean differences between taxonomic and phenotypic beta diversity values varied depending on the set of traits considered (above-ground traits < below-ground traits < whole-plant traits) (Figure S3; Table S3).

Phenotypic redundancy was very high immediately after fire, considering all traits together (Figure 5), and significantly decreased with time since fire (MCMCgImm post-mean estimate [95% credible interval] = -0.0016 [-0.0025, -0.0006]). A similar trend appeared considering the above-plant traits only (-0.0021 [-0.0033, -0.0009]), whereas the phenotypic redundancy for both the whole- (-0.003 [-0.006, 0.001]) and below-plant traits (-0.0002 [-0.0013, 0.0010]) did not show a significant trend with time (Figure 5).

### 4 | DISCUSSION

We quantified the post-fire trajectories of 23 traits from plant communities along three chronosequences in fire-prone Mediterranean drylands. Compared to long-unburned plots (i.e. plots with no fire records), our results showed a roughly complete recovery of community-level bud height, sclerophylly, plant height, SRL, root N



**FIGURE 2** Community-weighted means (CWM) calculated for each trait in 150 burned (grey) and long-unburned transects (green). The units for all variables depicted in Figure 2 are the same as those in Figure S2.

and root CN ratio in burned plots after 20 years since fire. After an initial drop due to fire, plant phenotypic diversity in burned plots described a positive trajectory across the chronosequences due to whole- and above-ground traits, while phenotypic diversity of (nine) below-ground traits remained unaffected.

#### 4.1 | Plant traits across species and communities

Our results highlight the importance of incorporating below-ground traits for a better modelling of the recovery trajectories of plant

communities after disturbance. This broader trait-based approach contributes to avoid a functional bias that could mask the keystone role of roots in the reassembly of plant communities and ecosystem functions after disturbance (Bardgett et al., 2014; Laliberté, 2016). During the last decade several authors have pointed out the relationships of above- and below-ground traits from plant communities across several biomes (e.g. Freschet et al., 2010, 2015; Pérez-Ramos et al., 2012; Shen et al., 2019), thus linking leaf, stem and root traits within a plant community economics spectrum. Nevertheless, other authors have shown that these above-below-ground trait correlations can change across different environmental gradients,

