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RESEARCH ARTICLE

Phenotypic rebuilding after fire: Understanding within-individual variability in a Mediterranean shrub

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Abstract

1. Due to the modular nature of plants, plant phenotypes are heterogeneous and dynamic within individuals. Previous studies have shown that certain environmental drivers can modulate variability within plant traits, but the effects of disturbances such as fires remain unknown. Fire may potentially act as a driving force of within-individual and population-level dynamics following resprouting. Specifically, we hypothesize that post-fire resprouting rebuilds plant phenotype by restarting plant development and erasing the previous developmental history. Consequently, we predict that burned (resprouting) and unburned plants differ in their phenotype and that this difference will have fitness consequences.
2. To test this hypothesis, we studied a population of the leguminous shrub *Anthyllis cytisoides* (Fabaceae) that was partially affected by a wildfire, allowing us to compare resprouting (burned) and undisturbed individuals in close proximity. We measured leaf, flower, seed and fitness traits, as well as global cytosine methylation—an indicator of epigenetic status, at a within-individual level.
3. Our results show that, for every study trait, burned and unburned individuals differed in at least one of the three dimensions we studied (mean value, total variability, within-individual variability). Burned plants showed a generalized increase in within-individual variability, including global cytosine methylation, as well as shifts in the relationship between this trait and several others, such as petal size and leaf shape. This pinpoints a possible epigenetic mechanism in explaining the phenotypic differences. Furthermore, higher seed set and altered floral–fruit set relationships in resprouting plants suggest fitness consequences of these phenotypic changes.
4. *Synthesis*. We found that burned resprouting individuals of *A. cytisoides* differed significantly in phenotype, global cytosine methylation, and the relationship between floral phenotype and fitness, compared to neighbouring undisturbed individuals. These findings support the idea that fire can alter the phenotype of individual plants, potentially through epigenetic mechanisms, and suggest that these changes may affect plant–animal interactions.

KEYWORDS
Anthyllis cytisoides, DNA methylation, epigenetics, fire ecology, flower traits, global cytosine methylation, leaf traits, plant phenotype, resprouting, trait variability, within-individual variability

1 | INTRODUCTION

Phenotype variability is key to evolution and is closely correlated to environmental heterogeneity and disturbances (Lazić et al., 2015; Lenormand et al., 2009; Stanton et al., 2000; Valladares et al., 2002). In plants, even though many functional traits are not individual but organ features (e.g. leaf mass, corolla diameter, petal size, fruit width, seed mass; Herrera, 2009; Pérez-Harguindeguy et al., 2013), individual phenotypes are typically characterized by the mean organ trait values or even by single organ measurements in the focal individuals (Harder & Johnson, 2009; Kingsolver et al., 2012). In recent years, the importance of considering within-individual variability to accurately describe the phenotype of modular organisms, such as plants, has gained attention. In these organisms, organ phenotypic traits vary both over time and across different parts of the plant, moving away from a static and uniform view of phenotypes, and making the phenotype more like a 'dynamic mosaic' (sensu Harder et al., 2019) or a distribution with a given life trajectory (sensu Herrera, 2024a, 2024b). The temporal and spatial variability dimensions within individuals are often closely correlated (e.g. the within-individual spatial variability of *Lavandula latifolia* Med. individuals' changes over its lifetime; C.M. Herrera, unpublished data). In fact, they arise from a diversity of shared, interrelated mechanisms such as ontogenetic changes, developmental stochasticity, architectural effects, environmental factors and phenotypic plasticity (Gómez et al., 2022; Harder et al., 2019; Herrera, 2009, 2024b). Both of these dimensions have important ecological consequences that are subject to phenotypic selection, like variance aversion behaviours by animal consumers or bet hedging (Ehrlén & Valdés, 2024; Shimada et al., 2015). For a synthesis on the ecological consequences of within-individual variability (see Harder et al., 2019; Herrera, 2017). Besides, both of these phenomena have heritable components (Herrera et al., 2015; Kulbaba et al., 2017), suggesting that within-individual variability might be a target on which natural selection may act.

Within-individual variability also occurs in epigenetic characteristics such as cytosine methylation, a key epigenetic mechanism that regulates gene expression and can be modulated by environmental factors (Zhang et al., 2018). For example, cytosine methylation in leaves can vary among different parts of the plant and along its life (Herrera et al., 2021; Yao et al., 2021). Furthermore, recent studies have found correlations between within-individual phenotypic and epigenetic variability (Alonso et al., 2018), even across generations (Herrera et al., 2022), suggesting a potential causal link between the two phenomena.

Although environmental changes and disturbances can serve as key drivers shaping spatial and/or temporal within-individual phenotypic variability (March-Salas et al., 2021; Møller et al., 2023; Stolter, 2008), for the moment, no attention has been given to the possible effects of wildfires on within-individual variability. Fires act as selective forces across spatial and temporal scales (He et al., 2019; Keeley et al., 2012; Pausas & Keeley, 2009), and they affect plants at the macroevolutionary (He et al., 2012; Lamont et al., 2019), community (Cavender-Bares et al., 2004; Verdú & Pausas, 2007) and population scales (Guiote & Pausas, 2023; Vandvik et al., 2014).

Post-fire resprouting (regeneration of above-ground tissues from dormant buds) is a survival strategy that can turn single-stem plants with strong apical dominance into multi-stemmed individuals lacking a clear hierarchical architecture (Figure 1). This structural change can have strong implications for the characteristics and variability of newly produced leaves, flowers, fruits and seeds. Thus, we hypothesize that post-fire resprouting modifies the phenotypic characteristics of burned individual plants in such a way that alters their within-individual variability and that these changes may be associated with within-individual global cytosine methylation variability. This should have an impact at a landscape (different phenotypes in burned and unburned patches) and temporal levels (different pre- and post-fire phenotypes in the same individuals) and have fitness consequences.

We tested these hypotheses by studying a population of the leguminous shrub *Anthyllis cytisoides* (L., Fabaceae) that was partially affected by a wildfire (Figure S1). We predict that (P1) burned individuals that were resprouting after fire differ in mean or variance of multiple phenotypic traits from undisturbed individuals, including within-individual variability (from now on also referred as WIV); (P2) phenotypic changes are correlated with variation in global cytosine methylation, suggesting that some epigenetic mechanism was involved in modifying either the mean phenotype or its variability; and (P3) post-fire phenotypic changes may affect fitness by modifying floral traits. We evaluate these predictions by comparing the phenotype of plants in pre- and post-fire conditions (i.e. burned and unburned individuals) considering mean values as well as two variability levels (subpopulation level—from now on 'total variability'—and within-individual level) and by exploring the relationships of mean and variance of the phenotype with global cytosine methylation and fruit set (fitness proxy).

