Zomer MA, Moreira B, Pausas JG. 2025. Pre-disturbance plant condition drives intraspecific resprouting variability in Mediterranean shrubs. *J. Exp. Bot*, https://doi.org/10.1093/jxb/eraf246

Original Research Paper

Pre-disturbance plant condition drives intraspecific resprouting variability in Mediterranean shrubs

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Running title: Intraspecific resprouting variability

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Highlight

Shrub resprouting depends on pre-disturbance condition, with aridity, soil fertility and fire history as secondary drivers. Repeated disturbance reduces resprouting, and adult plants are more resilient under low water conditions.

Abstract

Many Mediterranean plants persist after disturbances by resprouting from dormant buds, and understanding factors driving variability in resprouting is crucial for predicting regeneration under global change. We hypothesized resprouting is influenced more by long-term environmental factors (e.g., historical aridity, fire history, soil nutrients) that shape pre-disturbance plant condition than by immediate water availability or local adaptations. We applied an experimental disturbance of two consecutive cuts in a short interval (1) in the field, targeting adult *Anthyllis cytisoides* and *Globularia alypum* plants along an environmental gradient (in Spain), and (2) in a common garden, using *A. cytisoides* grown from seeds of contrasting aridity provenance and subjected to contrasted water treatments. Intraspecific variability in resprouting predominantly occurred within populations, and was primarily determined by pre-disturbance plant size, underscoring the importance of individual history. Secondarily, aridity had a positive effect on resprouting, while higher fire frequency and the second cut had negative effects. We found no evidence of local adaptations, but young plants in the garden were dependent on water availability. Adult plants may be resilient to disturbance under low water availability but sensitive to increased disturbance frequency, while young plants may be vulnerable in a drier world, emphasizing ontogenetic differences in resprouting vulnerabilities.

Keywords: disturbance, climate, resprouting, intraspecific variability, Mediterranean, shrubs

Introduction

Plant species in Mediterranean shrublands have an array of adaptive traits to persist with recurrent disturbances, such as fires and drought (Keeley *et al.*, 2012). One of the most widespread of these traits is basal resprouting, in which plants generate new shoots from a belowground bud bank that can be stored in the roots or root crown, non-woody swellings or woody structures such as lignotubers (Bond and Midgley, 2001; Clarke *et al.*, 2013; Pausas *et al.*, 2016). Belowground bud banks are well insulated from fire heat by the soil and allow vigorous resprouting after fire (Pausas *et al.*, 2016). Resprouting allows plant survival but carries a cost of storing carbohydrates and producing and maintaining a fire-resistant bud bank (Chapin *et al.*, 1990). This early allocation of resources to below-ground limits plant growth but results in deep root systems that can access more stable water reserves (Pausas *et al.*, 2016). Thus, resprouters tend to dominate the parts of the landscape with more reliable water, such as gullies and north facing slopes (Pausas and Keeley, 2014). Consecutive severe disturbances (droughts, fires, heat waves) are becoming common (Kane *et al.*, 2017; Nolan *et al.*, 2021), raising concerns about the possibility of reaching resprouting exhaustion (Nolan *et al.*, 2021). Although resprouting is often regarded as a binary trait at the species level, intraspecific variability exists and remains understudied (Vesk and Westoby, 2004; Moreira *et al.*, 2012; Pausas *et al.*, 2016). Thus, understanding the drivers of this variability is essential to predict future regeneration of Mediterranean ecosystems.

Water availability is expected to be an important limitation for resprouting (Nolan *et al.*, 2021), but current evidence is conflicting. On one hand, resprouting plants may be particularly vulnerable to water stress during the post-disturbance period due to reduced cavitation resistance (Jacobsen *et al.*, 2016). Once resprouting has been initiated, plants must grow new shoots quickly to re-establish their photosynthetic tissues to grow and compete for resources. As a consequence of this fast growth, xylem density and resistance to cavitation of the resprouting shoots is reduced (Jacobsen *et al.*, 2016). On the other hand, because disturbed plants mostly maintain their root system, resprouting plants benefit from increased root-to-shoot ratios and enhanced hydraulic conductance (Schafer *et al.*, 2014). In fact, previous drought experiments have had inconclusive results regarding the effects of water availability on resprouting. For instance, some studies found that when oak seedlings are subject to water stress closely before or after disturbance, the proportion of resprouting individuals, but not resprout growth, markedly increased with water availability (Dios *et al.*, 2020), whereas others reported no effect of water limitations on oak resprouting (Díaz-Guerra *et al.*, 2019). Similarly, field studies show contrasting results. In California chaparral, severe drought following fire led to a decline in resprouting species populations, due to their high levels of cavitation and embolism (Pratt *et al.*, 2014). Conversely, in South African and Mediterranean basin shrublands, resprouting populations were relatively insensitive to summer rainfall and drought (Parra and Moreno, 2018; Blerk *et al.*, 2021). As such, the importance of water availability during resprouting remains unclear.