**TABLE 1** Fire effects on the community weighted mean (CWM) of 23 traits in three 20-year fire chronosequences.

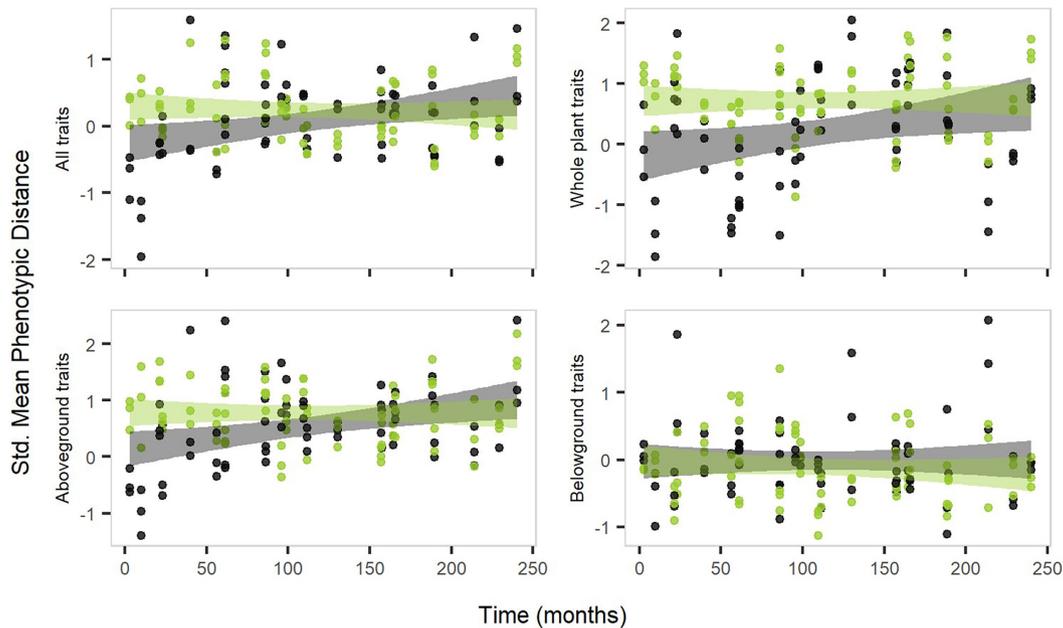
Trait CWM	Short-term fire effects paired <i>t</i> -tests	Long-term recovery post-mean estimate [95% CI]
<b>Whole plant traits</b>		
Bud height	-3.43**	<b>0.095 [0.015, 0.176]*</b>
Sclerophylly	-3.42**	<b>0.001 [0.0002, 0.002]**</b>
Xerophily	1.24	-0.0001 [-0.0008, 0.0005]
Resprouting ability	<b>2.64*</b>	-0.0000 [-0.0007, 0.0006]
<b>Above-ground traits</b>		
Plant height	-6.23***	<b>0.050 [0.015, 0.083]**</b>
Flowering	-0.85	-0.002 [-0.006, 0.001]
Flowering span	-2.95*	-0.001 [-0.005, 0.003]
Leaf size	-3.29**	0.028 [-0.047, 0.101]
Leaf area	-1.45	2.889 [-1.190, 7.519]
Leaf weight	-2.36*	0.587 [-0.397, 1.613]
Leaf thickness	-5.79***	0.000 [-0.002, 0.003]
SLA	<b>3.59**</b>	-0.001 [-0.005, 0.001]
Seed size	-1.77	0.006 [-0.003, 0.015]
Dispersal distance	0.05	0.027 [-0.016, 0.068]
<b>Below-ground traits</b>		
Root length	-3.6**	0.013 [-0.008, 0.173]
Root depth	-3.37**	0.009 [-0.010, 0.025]
Root laterality	-2.66*	0.004 [-0.019, 0.025]
Root depth/laterality	0.81	-0.0004 [-0.001, 0.0001]
Root weight	-1.78	0.016 [-0.076, 0.101]
SRL	<b>4.47***</b>	<b>-0.006 [-0.011, -0.002]**</b>
Root C	-5.68***	0.001 [-0.007, 0.008]
Root N	<b>5.33***</b>	<b>-0.0004 [-0.0007, -0.0001]*</b>
Root CN ratio	-6.50***	<b>0.055 [0.005, 0.104]*</b>

Note: Short-term effects describe paired *t*-tests between burned (<36 months after fire) and long-unburned transects (df = 11). Long-term recovery indicates post-mean estimates (and 95% CI, credible intervals) of the difference between burned and long-unburned transects regressed with time since fire throughout 20 years. Asterisks indicate significant CI ( $p \leq 0.05^*$ ,  $p \leq 0.01^{**}$  and  $p \leq 0.001^{***}$ ) and are in bold.

such as those related with soil properties or temperature (Craine et al., 2005; Geng et al., 2014). For Bardgett et al. (2014), Weemstra et al. (2016) and Kramer-Walter et al. (2016) root traits are multidimensional not only in a spatial sense (three-dimensional soil exploration) but also in a functional sense (resource acquisition, anchoring, vegetative reproduction and plant-microbial interactions). Hence, root traits might be integrated as a complementary part within trait-based approaches in order to a better knowledge of plant ecological strategies for acquiring and retaining limiting resources, and coping with stress factors. Our results show how above- and below-ground traits operate at the community level in a different way after a fire, thus informing on a decoupled post-fire plant recovery process.