2 | METHODS

2.1 | Species

Anthyllis cytisoides (L., Fabaceae) is a drought-deciduous shrub endemic to the western Mediterranean region that can reach up to 1.5 m in height. It thrives in open shrublands and abandoned

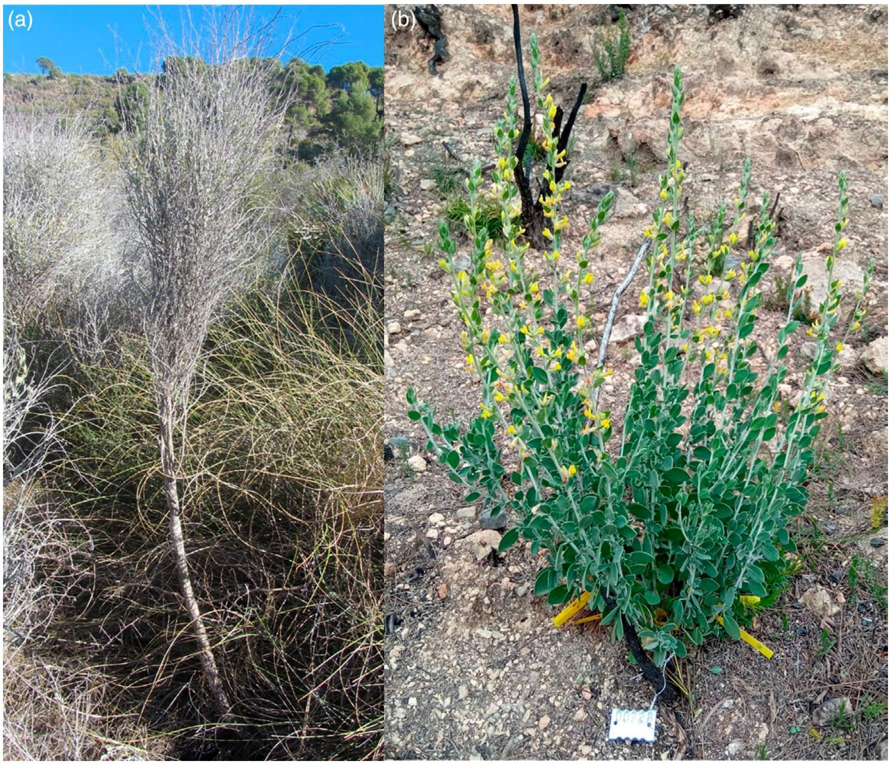

FIGURE 1 Architectural change produced by post-fire resprouting in *Anthyllis cytisoides*. Undisturbed individuals (a) usually have a single-stem, apical dominant structure. Individuals resprouting post-fire (b) have a multi-stem structure without apical dominance.

fields under dry and warm low-altitude environments (de Bolòs & Vigo, 1984), where it can become a dominant species (Haase et al., 1997). Each flowering season, it produces reproductive shoots that die back after seed dispersal (Escós et al., 1997). It has complex butterfly-shaped flowers ('papilionid' or 'keel' flowers, Westerkamp, 1997; Figure S2) that are insect-pollinated (Moragues & Traveset, 2004), produce nectar (Herrera, 1985) and are organized in spike inflorescences. Self-fertilization is prevented by the asynchrony of pollen and stigma maturity (Couderc, 1980). Fruits of *A. cytisoides* are single-seeded with hard, water-impermeable coats.

In terms of fire adaptation, *A. cytisoides* is a facultative resprouter, meaning that it resprouts (Moreira et al., 2012) as well as recruits from a soil seed bank after wildfires, with seeds exhibiting physical, heat-released dormancy (Moreira et al., 2010; Pausas & Lamont, 2022; Tavsanoglu & Pausas, 2018). *Anthyllis cytisoides* is characterized by basipetal shedding of branches and sympodial architecture. Undisturbed individuals are typically single-stemmed shrubs, while after severe disturbances that remove all above-ground biomass (like fires) plants resprout from the root crown and become multi-stemmed (Figure 1).

2.2 | Location

The study area is located on the edge of a wildfire that occurred during the summer of 2021 in Azuebar (365 m elevation, Castellón province, eastern Spain). This area comprises a terraced slope with abandoned fields colonized by pines (*Pinus halepensis*, Mill.) and shrubs, where *A. cytisoides* is common (Figure S1). We selected an *A. cytisoides* population at the fire's edge so that it was only partially affected by the wildfire. This unique natural setting provided both fire-affected (burned) and unaffected (unburned) individuals in close proximity. This design allows for sampling plant traits in different stages (resprouting and undisturbed) simultaneously and enabled us to sample under the same environmental conditions. In April 2022, we selected 31 individuals within a 0.5 ha plot—15 unburned and 16 burned and resprouting—that we will refer to as subpopulations hereafter. The distance between burned and unburned individuals ranged between 10 and 150 m (mean = 90 m). To minimize micro-topographical differences between the two subpopulations, we avoided selecting individuals located on slopes or rocky patches. Additionally, because we could not determine the pre-disturbance size of resprouting plants, we chose large individuals in both groups. Specifically, we selected only burned plants showing abundant resprouting (>15 shoots) and unburned plants taller than 1 m, and these criteria limited the number of available individuals for the study. For each individual, we selected and marked 6–7 modules totalling 213 modules (102 unburned, 111 burned; Figure S3). Modules in burned plants were single shoots resprouting from basal buds, while those in unburned plants were branches growing from the main stem that bore at least five dry reproductive shoots from the previous spring, used as a proxy for expected reproductive activity.

2.3 | Phenotypic characterization

As most fires occur in summer and our study species is summer deciduous, plant responses were studied during the first spring after the wildfire, in 2022. We measured 18 traits across the 31

A. cytisoides plants, including leaf, flower, inflorescence, seed and fitness traits as well as global cytosine methylation in leaf DNA. Most traits were assessed at the within-individual level, that is, either at the module or within-module levels (Table 1). All scans and digital measures in this study (leaves and flowers) were carried out using an Epson Scan Perfection 4490 and ImageJ software (Schneider et al., 2012). All weights (flowers, leaves, fruits) were measured to the nearest 0.01 mg using a Mettler Toledo AXE 205.