The above discrepancies may arise because resprouting is complex and not solely determined by extrinsic factors (e.g., resources, climate). A plant can only resprout after its aboveground biomass has been removed if it retains a reserve of dormant buds that can generate new growth (Vesk and Westoby, 2004). Additionally, it must rely on stored non-structural carbohydrates (NSC) and nutrients in its belowground organs to support respiration and initiate the resprouting process (Pate *et al.*, 1990; Canadell and López-Soria, 1998; Kabeya and Sakai, 2005; Paula and Ojeda, 2009). However, the history and development of individual plants is often overlooked in field studies. In Mediterranean shrubland species, intraspecific variability in resprouting is largely determined by the pre-disturbance state of the plant, including plant size and stored resources (Moreira *et al.*, 2012). Larger plants typically have larger roots systems and thus, greater reserves and higher capacity to mobilize resources after disturbance (Moreira *et al.*, 2012).

There are many spatially variable abiotic factors that may influence plant growth and allocation of resources in different ways (Clarke *et al.* 2013). For example, plant growth rates may be lower in sites with a shortage of nutrients and water, but allocation to belowground storage (root starch content, root-to-shoot ratios, fine root biomass) is often higher (Poorter *et al.*, 2012; Magaña-Hernández *et al.*, 2020). Long-lived resprouting shrubs also experience a large amount of environmental variability in their lifetime (Matesanz and Valladares, 2014) and may be shaped by the accumulation of ecological legacy (or memory) effects (Ogle *et al.*, 2015; Zweifel *et al.*, 2020). Indeed, species with long organ lifespans are often strongly connected to historical conditions, thereby buffering their responses to present conditions; the stronger these legacy effects, the less predictive current conditions become for a physiological response (Jump *et al.*, 2017; Zweifel and Sterck, 2018). Intraspecific variation of plant traits across geographic and climate gradients may also signify plasticity or local adaptation of populations to their parental environment (Westerband *et al.*, 2021). However, resprouting species have long generation times and slow population turnover compared to co-existing obligate post-fire seeders and consequently may have slower rates of natural selection (Pausas and Keeley, 2014). Thus, legacy effects on plant condition from historical climate and previous disturbances are likely key in resprouting species; to what extent these legacy effects are more important than immediate water availability during resprouting or local adaptations remains to be studied.

This study aims to understand the determinants of intraspecific variability in resprouting response. We hypothesize that this variability is primarily influenced by long-term environmental factors, such as historical aridity, fire history, and soil nutrients, that shape pre-disturbance plant size and belowground resource allocation. Given the accumulation of challenges endured by Mediterranean resprouting plants throughout their long lifespan, we predict that these long-term effects are more significant than immediate pre- or post-disturbance water availability, despite water being a limiting factor in Mediterranean ecosystems. We also explored whether resprouting variability is determined by the local adaptation of plant populations to their specific environmental conditions. To test our hypotheses, we conducted two experiments in which we applied a severe disturbance: 1) to adult plants in the wild along an environmental gradient on the eastern coast of Spain, with contrasting aridity, fire histories, soil nutrients, and precipitation; and 2) to plants in a common garden experiment grown from seeds collected from populations at opposite ends of the aridity spectrum (High *vs.* Low) and subjected to contrasting water treatments (Drought *vs.* Watered). The severe disturbance involved two consecutive experimental cuts, removing all aboveground biomass in a short interval, and pushing the plants to their physiological limits to better capture resprouting variability. In fact, compound disturbances are becoming common in Mediterranean ecosystems due to events like consecutive severe droughts and/or fires (Batllori *et al.*, 2019).

Materials and Methods

Species

Our study species are *Anthyllis cytisoides* L. (Fabaceae) and *Globularia alypum* L. (Globulariaceae), two shrub species common in eastern Spain and with a wide distribution in the western Mediterranean Basin (from southern France to northern Africa; Bolòs and Vigo, 1984; 1995). *Anthyllis cytioides* is summer deciduous, losing all leaves during prolonged summer droughts (Haase et *al*., 2000), while *G*. *alypum* is evergreen, with sclerophyllous leaves (Estiarte *et al.*, 2011). These species are shade intolerant, grow in shrublands with typically Mediterranean climate, with high interannual rainfall and temperature variability, and summer droughts (Keeley *et al.*, 2012). They are facultative resprouters, ie. after fire they can regenerate both by resprouting (from the root crown) and by seedling establishment (Moreira *et al.*, 2012). Facultative resprouters constitute a large proportion of the Mediterranean Basin biodiversity hotspot and their ecology is understudied. In addition, there is known to be wider intraspecific variability in resprouting ability (i.e., lower resprouting success and vigour) within facultative than within obligate resprouting species (Maitre *et al.*, 1992; Pratt *et al.*, 2014). For the field study, we used *Anthyllis cytisoides* and *Globularia alypum* as model species, while *A. cytisoides* was used in the common garden experiment.