Historically, specific leaf area (SLA) and other leaf traits are among the most studied traits in plants, with a predominance of trait-by-trait and species-by-species analyses (Laliberté, 2016). In North American fire-prone ecosystems, Anacker et al. (2011) modelled how SLA was

affected by different gradients including climate, soil properties and fire at the community level. They found that in harsh climates SLA was higher on more fertile soils and on more recently burned sites. In Mediterranean burned areas, Parra and Moreno (2017) quantified increased SLA after fire in different plant species. At the plant community level, our results also showed a short-term increase in SLA after fire compared to adjacent unburned plots, with no significant recovery trend after 20 years. The resemblance of the mean SLA in Anacker et al. (2011) to our mean SLA is very high (8.74 vs. 8.87 mm<sup>2</sup> mg<sup>-1</sup>), resprouters being dominant in both areas (63% vs. 56%). This similarity supports the idea of geographically distant plant communities exhibiting similar syndromes as a result of similar selection pressures imposed by fire in drylands (Pausas & Keeley, 2014). Nevertheless, the results by Verdú et al. (2003) on trait convergence of Mediterranean woody plants from lineages prior to the Mediterranean climate would question this hypothesis.



**FIGURE 3** Standardised mean phenotypic distance based on all traits ( $n=23$ ), whole-plant traits ( $n=4$ ), above-ground traits ( $n=10$ ) and below-ground traits ( $n=9$ ) in 150 burned (grey) and long-unburned transects (green).

The specific root length (SRL) is probably the most used below-ground trait as an indicator of plant economic aspects under environmental changes (Ostonen et al., 2007). Kramer-Walter et al. (2016) found a lack of correlation between SRL and SLA, and a negative correlation between SRL and soil fertility. In our chronosequences, Pérez-Valera et al. (2020) found a positive recovery trend of soil fertility (total organic carbon, total nitrogen and gravimetric humidity) after 20 years. Contrarily to the observations by Kramer-Walter et al. (2016), the fertility improvement in our case was associated to an analogous decrease of SRL in burned plots, which tended to converge towards long-unburned plots. This mismatch with the results by Kramer-Walter et al. (2016) can be due to the fact that they measured SRL from shallow fine roots sampled in planted seedlings, whereas our traits were estimated from the whole root system of adult or sub-adult individuals. Therefore, most root systems in our study were fully sampled, reaching up to 70 cm sampling depths. To put these figures into context, Jackson et al. (1997) estimated that globally, 79% of root biomass is located in the upper 30 cm in dryland vegetation. These differences alert us to the need for a complete characterisation of root systems in order to understand their role in the assembly of communities.

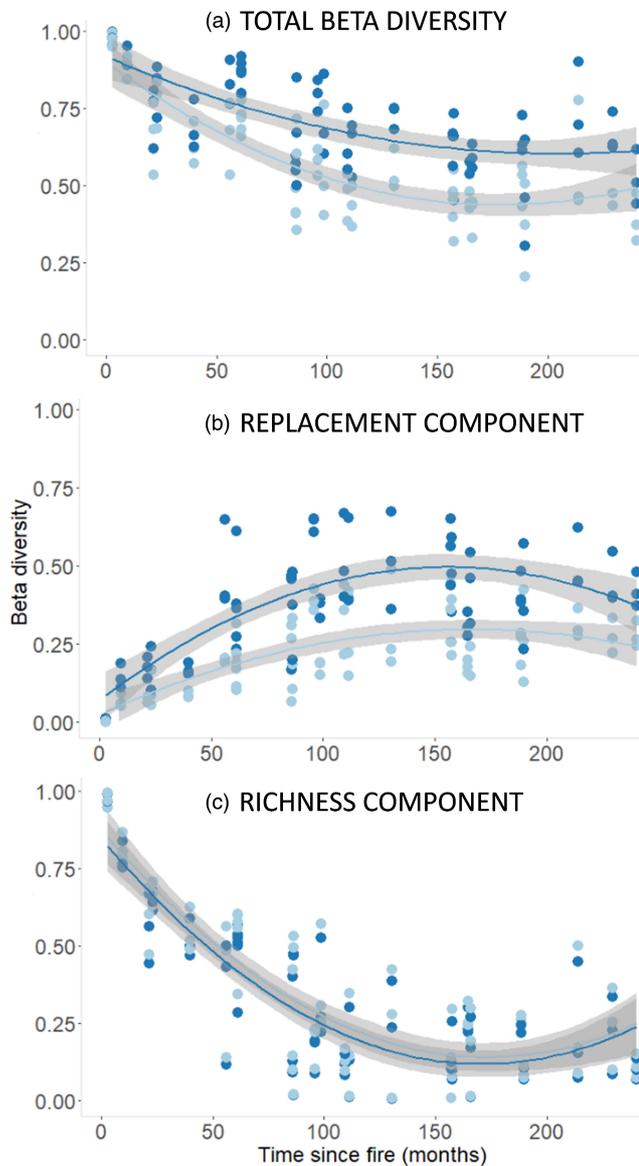
## 4.2 | Fire effects on phenotypic diversity