2.3.1 | Leaf traits

We distinguished between two leaf types: vegetative leaves (produced by the perennial part of the plant) and reproductive leaves (produced by annual reproductive shoots) and collected three leaves of each type per module. For each leaf, we measured four traits: leaf area, leaf mass, specific leaf area (from now on SLA; m^2/kg) and leaf shape. In Mediterranean ecosystems, SLA is related to relevant physical traits such as sclerophylly (Filella & Peñuelas, 2003), fire persistence mechanisms (Hernández et al., 2011; Paula & Pausas, 2006) and community-level factors such as fire history (Anacker et al., 2011). Intraspecific variation in SLA, leaf area and shape also correlates with environmental conditions across multiple Mediterranean species (Kassout et al., 2024; Valladares et al., 2002). Leaves were scanned while fresh, then dried and weighed after petiole removal. The leaf scans provided data on leaf area and leaf shape (slenderness = length/width). SLA was estimated as the ratio between leaf area and mass (m^2/kg). Since vegetative leaves live longer and have lower SLA than reproductive leaves (Estimate = −2.16; $\chi^2 = 1940$; $p < 0.001$), these two types of leaves can be considered functionally different (i.e. they occupy different positions on the leaf economical spectrum: Vegetative leaves are more conservative while reproductive leaves are more acquisitive; Wright et al., 2004).

2.3.2 | Inflorescence traits and floral production

At the time of fruiting, we recorded total inflorescence production and the length of five inflorescences per individual. Due to the slow acropetal development of *A. cytisoides* inflorescences (with distal parts still producing new flowers while basal ones are already fruiting), flower density per inflorescence (number of flowers per cm) was calculated from the basal part (i.e. the section bearing wilted flowers or fruits). Total flower production per individual was calculated as the product of flower density, mean inflorescence length and total inflorescence production.

2.3.3 | Flower traits

Following previous studies conducted with papilionid flowers, we selected three flower traits: standard petal area, nectar guides area and flower size (Castellanos et al., 2023). The standard petal is the upright standing petal of papilionid flowers (i.e. banner or flag petal; Figure S2b), and it is the most visible flower part. In *A. cytisoides*, this petal has nectar guides that, together with the flower structure, direct pollinators into the nectaries (Hansen et al., 2012; Westerkamp, 1997). In addition, the size of papilionid flowers is correlated with the ability of insects to trigger the pollen release mechanism, meaning that larger flowers usually require larger insects for effective pollen transfer (Córdoba & Cocucci, 2011; Figure S2c). In fact, the standard petal area and the flower size are correlated with fruit set in other Fabaceae (*Ulex parviflorus*; Castellanos et al., 2023), highlighting the potential of these two traits as key display features. We collected 3–8 mature flowers from each module (i.e. flowers with the standard petal completely extended and without withering signals). In the laboratory, we removed the standard petals while still fresh and

TABLE 1 The studied traits classified by plant organ (different colours) and sampling level.

Plant organ	Trait	Sampling level
Vegetative and reproductive leaves	Leaf area	Within module
	Leaf dry mass	Within module
	Specific leaf area (SLA)	Within module
	Slenderness (Length/Width)	Within module
Inflorescence	Inflorescence length	Module
	Inflorescence production	Individual
	Total flower production	Individual
Flower	Standard petal area	Within module
	Nectar guides area	Within module
	Flower dry mass	Within module
Seed	Seed mass	Within module
Fitness	Fruit set	Module
	Seed set	Module
Epigenetic	Global cytosine methylation	Module

Note: The three levels are nested as follows: Individual ($n = 31$) > Module (5–7 in each individual) > Within module (3–8 leaves, petals or seeds in each module).

immediately pressed them using a plant press for 24 h. Then, we scanned and measured total petal area and nectar guide area. Given the complex shape of these flowers, we estimated flower size based on the dry mass of the remaining flower parts, excluding pollen and anthers. To avoid variance in tissue hydration, flowers were oven-dried at 100°C for 12 h and kept in the oven until weighing.

2.3.4 | Seed and fitness traits

Seed mass, fruit set and seed set were measured in the same basal section of the inflorescences considered for floral density and flower production. To collect all fruits produced in this section, we enclosed them in a mesh bag. Fruit set was calculated as the ratio of fruit to flower production. Since *A. cytisoides* fruits bear a single seed, the difference between the number of fruits and seeds is due to empty fruits that may result from either fruit predation or seed abortion. Thus, we defined 'seed set' as the proportion of fruits without *Curculionidae* marks (predated seeds) that successfully bore seeds for each module. Lastly, seed mass was measured using 10 seeds per module.

2.3.5 | Epigenetic characterization

We measured the percentage of methylated cytosines genome-wide in leaf DNA. This is a highly variable characteristic at the intraspecific level (Alonso et al., 2014; Alonso, Balao, et al., 2016), and, in some species, it is also correlated to fitness traits at a within-individual level (Alonso et al., 2018). Global cytosine methylation was calculated at a within-individual level using one vegetative leaf per module. We used this organ since they are the first ones produced after resprouting and, thus, their DNA methylation characteristics could be related to organs built later along each branch. We estimated it using reversed-phase high-performance liquid chromatography (HPLC) with spectrofluorimetric detection (see Alonso, Pérez, et al., 2016 for details). To do so, we first extracted total genomic DNA from dried leaf samples, which was then enzymatically digested to its nucleoside components. Two independent replicates of DNA hydrolysate were prepared for each sample. Digested samples were stored at −20°C until analysis. Chemical derivatization was conducted just before running the HPLC analyses. We then calculated global cytosine methylation as $100 \times 5\text{mdC}/(5\text{mdC} + \text{dC})$, where 5mdC and dC represent the integrated peak areas for 5-methyl-2′-deoxycytidine and 2′-deoxycytidine respectively.

2.4 | Statistical analysis

All statistical analyses were conducted in the R environment (R Core Team, 2023), employing the lmer and glmer functions from 'lme4' package for fitting LMMs and GLMMs, and the Anova function from 'car' package to perform ANOVA tests for each model. Marginal R^2 was calculated using the "r2_nakagawa" function of the 'performance package' (Lüdecke et al., 2021).