Field experiment

Aridity gradient

We selected 13 sites, where one or both study species were abundant, along the eastern coast of Spain, spanning a climate gradient with contrasting aridity (Fig. 1; Supplementary Table S1). All sites were mature shrublands free of fire disturbance for at least 5 years. Sites were selected across 150-650 m a.s.l. with comparable slope and habitat ‘openness’ (shrublands with minimal tree cover and avoiding shady microsites), although the nature of the climate gradient inevitably resulted in lower vegetation density and higher amounts of bare ground in more arid sites (Supplementary Fig. S1 – S2). Thus, plants in wet sites were more likely competing for light while plants in dry sites were more likely driven by competition for water (Gross *et al.*, 2013). *Globularia alypum* was present along the whole latitudinal gradient studied (10 sites along ca. 400 km), while populations that fit the requirements for the cutting experiment (i.e., numerous plants in homogeneous conditions and accessible terrain) of *A. cytisoides* was only found in the southern half (6 sites along ca. 200 km) of the gradient (Fig. 1). As the two species co-occur in some locations, the 16 populations considered were distributed in 13 sites along the aridity gradient. In fact, the wider environmental range of suitable *G. alypum* populations was a reason for adding this species to the field sampling.

For each site, we obtained accumulated precipitation (mm) data for the 5 months post-cutting (August – December) in 2018 and 2020, from a daily gridded ensemble observation dataset for Europe with 0.1-degree resolution (Cornes *et al.*, 2018). Historical aridity index values for each site were obtained from the Global Aridity Index v3 for the years 1970 - 2000 with 30 arc second spatial resolution (Zomer *et al.*, 2022). This aridity index represents the ratio between mean annual precipitation and mean annual potential evapotranspiration, with lower values indicative of more arid conditions. We termed 1- aridity index as our aridity index, so higher values indicate higher aridity.

Fire history

An estimation of the recent fire history was determined from historical fire records obtained from local governments (Generalitat Valenciana and Generalitat de Catalunya). Records were available from 1976 – 2014 for the province of Valencia, 1993 – 2014 for the provinces of Castellon and Alicante, and 1987 – 2017 for the provinces of Tarragona and Barcelona. From these records, we determined years since last fire in each study site. The study region typically has intense crown fires concentrated within the summer months, with fire intervals in the order of decades, thus the fire data available (20 - 40 years) was considered too short to correctly determine fire frequency for our sites. Considering some spatial extent is a way to minimize the problem of the short temporal extent in the fire data (Guiote and Pausas, 2022). Thus, we estimated annual fire activity for each site by considering the cumulative area burned within a 10 km radius buffer circle surrounding each sampled site. We then calculated the average area burned annually to account for the differences in the number of years with fire records between provinces. To account for sites with buffer circles that overlapped with the sea, we converted these values to the percentage of buffer area (hectares on land) burned annually (hereafter, fire activity). Bioclimatic variables were extracted for sites, and site buffer zones intersected with fire maps using ArcGIS Pro 2.8 (Esri Inc. 2021).

Soil nutrient content

In August 2018, a composite soil sample was collected from each of the 13 sites, transported to the laboratory, dried for 24 hours at 105 °C, and sieved to 2 mm. Total carbon and total nitrogen of the soil samples were determined by dry combustion with the LECO CNS928 elemental analyser

(LECCO Corporation) in the CIDE-CSIC Department of Environmental Quality and Soils. Inorganic carbon was measured using the Bernard calcimeter method (MAPA, 1994). Organic carbon was calculated by difference as the difference between total and inorganic carbon. All results were expressed as percentages of dry material. Note that some nitrogen values were between the limit of detection (0.014) and the limit of quantification (0.5). Nitrogen content in one site was below the level of detection (0.014) and was assigned a truncated value of 0.005% for statistical analyses.