Shifts in individual traits underlay a drop in plant phenotypic diversity (stdMPD) after fire. This pattern fits well with the idea of an abiotic filter, with increasing stress factors linked to the disturbance, reducing the suite of traits displayed in the community (Pérez-Valera et al., 2020). Nevertheless, a separate analysis by sets of traits shows that, unlike above-ground diversity, below-ground phenotypic

diversity was resistant to fire. The short-term abiotic filtering imposed by fire induces the above-ground dominance of some phylogenetically related pyrophytic species (Pérez-Valera et al., 2018; Verdú & Pausas, 2007). These are mainly seeders belonging to families such as *Cistaceae*, *Fabaceae* and *Lamiaceae*. According to the single 'fast-slow' plant economics spectrum (Lipoma et al., 2016; Reich, 2014), these species have acquisitive traits for a rapid response to disturbance. Nevertheless, their relative abundance decays with time. On the contrary, species with typical conservative traits (long life span, resprouting structures, low SRLs, low root N and high root CN) contribute to keep below-ground phenotypic diversity steady through time. Plant communities dominated by species from the genera *Quercus*, *Olea*, *Pistacia*, *Rhamnus* and *Phyllirea*, were the main representatives of this group of traits in our region.

## 4.3 | Taxonomic and phenotypic beta diversity across chronosequences

The recovery of plant communities induced a decline with time since fire both in taxonomic and phenotypic beta diversity, both metrics reaching minimum levels after approximately 160 months. Taxonomic beta diversity has been shown to drop along gradients of decreasing resource availability in grasslands (Li et al., 2021; Tang et al., 2018). Abedi et al. (2022) found a general decrease of taxonomic  $\alpha$ -diversity after fire in mountainous areas from Iran, whereas beta diversity patterns varied depending on the slope aspect (increasing in southern slopes and decreasing in northern slopes). Neither phenotypic alpha nor beta diversity were affected by fire. Our results partly agree with these observations, since fire triggered



**FIGURE 4** Beta diversity calculated based on species (dark blue) and traits (light blue). Total beta diversity (a) was divided in species replacement (b) and richness components (c).

a negative effect on soil functions, such as fertility or microbial productivity, that only recovered in the mid- to long-term (Pérez-Valera et al., 2018, 2020) when the decline in beta diversity reached a plateau. Nevertheless, the effect of fire on soil properties may be rather dependent on fire intensity and severity, as well as the subsequent rainfalls, that can trigger intensive erosive processes in the following years (Keeley, 2009), altering the recovery trajectory of vegetation (González-De Vega et al., 2016).