2.4.1 | Phenotypic consequences of post-fire resprouting

First, we studied the effects of post-fire on the mean as well as on two variability metrics (total variability, WIV) for each measured trait (P1). When studying effects on the *mean*, we assessed divergence between the two subpopulations (burned/unburned, where 'burned' refers to resprouting plants) by fitting random intercept mixed models in which each of the trait values entered as the response variable and the plant's subpopulation as the single categorical fixed predictor (see Table S1 for more details). The sampling structure, with the trait data (from now on 'measurements') nested within modules, and modules nested within individuals, was incorporated as a random effect. Second, to assess the effects of post-fire resprouting on *total variability* at the subpopulation level, for each trait we compared the coefficients of variation (CV) across the two subpopulations. The CV of a subpopulation for a given trait was calculated as the standard deviation divided by the mean, and the confidence intervals (from now on 'CIs') were calculated through bootstrapping. We selected this method instead of comparing individual CV values of burned and unburned plants since we were interested in the total variability of each subpopulation and not in the variability of the individuals of each population.

Finally, in order to fully understand within-individual variability, it is important to consider that, in our sampling design, the total variability analysed for traits sampled at the 'within module level' (Table 1) includes three nested levels: variation between individuals, among modules within individuals, and within each module. Note that the last two levels refer to variability occurring *within individuals* (i.e. WIV).

For 'Inflorescence Length', 'Fruit Set', 'Seed Set' and 'Global Cytosine Methylation', we recorded one value per module, thus, variability was partitioned into two levels, that is between individuals and between modules (i.e. within individuals, also termed WIV). To analyse differences in *WIV* between burned and unburned plants, we calculated the variance partition values by fitting a separate random intercept model for each subpopulation (burned/unburned) and trait. In these models, the response variable were the raw values of the studied traits. We standardized the response variable to allow the comparison among subpopulations and traits with different variance magnitudes. As a predictor, we only included the random effect, with trait data nested within modules and modules nested within individuals. For each trait, we compared the models between subpopulations (burned/unburned) using confidence intervals (CIs) calculated through bootstrapping (confint.merMod function from the 'lme4' package, nsim = 1000, see Figure S4 for a comprehensive summary of this method). Since binary traits cannot be standardized (i.e. Fruit set and Seed set), we calculated the CIs for the ratio between within individual variability and total variability. Significant differences were considered when the subpopulation CIs for the same variability level for a given trait did not overlap (Figure S4a) or when the CIs of two variability levels for a given trait overlapped in one subpopulation but not in the other (Figure S4b). Changes in CV and WIV were not analysed for number of inflorescences or overall flower production since we only had one data per individual ($N=31$).

2.4.2 | Effect of post-fire resprouting in the relationship between global cytosine methylation and measured phenotype

We assessed the effects of fire on the relationship between global cytosine methylation and organ phenotype (P2) by analysing linear and quadratic relationships between either the mean, variance or CV of each trait and the global cytosine methylation level. This analysis was performed with modules serving as the primary sampling units (Unburned: 46 modules across 9 plants; Burned: 43 modules across 8 plants). In all cases, the random effect included modules nested within individuals. This means that for each trait, we fitted 6 random intercept mixed models (see Table S1 for a summary of the statistical analysis). Model selection between linear and quadratic forms was determined using likelihood ratio tests ('lrtest' function from the 'lmtest' package). We then adjusted the resulting p-values through the Benjamini–Hochberg procedure to control the false discovery rate ('p.adjust' function from 'Stats' package).

2.4.3 | Effect of post-fire resprouting in the relationship between floral traits and fruit set

Finally, we explored the fitness consequences of the differences in floral phenotype between burned and unburned plants (P3). To do this, we performed an analysis using a random intercept generalized mixed model (GLMM) where the response variable was the fruit set, the predictors were the standardized means and variances per module of the three floral traits measured (standard petal area, nectar guides area, flower dry weight) and its interaction with the state of the plant (burned/unburned). The random component included the modules nested within individuals. For every model we fitted in this work, diagnostics were assessed using the 'performance' and 'DHARMA' packages (Hartig et al., 2024; Lüdecke et al., 2021).

3 | RESULTS

3.1 | Phenotypic consequences of post-fire resprouting

Post-fire resprouting affected all traits at least in one of the three dimensions studied (Figure 2). Changes in means after resprouting were usually not directly related to changes in total variability or within-individual variability for the same trait, and the effect of resprouting can be different in total variability (CV) and in WIV.

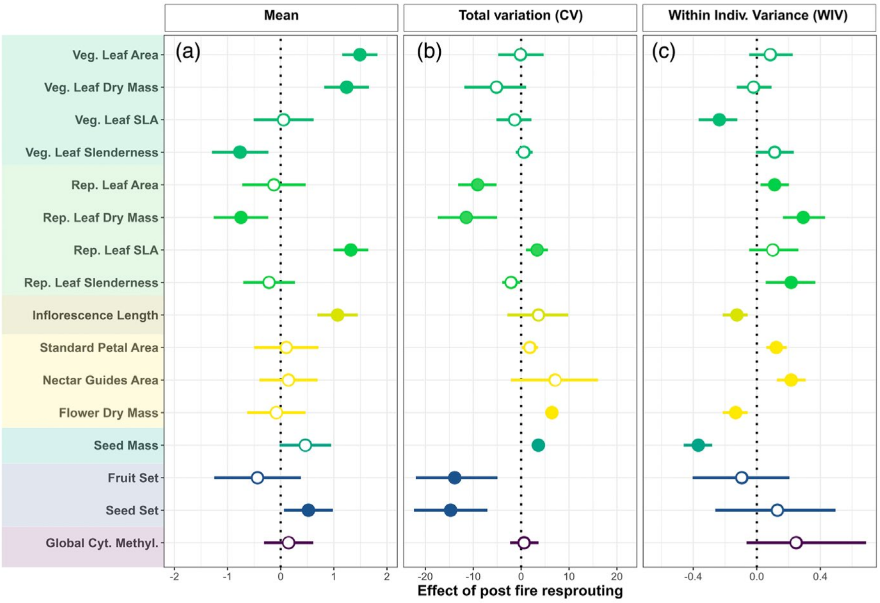

FIGURE 2 Effects of post-fire resprouting on the (a) mean, (b) total variability (CV) and (c) within-individual variance (WIV) for the traits considered. Positive values indicate an increase in the burned subpopulation. For mean, symbols (circles) represent the effect size of post-fire resprouting (i.e. estimate of the fitted models) and bars ±1.96 × SE (see Table S2). For total variability and WIV, symbols represent the difference between the variance values obtained for burned and unburned plants (see Table S3 for total variability values and Table S4a,b for WIV values). Bars represent the confidence intervals of these differences, calculated through bootstrapping. In both cases the significance of the change was determined using confidence intervals (see Section 2.4.1). Note that within-individual variability is the metric where most traits change and that significant changes in mean values are usually de-coupled from those in WIV (i.e. for a given trait, only one of the two metrics changes).