Field Sampling

The cutting-resprouting experiment consisted of two consecutive cuts with two years between them (first cut in 2018 and second cut in 2020). Cutting was performed during the summer, when physiological activity is low, and plants are mostly likely to lose aerial biomass due to both drought and fire. In August 2018, 25 plants per population were chosen (tagged and georeferenced); they were spaced at least 1 meter apart from each other. Selected plants had no visible signs of recent disturbance (no burned or broken main stems), and plant size was not correlated with years since last burn (all free of fire disturbance for at least 5 years). But certainly, some plants may have been disturbed and resprouted in the past (the lifespan of these resprouting species is unknown).

Before cutting (pre-disturbance data), plant height, crown length and width, number of stems at base (as an indicator of the bud bank size; Malanson and Trabaud, 1988), and diameter of largest stem were measured for each individual. Plants were then cut at the base of the stem so that all aboveground biomass was removed (Supplementary Fig. S3-S4). Cut biomass was weighed onsite using a hanging scale and transformed to dry mass using the fresh-dry mass relation from plants growing under experimental water treatments (see Supplementary Table S2 for details). The surrounding above-ground biomass in a 50 cm radius circle of each target plant was also removed to avoid differential competition for light by neighbouring vegetation (Zhu *et al.*, 2012). There were no visible signs of herbivory by vertebrates in the sites.

We monitored resprouting success and vigour two years after the cut (i.e., August 2020). In a few cases, plants were missed when assessing success but were located in a following visit. These plants were only cut once; thus, were excluded from the remaining analysis (Supplementary Table S3). Some plants could not be found at all, probably due to detached tags (6.6% *A. cytisoides* and 4.8% *G.*

alypum; Supplementary Table S3) and thus were excluded from all analysis. There was no significant association between the number of missing plants and aridity for either species, although, in the case of *A. cytisoides,* the wettest site had the highest number of plants not found (n = 7, 28%). For each plant that resprouted, we measured resprouting height, crown length and width, number of resprouting stems at base, and diameter of largest resprouting stem. Resprouts were then re-cut at the base (second cut), and the aerial biomass was transported to the lab in paper bags, oven dried for 48 hours at 60 °C and weighed for dry biomass. We recorded resprouting success (yes/no) after this second cut (i.e., resprouting success of plants that had resprouted after the first cut and were re-cut two years later) in June 2024. Again, some additional plants (7.9% *A. cytisoides* and 11.3% of *G. alypum*; Supplementary Table S3) were not retrieved and were thus excluded from further analysis.

In June 2022, we selected two populations of each species; one at the arid extreme and one at the wetter extreme of the gradient (sites 1 and 6 for *A. cytisoides;* and sites 1 and 10 for *G. alypum* in Supplementary Table S1). In each population, we extracted a lateral root sample (~ 1 cm in diameter) from 8 undisturbed plants. Root samples were immediately stored in a sealed plastic bag with silica gel and transported in a cooler with freezing packs (5°C) to the laboratory. Root samples were oven-dried at 80°C for 24 hours to stop root respiration. Samples were stored in the freezer at -18°C in hermetic bags with silica gel until analysed (Moreira *et al.*, 2012). Starch was determined by an enzymatic procedure and measured colorimetrically using a coupled glucose oxidase/peroxidase reaction and spectrometric analysis (Agrolab Analítica, SL; Rasmussen and Henry, 1990). Total soluble sugars (SS; sucrose, fructose, and glucose) were measured through colorimetric reaction and spectrometric analysis (Green et al. 1989). Starch and SS concentrations were expressed as g 100 g^{-1} dry material. Starch concentrations below the level of detection (0.10) were given a truncated value of 0.10 for the statistical analyses.