Taxonomic beta diversity was larger than phenotypic beta diversity across the chronosequences, that is, there were larger compositional shifts in species than traits. This pattern was mostly due to a larger replacement of species than traits, despite a lower gain of species than traits (note that the richness component was slightly but still significantly lower for species than traits). The pattern held for whole-, above- and below-ground traits. The

relevance of splitting beta diversity components lies on the fact that the replacement component is mainly determined by abiotic factors and negative biotic interactions, whereas the richness component is more influenced by stochastic processes determining species extinction and/or colonisation (Baselga, 2010; Bergamin et al., 2017; Fu et al., 2019). The trait-based trajectory described by our plant communities suggests that, in spite of a dominance of short-distance dispersal species, opening of gaps after fire favours recruitment of new colonisers with particular traits. Contrarily to our results, Joner et al. (2021) found that at the community level phenotypic beta diversity (based on leaf traits) increased and taxonomic beta diversity remained steady after 9 months since a prescribed fire in subtropical grasslands. The different type of fire, time frame and location of the experiments makes comparisons difficult. Moreover, trait-based approaches are usually idiosyncratic regarding the selected traits for diversity estimation (Van der Plas et al., 2020). Hence the need to approach these studies with a range of traits as wide as possible.

Phenotypic redundancy had a maximum value after fire and progressively decreased with time. This trajectory was mainly influenced by above-ground traits, whereas below-ground traits remained unaffected across the chronosequences. A higher phenotypic redundancy has been traditionally associated to a higher resistance to environmental changes, which strengthens ecosystem stability (Biggs et al., 2020; Fonseca & Ganade, 2001; McCann, 2000; Pillar et al., 2013). Therefore, identifying the post-fire re-assembly of as many traits as possible might help identify the key traits behind the stability of fire-prone ecosystems and the mechanisms behind such stability. The fact that our below-ground traits remained stable at the community level suggests that root traits are fundamental for conferring such a resistance to disturbed plant communities. According to the single 'fast-slow' plant economics spectrum (Reich, 2014), species with high tissue density, long tissue life span and low rates of carbon and nutrients acquisition and flux are better protected from high carbon losses and drought stress. This 'slow' strategy matches with the results by Lipoma et al. (2016), who found that conservative resource-use strategies were responsible for post-fire community re-assembly in Argentinian mountain shrublands. They determined that traits associated to larger life spans and resprouting abilities, instead of acquisitive strategies (annual plants, seeders) increased resilience of plant communities to fire. In our system, shrubs and trees from the genera *Quercus*, *Olea*, *Phyllirea*, *Rhamnus* or *Pistacia*, among others, exemplify typical sclerophyllous resprouters that define this 'slow' strategy. They dominate the secondary succession in fire-prone Mediterranean ecosystems (Fournier et al., 2020). Our results also provide a below-ground characterisation of the sclerophylly at the community-level. We found that SRL, root N and root CN ratio are highly correlated with whole-traits as bud height or sclerophylly and less correlated with above-ground traits (Figure S4). These observations encourage to study several across-level traits to better understand the community phenotypic re-assembly of disturbed ecosystems, as suggested by Reich (2014),