For leaf traits, post-fire resprouting had different effects in vegetative and reproductive leaves. In particular, vegetative leaves changed mainly in the mean of shape and size, while reproductive leaves changed more in total variability and WIV (Figure 2; Tables S2, S3, and S4a,b). Burned plants had bigger and rounder vegetative leaves with similar SLA. Total variability in those traits was also similar between the two subpopulations, and vegetative leaves of burned plants had a more variable SLA within individuals than those of unburned plants. Furthermore, reproductive leaves of burned plants were on average lighter and had a higher and more variable SLA, and, despite their more homogenous size at the subpopulation level, they had a higher WIV in every trait except for SLA.

When considering reproductive traits, burned and unburned plants did not differ in inflorescence production (Unburned: Mean = 71.86, SD = 16.65; Burned: Mean = 66.67, SD = 24.92; $\chi^2 = 127.2$; df = 1; $p = 0.6$) but differed in average inflorescence length, which was longer for burned plants (Figure 2a), and overall flower production with burned plants producing almost twice the number of flowers as the unburned plants (Unburned: Mean = 3868.47, SD = 1636.83; Burned: Mean = 6453.57, SD = 4100; $\chi^2 = 46{,}779{,}362$; df = 1; $p = 0.038$).

For flower traits, burned plants differed from unburned plants in total variability and WIV but not in mean values. Although burned plants had a higher total variability in flower mass, less of that variability was due to differences within individuals, since they had lower WIV than unburned plants (Figure 2b,c). For petal traits, nevertheless, post-fire resprouting increased WIV (Figure 2c). In fruit and seed mass, resprouting effects were also restricted to variance, increasing its total variability at a subpopulation level but reducing it within individuals (Figure 2b,c). Burned plants had more homogenous fruit and seed sets (Figure 2b) and less of their fruits were empty (i.e. they had a higher seed set; Figure 2a). Finally, the two subpopulations did not differ in the average cytosine methylation of vegetative leaves' DNA, while post-fire resprouting increased the WIV component of global DNA cytosine methylation (Figure 2c).

3.2 | Effect of post-fire resprouting in the relationship between global cytosine methylation and measured phenotype

Post-fire resprouting altered the linear relationship between global cytosine methylation in vegetative leaves and some of the leaf and flower traits analysed (Table 2; Figure 3). Four of the linear models (mean size of the standard petal, variance of nectar guides, variance of seed mass, and mean of slenderness of reproductive leaves) showed a significant effect of subpopulation in the relationship between global cytosine methylation and phenotype, while three others (mean flower mass, mean SLA of vegetative leaves and seed set) exhibited marginally significant effects (Table S5a). In unburned plants, there was a positive association between methylation level and trait value for most significant traits with linear relationships (Figure 3). These relationships either disappeared (in the case of petal size) or reversed (variance of nectar guides area, variance of seed mass) in burned plants (Figure 3). Furthermore, only in the case of seed set, quadratic interaction models significantly improved the fit: seed set was lower at intermediate levels of leaf DNA methylation, with a marginally significant effect of the subpopulation on this relationship (Table S5b). Burned plants showed a reduction in the strong convex relationship between seed set and leaf DNA methylation level found in unburned plants (Figure S5).

TABLE 2 Results of the ANOVA tests of the LMMs analysing the differences between subpopulations (burned/unburned) in the relationships between global cytosine methylation and phenotype.

Response trait	Predictor	χ^2	df	*p*-Value	Marginal R^2
Mean standard petal size	Global cytosine methylation (GCM)	2.393	1	0.122	0.024
	Subpopulation	0.015	1	0.903	
	GCM: Subpopulation	4.372	1	**0.037**	
Variance of nectar guides area	Global cytosine methylation	0.985	1	0.321	0.123
	Subpopulation	3.748	1	0.053	
	GCM: Subpopulation	4.494	1	**0.034**	
Mean reproductive leaf slenderness	Global cytosine methylation	0.769	1	0.380	0.088
	Subpopulation	1.191	1	0.275	
	GCM: Subpopulation	4.273	1	**0.039**	
Variance seed mass	Global cytosine methylation	2.821	1	0.093	0.068
	Subpopulation	0.009	1	0.927	
	GCM: Subpopulation	5.413	1	**0.020**	

Note: Here we only include the four traits where post-fire resprouting had a significant effect on this relationship (see Figure S5 for the marginally significant interactions and Table S5a–c for the results of all performed models). Bold values indicate significant ($p < 0.05$).