Common garden experiment

Common garden experiments, in which offspring from different populations are grown under the same environmental conditions, allow us to disentangle the role of local adaptation from plasticity and ecological processes (de Villemereuil *et al.*, 2022). The common garden experiment consisted of plants grown from seeds collected from populations with two distinct climates (High and Low aridity), with half of the plants given a Drought treatment, and the other half a Watered treatment. Seeds were collected in June and July 2018 from populations of *A. cytisoides* representing the extremes of a climate gradient along the eastern coast of Spain (ca. 300 km) (Fig. 1). Two populations were from the high arid extreme and two populations from the low aridity extreme (Supplementary Table S4). Some of these populations differ from the field experiment, because while cutting required sites with numerous plants and flat terrain, seed collection required availability of seeds and was possible in a wider range of conditions; we thus chose to maximise differences in aridity. Fruits were stored in paper bags in a chamber in darkness and controlled temperature at 20°C until the experiment began. In September 2019, seeds were removed from fruits with an electric sander. *Anthyllis cytisoides* seeds have physical dormancy; thus, to break seed dormancy and maximise the percentage of germination, seeds were pre-treated with 15 min immersion in sulfuric acid, soaked in distilled water at 4°C for 17 h, and then immediately sown directly into pots with substrate. Pots were made of PVC pipes (16 cm diameter x 60 cm height) and arranged randomly in three pallet tables, in a large, netted tunnel in the infrastructures of the Centro para la Investigación y Experimentación Forestal (CIEF), in Manises, Valencia (Spain) (Supplementary Fig. S5). Each table had two automatic drip irrigation watering systems (Netfim Inc), for contrasting water treatments (Supplementary Fig. S5). Pots contained as substrate 500 ml of arlite at the bottom for drainage; a mixed substrate composed of 50% peat, 20% sand, 20% perlite, and 10% sandy soil collected from the field; and 30 g of NPK slow releasing fertilizer (Planta Plus). Pots were watered to field capacity for the first month to optimize conditions for germination. From the beginning of the second month, two watering treatments were applied, i.e., Drought and Watered. During the autumn, winter, and spring months watering was 200 ml and 400 ml weekly, in the Drought and Watered treatment respectively, plus the local rainfall (Supplementary Table S5). During the summer months, water was increased to 300 ml and 600 ml weekly, respectively, to maintain the plants alive, given the increased evapotranspiration in the summer (Supplementary Table S5). Although the quantity of water varied seasonally, the Watered treatment was always double that of the Drought treatment.

After one year of plant growth, the Drought treatment contained 15 plants from High and 15 plants from Low aridity sites, while the Watered treatment had 14 plants from High and 13 plants from Low aridity sites (Supplementary Table S4). In August 2020, measurements of plant height, crown length and width, number of stems at base, and diameter of largest stem were taken for each individual. Plants were then cut at the base of the stem (Supplementary Fig. S6), removing all aboveground biomass, weighed with a hanging scale onsite (fresh mass), and oven dried for 48 hours at 60°C, and weighed again (dry mass). At the end of July 2021, the same measurements and cutting were repeated for plants that successfully resprouted (Supplementary Fig. S6). Resprouting occurred very quickly (within days of cutting), thus resprout success (yes/no) after the second cut was monitored in September 2021 and rechecked in January 2022.

Statistical analysis

Our data were split into three distinct resprouting stages: (1) resprouting success after first cut, represented by the binary variable of resprout success (yes/no); (2) resprout vigour after first cut, represented by plant above-ground biomass (dry mass) of plants that resprouted after disturbance (2 years after, in the field study; 1 year after, in the common garden experiment); and (3) resprouting success after second cut (yes/no). In the field, we measured resprouting response after two years to capture more variability in resprouting vigour, but in the common garden we measured after only 1 year as to avoid the plants outgrowing their pot size. We don't expect the difference to affect the patterns observed, as the majority of resprouting mortality typically occurs in the first year after disturbance (Pratt *et al.*, 2014). Statistical analyses were performed using R software version 4.4.1 (2024).

Variation Components

We used linear mixed-effects models to partition variance in pre-disturbance biomass and resprouting response across three nested hierarchical levels, using the varcomp function from the R package ape (Paradis and Schliep, 2019). For field data from *A. cytisoides* and *G. alypum* along the aridity gradient, variance was decomposed into components attributable to differences between species, among populations within species, and among individuals within populations. For the common garden data of *A. cytisoides*, variance was partitioned into components attributable to differences between water treatments, between seed provenances within treatments, and among individuals within provenances and treatments.

Structural Equation Modelling (SEM)

SEM unites multiple variables in a single causal network. Because variables can be both predictors and responses, SEM can quantify both direct and indirect (cascading) effects. We used the R package piecewiseSEM version 2.1.0 (Lefcheck, 2016), which combines multiple linear mixed models (LMM), or general linear mixed models (GLMM) constructed from the package lme4 (Bates *et al.*, 2015).

For field data, we constructed two multigroup SEM models (SEM 1 and SEM 2) based on our hypothesis (Supplementary Fig. S7a), in which we assumed long-term environmental variables (aridity, fire history, soil nitrogen), and immediate post-cutting rainfall had effects directly or indirectly on resprouting response (resprouting success and resprouting vigour) *via* pre-disturbance plant condition. From preliminary linear analyses, we determined that pre-disturbance biomass was the most influential plant condition variable for resprouting response. Soil nitrogen and soil organic carbon were positively correlated; thus, to avoid collinearity, we included only soil nitrogen in the model as the more directly relevant variable for plant growth. SEM 1 consisted of two model components, an LMM with response variable pre-disturbance biomass (log transformed, scaled and centred), and a binomial GLMM with a "bobyqa" optimizer and response variable of resprouting success after first cut. SEM 2 analysed only the plants that successfully resprouted, and consisted of three model components, an LMM with response variable pre-disturbance size (log-transformed, scaled and centred), an LMM with response variable resprouting vigour (log-transformed, scaled and centred), and a binomial GLMM with a "bobyqa" optimizer and response variable resprouting success after second cut. Site was included as a random effect in all models and all environmental explanatory variables were centred and scaled. We used the ‘multigroup’ function for both SEM, implementing a model-wide interaction where each term in the model interacts with the grouping variable (species). If the interaction is significant, the path is free to vary by group, otherwise, the path takes on the estimate from the global dataset (then the model is termed “constrained”).