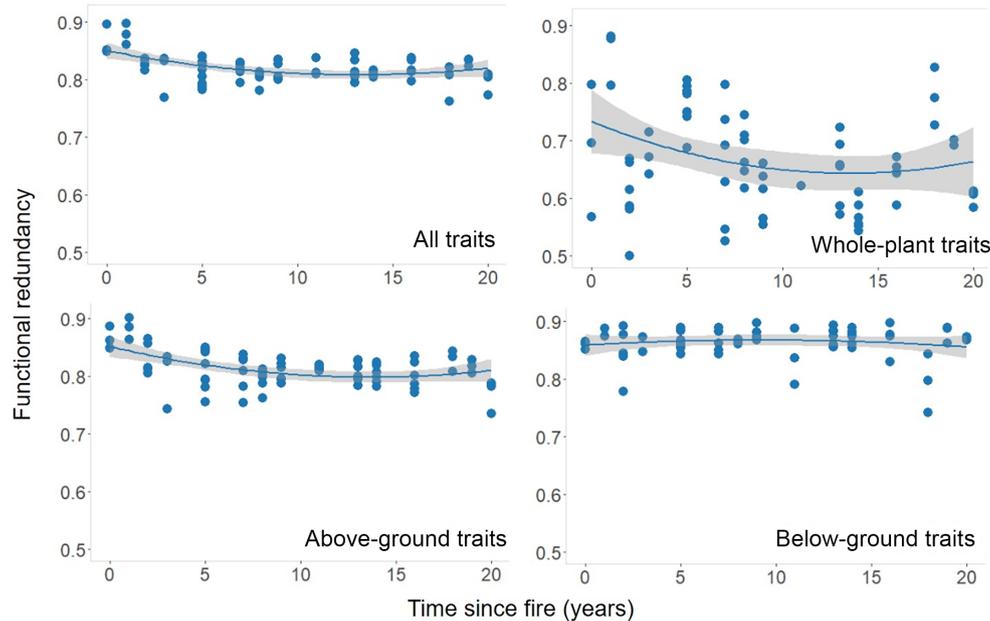


FIGURE 5 Phenotypic redundancy for all the traits and each set of traits (whole-, above- and below-plant traits) separately.

Kramer-Walter et al. (2016) or de la Riva et al. (2018). Moreover, multi-trait approaches are also emerging as useful for a better selection of species in restoration programmes (Wainwright et al., 2018). Jaureguiberry and Díaz (2023) recently proposed an identification method of dominant fire syndromes in plant communities. Recognising functional syndromes to select species aimed at promoting ecosystem functions has also been suggested in barren soils (Navarro-Cano et al., 2018). Moreover, under the current climate emergency, the inclusion of traits to cope with extreme droughts is mandatory (del Campo et al., 2020). These multitrait-based approaches might help to select plant communities that contribute to the ecosystem resilience by increasing resprouting abilities, decreasing flammability, promoting fertility and resistance to drought events. They might contribute to recover ecosystem functions driven by plant community traits (Laughlin, 2014; Montoya et al., 2012). The unsolved challenge is to develop easy implementation methods for an operatively and environmentally broad applicability of this approach.

## 5 | CONCLUSIONS

The study of plant community re-assembly after disturbance requires a special attention to below-ground-plant traits. Root traits provide a general resistance to fire that contribute to the ecosystem stability, whereas above-ground traits are more resilient in the sense of rapid changes in phenotypic diversity after fire, that progressively recover after two decades. Taxonomic and phenotypic betadiversities exhibit decoupled trajectories due to a larger species replacement than traits across time since fire. Our results highlight the importance of considering multi-dimensional trait-based approaches to understand the mechanisms behind the plant

community reassembly after fire. We suggest that trait-based approaches including both types of traits can be also useful in restoration programmes that pursuit not only a taxonomic recovery but restoring ecosystem functioning.

## AUTHOR CONTRIBUTIONS

All the authors designed the study and collected field data. Jose Antonio Navarro-Cano, Marta Goberna and Miguel Verdú performed analyses and wrote the first draft of the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare having no conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14379>.

**DATA AVAILABILITY STATEMENT**

All data used for analyses are available on Dryad Digital Repository: <https://doi.org/10.5061/dryad.c2fqz61jc> (Navarro-Cano, 2024).

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SUPPORTING INFORMATION

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

**Table S1:** Description of the 23 plant phenotypic traits used to assess the phenotypic diversity of plant communities in the three fire chronosequences studied.

**Table S2:** Functional trait matrix (117 species × 23 traits) of Mediterranean plant species.

**Table S3:** Paired t-tests for taxonomic and phenotypic betadiversity between burned and long unburned transects. Mean differences and t statistics (df = 71) for whole-plant, aboveground, and belowground traits are given. Asterisks indicate  $p \leq 0.001$ .

**Figure S1:** Location map of the three chronosequences (North, Centre and South) in the Valencian Region (Eastern Spain).

**Figure S2:** Distribution of whole-plant traits (grey), aboveground traits (green) and belowground traits (blue) in 117 Mediterranean species detected in 150 burned and long-unburned transects.

**Figure S3:** Taxonomic (deep blue) and phenotypic (light blue) beta diversities for whole plant, above-, and belowground traits.

**Figure S4:** Relationships among the six whole-plant, above- and belowground trait community-weighted means [CWM] whose differences between paired burned and unburned transects were significant across time (see Table 1).

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