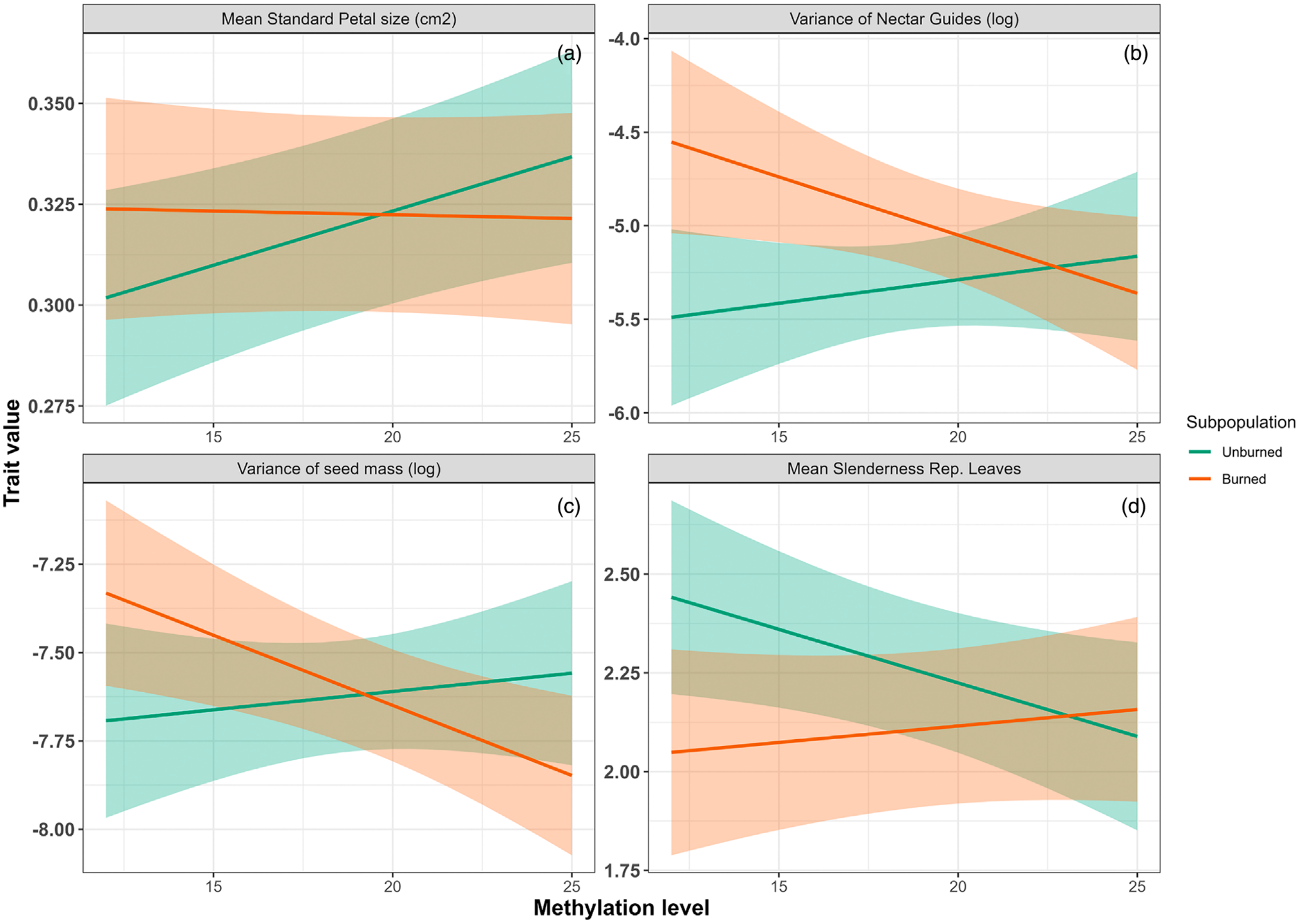

FIGURE 3 Effect of post-fire resprouting in the relationship between global cytosine methylation and plant phenotype. Only the four traits with significant interactions are represented (Table 2; Table S5a–c): (a) Mean standard petal size; (b) Variance of nectar guides; (c) Variance of seed mass; (d) Mean slenderness of reproductive leaves. Note that in burned plants, relationships either reverse (b, c, d) or disappear (a).

3.3 | Effect of post-fire resprouting in the relationship between floral traits and fruit set

Our analyses showed that for standard petal size and flower dry mass, the relationship between means and variances of trait values with fruit set was different in burned and unburned plants (Table 3). In unburned plants, fruit set was higher when having small, homogenous petals and variable-sized flowers (Figure 4a,c,d), while in burned plants, fruit set was only positively related to flower mass (Figure 4b).

4 | DISCUSSION

Phenotypes are by no means constant in plants. Fire, through post-fire resprouting, can drastically reshape the individual phenotypes, as we have shown in the shrub *Anthyllis cytisoides*. This phenotypic rebuilding included obvious changes in individual plant architecture (from a single-stemmed to multi-stemmed plant; Figure 1), and subtler but significant changes in a suite of leaf, flower, and seed traits. Given that the capacity to resprout in response to disturbances is widespread among angiosperms (Del Tredici, 2001), these results are likely to have broad, yet understudied, implications.

Post-fire phenotypic changes in *A. cytisoides* led to divergence between co-occurring burned and unburned individuals in terms of mean, total variability and within-individual variability (WIV) of organ traits. Consequently, resprouting could imply a change in the dynamics of individual phenotypic mosaic (sensu Harder et al., 2019) or, in other words, a breakpoint in individual phenotypic trajectory (sensu Herrera, 2024b). Furthermore, fire also affected within-plant variability of global cytosine methylation and its relationship with some organ's phenotype, as well as the fecundity correlates of variability in floral traits. In the following paragraphs we will discuss the effects of post-fire resprouting on all studied traits and the relationships between some of them. Although we will address vegetative and reproductive traits separately, almost all phenotypic changes can be attributed to either the environmental changes post-fire (e.g. abiotic resource pulses, reduced competition, shifts in pollinator abundance), the consequences of resprouting per se (e.g. stimulation of multiple dormant buds, architectural changes), or a combination of both. However, it is important to note that some of the observed phenotypic divergence between subpopulations will be influenced by ontogenetic differences between newly resprouted and mature shoots, meaning that these differences could diminish with time since fire. Pre-existing inter-individual variability between unburned and burned plants could also

TABLE 3 Results of the ANOVA tests of the LMMs analysing differences between subpopulations (burned/unburned) in the relationships between fruit set and floral traits (scaled previous to the analyses).

Predictor	χ^2	df	*p*-Value
Mean standard petal area	14.482	1	**<0.001**
Mean nectar guides area	0.984	1	0.321
Mean flower dry mass	20.724	1	**<0.001**
Var. of standard petal area (log)	2.041	1	0.153
Var. of nectar guides area (log)	0.000	1	0.997
Var. of flower dry mass (log)	7.377	1	**0.006**
Subpopulation	1.156	1	0.282
Mean standard petal area: Subpopulation	24.762	1	**<0.001**
Mean nectar guides area: Subpopulation	0.170	1	0.680
Mean flower dry mass: Subpopulation	6.198	1	**0.013**
Var. of standard petal area (log): Subpopulation	11.257	1	**<0.001**
Var. of nectar guides area (log): Subpopulation	0.057	1	0.811
Var. of flower dry mass (log): Subpopulation	8.959	1	**0.003**

Note: Bold values indicate significant ($p < 0.05$).