For common garden data of *A. cytisoides*, we again constructed two SEM models based on our hypothesis (Supplementary Fig. S7b), in which we assumed water availability and climate at seed provenance had effects directly or indirectly on resprouting response (resprouting vigour and resprouting success) via pre-disturbance plant condition. Again, pre-disturbance biomass was the most influential plant condition variable (preliminary linear analyses). SEM 1 consisted of two model components, an LMM with response variables pre-disturbance biomass, and a binomial GLMM with response variable resprouting success after the first cut. SEM 2 analysed only the plants that successfully resprouted, and consisted of three model components, an LMM with response variables pre-disturbance biomass, an LMM with response variable resprouting vigour, and a binomial GLMM with response variable resprouting success after the second cut. Site was included as a random effect in all models. Fixed effects of water availability and climate at seed provenance were categorical variables, thus, piecewise SEM uses a two-step procedure of ANOVA (for the categorical variable) and the calculation of marginal means (for each level of the categorical variable). Marginal mean is the expected average value of one predictor given the other co-variables in the model.

All SEM were assessed by a test of directed separation to determine if there were any missing pathways between variables, a Fisher's C test to determine goodness-of-fit ($p > 0.05$ indicates that the data supports the model structure), Akaike's information criteria (AIC) and Bayesian information criterion (BIC) (Lefcheck, 2019). Temporally implausible direct pathways (e.g., from pre-disturbance biomass to resprout success after cut 2) were suppressed. Additionally, non-significant pathways were eliminated sequentially in order of their contribution to the explained variance (smallest standardized estimates) of each component of the SEM to improve overall model fit. Normality of model residuals were tested with DHARMa (Hartig *et al.*, 2017).

Regression models

Root NSC concentration (starch and SS) data for plants from field aridity extremes were analysed using linear models. Most root starch measurements for *G. alpyum* were below the level of detection and we were unable to construct a model that fit the data (Supplementary Table S6). Thus, we first constructed a model for *A. cytisoides* with starch as the response variable, and aridity as a fixed effect. A second model for both species had SS as the response variable, and aridity and species were fixed effects. We used the 'anova' function for a Type III analysis of variance with Satterthwaite's method.

To evaluate the effect of repeated disturbances on resprouting success (i.e., survival) in the two species, we fitted binomial GLMMs using combined survival outcomes from both disturbance events (Cut 1 and Cut 2). In the field data model, fixed effects included: disturbance number (Cut 1 or 2), species (*G. alypum*, *A. cytisoides*), and pre-disturbance plant biomass (log-transformed; either initial biomass before Cut 1 or resprouting vigour before Cut 2), and their interactions. For the common garden data model, fixed effects comprised disturbance number (Cut 1 or 2), pre-disturbance plant biomass, water treatment (Drought / Watered), and seed provenance climate (High / Low aridity), along with their interactions. In both models, plant identity nested within site was included as a random effect, and the field data model used a “bobyqa" optimizer.

Results

Field experiment

Resprouting success of wild populations ranged from 48% to 100% (mean = 88%) after the first cut, and from 68% to 100% (mean = 90%) after the second cut (Supplementary Table S3). Overall, the survival after two cuts ranged from 36% to 100% (mean = 77%). Most of the variation across nested levels occurred between individuals within populations of the same species, for the four variables considered (see proportions in Table 1). Total variance in biomass was reduced after disturbance in all three hierarchical levels (compare pre-biomass vs resprouting vigour; Table 1).