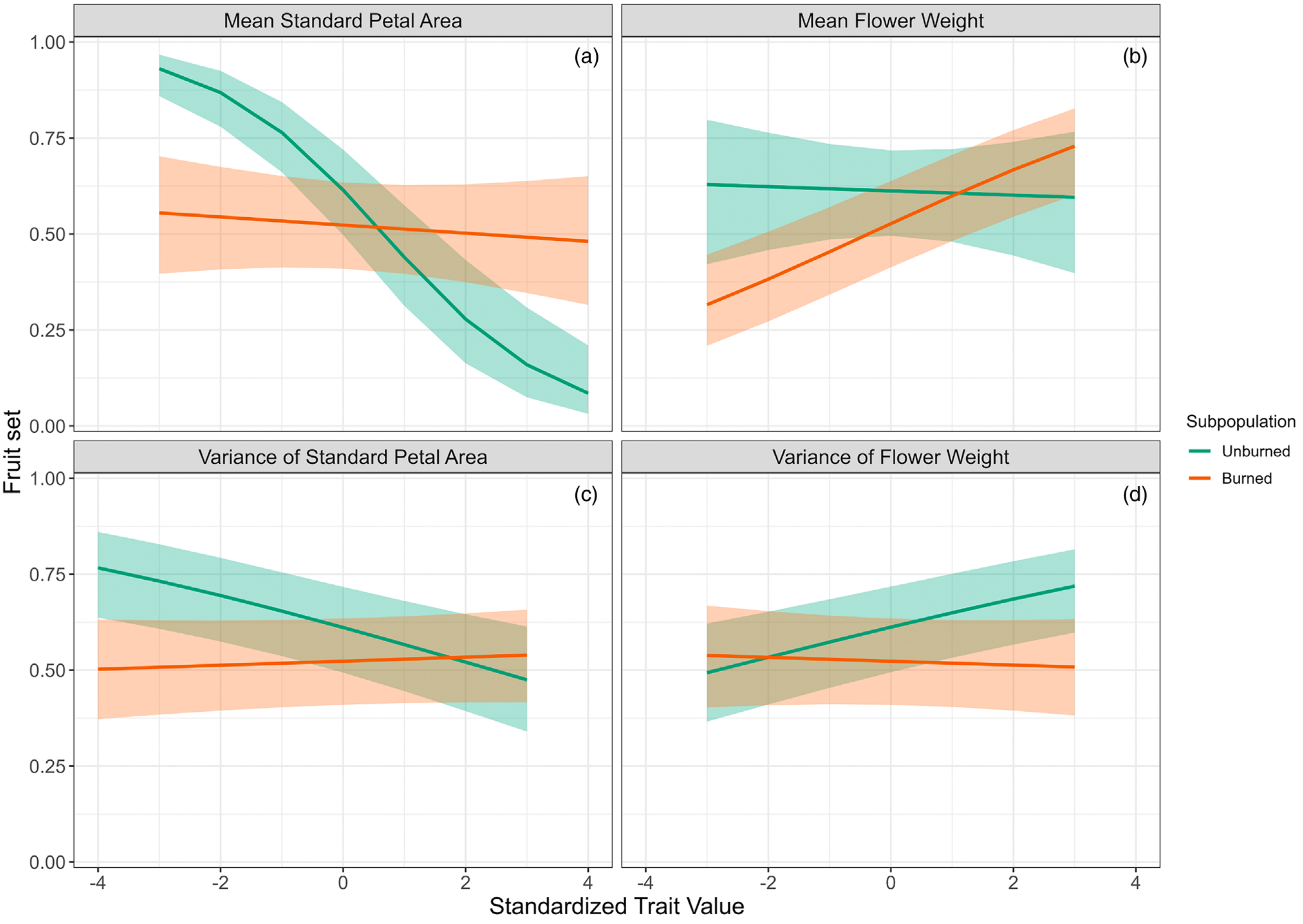

FIGURE 4 Effect of post-fire resprouting in the relationship between floral phenotype and fruit set. Only the four traits with significant interactions are represented: (a) Mean standard petal area; (b) Mean flower weight; (c) Variance of standard petal area; (d) Variance of flower weight (Table 3). Flower traits undergo different selective pressures on the two groups of plants: The trait not under selection in unburned plants (mean flower mass) becomes the primary trait under selection in burned plants (Table 3). Note that the mean of these two traits also has a different relationship with global cytosine methylation (Figure 3; Figure S5; Table S5a).

affect these differences, although we assumed that this has a minor effect given the reduced extension of the study area as well as the continuity and lack of strong microhabitat differences. Moreover, we are aware of our small sample size, although it is typical for WIV studies due to the amount of work involved.

4.1 | Resprouting and vegetative traits

The two leaf types responded to the disturbance in different ways, corresponding to their position in the leaf economic spectrum, with long-lived vegetative leaves increasing their conservative strategy and the short-lived reproductive leaves increasing their acquisitive strategy. Vegetative leaves of resprouting individuals showed a reduction in WIV of their SLA values. This may be driven by the increase in light availability post-fire, as the shade is known to increase the WIV in this trait (Møller et al., 2023). Meanwhile, the increase in mean SLA values of reproductive leaves may favour rapid resource acquisition during the early stages of resprouting. Although higher SLA values are typically associated with lower water-use efficiency, resprouting individuals retain their root systems, allowing them access to deep water reserves (Bell & Pate, 2001; Vilagrosa et al., 2014). Similar responses involving high growth rates despite reduced water efficiency have already been observed in other resprouting species (e.g. low xylem density after resprouting; Jacobsen et al., 2016). These strategies might enable burned individuals to quickly rebuild their above-ground structures following disturbance, thereby replenishing their reserves for future disturbances (Saiz-Blanco, Alonso, & Pausas, 2025). The observed shape changes in vegetative leaves of burned plants make them resemble those produced by *A. cytisoides* seedlings (i.e. large, thick and round). Given that they are the first plant organ produced during resprouting and that these characteristics dilute in successive leaf flushes (pers. obs.), this shape change likely reflects a temporary ontogenetic flashback occurring in the early stages of resprouting which suggests that the short-term divergences here reported could be reduced with time and it would be worth monitoring them along several reproductive events.

4.2 | Resprouting, reproductive traits and plant fitness

Burned plants produced nearly twice as many flowers as unburned plants, owing to their longer inflorescences. Sharp increases in floral display are common in the first years after fire in many ecosystems (LoPresti et al., 2018; Richardson et al., 2023), including Mediterranean ones (Potts et al., 2001). Despite this larger floral display in burned plants, fruit set did not differ between the two subpopulations; however, seed set was higher in burned plants. A similar pattern was described in tallgrass prairies (Richardson et al., 2023), and might be due to interactions with animals (see Charles et al., 2025 for a review) such as a higher pollinator efficiency in post-fire conditions (Banza et al., 2021) or a reduced pre-dispersal seed predation in our particular study case. However, other mechanisms, such as the production of parthenocarpic fruits in order to reduce seed predation, might also play a role in other species (Zangerl et al., 1991). Combining the effects on flower production, fruit set, and seed set, we estimated that burned plants produced nearly twice as many seeds (mean: 2338.2, SD: 1731.4 seeds/plant) as unburned plants (mean: 1300.4, SD: 996.4 seeds/plant), suggesting a considerable post-fire increase in fitness. A combination of abiotic resource pulses and changes in plant–animal interactions may contribute to this effect (Carbone et al., 2019; Muñoz et al., 2005).