The SEM showed both direct and indirect effects of environmental factors on plant resprouting outcomes (Table 2; Fig 2). In both SEM, pre-disturbance biomass was positively correlated with soil nitrogen and aridity, and negatively with fire history ($R^2 = 0.68$ for SEM 1; $R^2 = 0.49$ for SEM 2; Table 2a,b). In SEM 1, pre-disturbance biomass explained little variation in resprouting success after the first cut ($R^2 = 0.10$; Table 2a) and the pathway was not statistically significant ($p=0.829$), likely contributing to the marginal model misfit indicated by the Fisher’s C test ($P = 0.042$). We retained the SEM 1 model structure to ensure continuity across models, and because the same structure showed strong fit and meaningful relationships in subsequent models. SEM 2 showed that pre-disturbance biomass significantly increased resprouting vigour in both species, and that aridity had an additional direct positive effect in *G. alypum*, together explaining substantial variation in resprouting vigour ($R^2 = 0.52$; Table 2b). In turn, resprouting vigour had a significant direct positive effect on resprouting success after the second cut, although the proportion of variance explained was low ($R^2 =0.12$; Table 2b). Consequently, a cascading indirect effect was observed, where higher aridity, lower fire activity, and increased soil nitrogen each enhanced resprouting responses through their impact on pre-disturbance plant biomass (Fig. 2). These results were consistent using either the corrected pre-disturbance dry biomass or the original pre-disturbance fresh biomass values (Supplementary Table S7). The interactions between environmental variables were not significant. Rainfall immediately post-cutting had no significant effects on resprouting outcomes.

Linear models of root starch concentrations for *A. cytisoides* showed no differences between aridity (Low *vs* High; Supplementary Table S8). In contrast, plants from High aridity populations had higher root total SS concentrations than plants from Low aridity populations for both species (Fig. 3; Supplementary Table S8).

The binomial GLMM of survival outcomes showed a general decline in resprouting success from the first to the second cut (Fig. 4; Supplementary Table S9). In that same analysis, greater plant biomass prior to the second cut (i.e., resprouting vigour after the first cut) significantly increased survival probability following the second disturbance, consistent with the SEM results. *G. alypum* showed a smaller reduction in survival following repeated disturbances than *A. cytisoides*.

Common garden

Resprouting success for each seed provenance and water treatment combination ranged from 80% to 100% (mean = 89%) after the first cut, and from 50% to 93% (mean = 68%) after the second cut (Supplementary Table S10). The survival after the two cuts ranged from 40% to 79% (mean = 62%). The majority of variance in pre-disturbance biomass and resprouting vigour occurred between water-treatments (59% and 83% respectively; Supplementary Table S11). Variance of success after first and second cut were almost entirely between individuals (99.6% and 86% respectively).

The SEM showed direct and indirect effects of water availability on resprouting outcomes (Table 3; Fig. 5). Plants in the Watered treatment accumulated more pre-disturbance biomass ($R^2 = 0.41$ for SEM 1; $R^2 = 0.47$ for SEM 2; Table 3a,b). In SEM 1, this increased pre-disturbance biomass strongly promoted resprouting success after the first cut ($R^2 = 0.54$, Table 3a). In SEM 2, pre-disturbance biomass showed a positive but marginal effect on resprouting vigour ($p = 0.06$), while water availability directly increased vigour, together accounting for most of its variation ($R^2 = 0.73$, Table 3b). Thus, higher water availability increased vigour both indirectly (via pre-disturbance biomass) and directly. After the second cut, resprouting success was higher under the Watered treatment ($R^2 = 0.12$, Table 3b), while no other pathways (including the impact of vigour on success) were significant. Finally, climate at seed provenance had no significant effects on either pre-disturbance biomass or resprouting outcomes.

The binomial GLMM of survival outcomes indicated that resprouting success increased with pre-disturbance biomass, with no significant difference between the first and second cuts (Supplementary Table S9; Supplementary Fig. S8).

Discussion

Our current understanding of the drivers of resprouting is limited and may lead to uncertainties when considering the resilience of resprouting species to global change. Our study indicates that most intraspecific variation in resprouting response (in field conditions) occurred within, rather than among populations across the environmental gradient (Table 1), suggesting a limited role of climate on resprouting variability. In agreement, the SEM showed that the condition of the plant prior to disturbance was a key determinant of resprouting capacity in the field. Specifically, pre-disturbance biomass had a strong positive effect on resprouting vigour, which in turn significantly influenced the probability of resprouting success following a second disturbance (Table 2; Fig. 2). These results align with previous studies that document the importance of pre-disturbance plant size, which likely reflects a larger and more developed root system capable of mobilizing resources rapidly after a disturbance, leading to more vigorous resprouting (Moreira *et al.*, 2012; Nolan et *al.*, 2021). Resprouting vigour determines the plant capacity to photosynthesize after disturbance, which is important for post-resprouting survival, growth and NSC storage, in preparation to survive the next disturbance (Moreira *et al.*, 2012). Variation between individuals may be attributed to intrinsic factors of the plants, such as, plant age, historical disturbances, or microsite variability, that are not easily detectable. Our results also highlight that resprouting is not necessarily a binary trait at the species level (as often considered), at least in Mediterranean resprouters that can recruit postfire from a seed bank (postfire facultative resprouters). This pattern is also consistent with findings from other disturbance contexts: in California chaparral shrublands, larger resprouting plants had lower mortality during severe drought (Venturas *et al.*, 2016), demonstrating the broader importance of plant condition for disturbance resilience.