In relation to the floral phenotype, it is noteworthy that post-fire resprouting had opposite effects on WIV of petal and flower size, two highly correlated traits ($r^2=0.33$). This could be a consequence of the two traits being subject to different selective pressures, as has been observed in *Ulex parviflorus* (a closely related Mediterranean Fabaceae with papilionid flowers; Castellanos et al., 2023). In our case, there seems to be different selective pressures on the mean and variance of the two traits in burned and unburned plants (Figure 4) further supporting this idea. This divergence could also be related to the architectural change caused by basal resprouting, which could homogenize resource access across different plant parts within an individual and might explain the lower WIV of flower and seed mass in burned plants. Since this phenomenon would only affect WIV, it could be compatible with the observed increase in total variability (CV) for these traits (Figure 2b). Changes in total variability could be influenced by other factors such as heterogeneous reserve availability, resource access, or competition abilities across burned individuals. Additionally, a reduction in WIV in seed mass could translate into more homogeneous progeny per individual, as seed mass usually influences seedling fitness (for examples in other Fabaceae, see Marshall, 1986; Souza & Fagundes, 2014). Although behaviours in animal consumers, such as variance aversion (Shimada et al., 2015), could lead us to predict negative relationships between WIV in floral traits and fitness, no consistent pattern has been described so far (positive: Paglia et al., 2023; negative: Arceo-Gómez et al., 2017; both: Dai et al., 2016), suggesting a complex and context-dependent reality. In any case, the changes in WIV in floral traits of *A. cytisoides* do not appear to negatively affect overall fitness (Figures 2a,c and 4c,d). Moreover, the homogenization of both fruit and seed set in burned plants (Figure 2b) might result from the combined effect of their competitive advantage for attracting pollinators (due to the larger floral displays) and, possibly, a broader range of floral signalling traits within individuals (increased WIV in standard petal area and nectar guides). This could be linked to the higher abundance and richness of pollinators in post-fire scenarios (Carbone et al., 2019 and references therein) or to the changes in the pollination community structure (LaManna et al., 2021; LoPresti et al., 2018; see García et al., 2018; Potts et al., 2001 for community level effects on the Mediterranean). In fact, the contrasting selective pressures on the floral phenotype of burned and unburned plants (Figure 4) support the idea of a fire-driven change in the plant–pollinator interactions. Although we do not know if the changes in the relationship between floral phenotype and plant fitness are the cause or consequence of this change in the pollinator community, the fact that we observed a divergence between subpopulations highlights the potential of wildfires to generate different selective pressures on the floral phenotype even at very local spatial scales (the two furthest plants were 150 m apart).

Finally, global cytosine methylation showed higher WIV in burned plants, suggesting the promotion of a within-individual epigenetic mosaic (Herrera et al., 2022) due to the activation of dormant buds. Additionally, changes in the relationship between global cytosine methylation and some organ traits (Figure 3) might indicate that some of these phenotypic changes could be mediated through epigenetic changes (Herrera & Bazaga, 2013). These findings are especially appealing, since they provide insight into the mechanisms behind the potential ability of wildfires to drastically alter the phenotypic trajectory in resprouting plants: fire would wipe out the previous developmental history of the aerial plant parts and establish a new and more variable starting point.

5 | CONCLUDING REMARKS

Post-fire resprouting significantly altered vegetative and reproductive traits in *Anthyllis cytisoides* in mean, total variability and within individual variability (P1). These changes might be due to effects derived from the new environment experienced after fire and/or from the basal resprouting per se (i.e. the stimulation of multiple dormant buds and resultant structural changes). Since, in burned plants, global cytosine methylation is more variable within individuals and has different relationships with its phenotype, these phenotypic changes can be mediated by epigenetic mechanisms (P2), affect floral traits and, very likely, plant–pollinator interactions (P3). They can also influence the variability of the next generation, as seed production becomes more homogenous among individuals, and seed mass within individuals exhibits reduced variability. Thus, we propose that fires can fundamentally change the expression of an individual's phenotype. The extent of how these modifications follow post-fire dynamics and vary with recurrent fires remains to be explored. In any case, our results contribute to the growing body of literature showing that plant traits vary within populations and even within individuals and that this variability is dynamic. Disturbance acts as a source of this variability, which, unsurprisingly, has significant implications.

AUTHOR CONTRIBUTIONS

Jaime Saiz-Blanco and Juli G. Pausas designed the study and Jaime Saiz-Blanco performed it. Jaime Saiz-Blanco analysed the data with the support of Conchita Alonso, Carlos M. Herrera and Juli G. Pausas. Jaime Saiz-Blanco wrote the draft and all authors contributed substantially to the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data associated with this study are publicly available in Figshare https://doi.org/10.6084/m9.figshare.29493254.v1 (Saiz-Blanco, Alonso, Pausas, et al., 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. Study location in Azuebar (Castellon province, Spain).

Figure S2. Floral morphology of *Anthyllis cytisoides*.

Figure S3. Conceptual scheme representing an unburned (a) and a burned (b) plants with seven modules.

Figure S4. Examples of variance partition analysis for three traits which exemplify the two different types of results.

Figure S5. Marginal effects of post-fire resprouting in the relationship between global cytosine methylation and plant phenotype.

Table S1. Summary of the different statistical analyses carried out in this study.

Table S2. Mean values-estimates of the effect size of post-fire resprouting on the scaled mean values of each study trait based on LMMs.

Table S3. Total variability-coefficient of Variation estimates and 95% CI for each trait and subpopulation.

Table S4. Within individual variability-variance partition and CIs for each variance level of (a) each leaf trait studied and (b) every reproductive trait studied.

Table S5. Global Cyt. Met. and phenotype-results of the ANOVA tests of the LMMs analyzing the differences between subpopulations (burned/unburned) in the relationships between (a) global cytosine methylation and mean values of the phenotype, (b) global cytosine methylation and variance values of the phenotype and (c) lobal cytosine methylation and CV values of the phenotype.

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