While most variation occurred at the individual level, the SEM indicated that among-population variability, though relatively small, also contributed to resprouting outcomes. There was a cascading indirect effect in which higher aridity, increased soil nitrogen, and lower fire activity all enhanced population-level resprouting vigour and subsequent success following the second disturbance via pre-disturbance plant size (Table 2; Fig. 2). There was also a species-specific direct effect, whereby aridity increased resprouting vigour for *G. alpyum* (Fig. 2). In contrast, immediate rainfall conditions did not significantly influence resprouting outcomes. These results support our hypothesis that resprouting is shaped by complex interactions with environmental variables, mediated by pre-disturbance plant condition, underscoring the influence of long-term environmental legacies over short-term weather variability.

Differences in NSC concentrations across the aridity gradient may reflect physiological adjustments that help sustain plant condition and support resprouting vigour under resource-limited conditions. We found that root SS (ie., glucose, fructose, and sucrose), but not starch, concentrations were significantly higher in plants from the more arid regions of our gradient (Fig. 3; Supplementary Table S8). This is consistent with the concept of functional equilibrium; that is, plants allocate more biomass to their root systems when growth-limiting factors such as nutrients or water are predominantly belowground (Poorter *et al.*, 2012). Thus, in arid regions, plants often allocate to roots and NSC reserves that can buffer water stress, at least to some extent (Qi *et al.*, 2019; Tumber-Dávila *et al.*, 2022). This is supported by studies that found resprouting plants had higher concentrations of root NSC on arid ridges compared to humid gullies (Mexican ecosystems; Magaña-Hernández *et al.*, 2020), and enhanced root length and density with a 30% reduction in annual rainfall (Mediterranean semi-arid shrubland species; Padilla *et al.*, 2015). However, opposite trends have also been observed, with decreased root NSC pool size and reduced resprouting vigour in lower-productivity, higher-altitude sites on the eastern Qinghai-Tibet Plateau (Zhu et al., 2012).

Our June sampling of root NSC coincided with the midsummer period when SS typically peak (Martínez-Vilalta *et al.*, 2016). SS support a variety of functions, including growth, but are also involved in turgor maintenance, phloem transport and xylem repair (Martínez-Vilalta *et al.*, 2016). Starch is a storage compound for future use (e.g., resprouting), and under drought stress is converted to SS to maintain metabolic functions (Guo *et al.*, 2021). The mostly undetectable root starch levels for *G. alpyum* were unexpected, but as an evergreen species, it may maintain higher SS levels to support continuous physiological processes (in contrast to drought deciduous species such as *A. cytisoides*) and increase starch reserves later in the summer (Palacio *et al.*, 2007). Elevated SS levels suggest that plants in arid regions are effectively mobilizing their NSC reserves under stressful conditions. Indeed, it could be possible that the remobilisation of NSC contributes to the maintenance of plant biomass and to resprouting vigour in higher aridity sites. This contrasts with studies of the Mediterranean shrub *Erica australis* that resprouted better in sites with higher water availability (Cruz *et al.*, 2002; 2003) but is consistent with the physiological response observed in *Erica arborea*, where an increase in relative growth rate during water stress was likely driven by the remobilization of starch (Ramírez *et al.*, 2012). Note that our study focused on spatial variability in aridity rather than acute drought events that vary through time. It is possible that plants from more humid environments, that invest less resources belowground, may be more vulnerable to mortality in acute drought events than those in arid sites (Magaña-Hernández *et al.*, 2020).

Aridity, soil nutrients, and fire interact in complex ways to shape plant growth, physiology, and resprouting responses across environmental gradients. Soil nitrogen is the most limiting factor, after water, for plant growth in drylands (Robertson and Groffman, 2007), and indeed we found a positive impact of soil nitrogen on pre-disturbance plant size (Fig. 2). Furthermore, in regions with high aridity, despite frequent occurrences of flammable conditions, the actual extent of burned areas tends to be limited due to the reduced fuel loads and continuity (fuel-driven fire regime; (Pausas and Paula, 2012). In our study, we observed a trend toward lower fire activity and a longer time since the last fire in the most arid sites (Supplementary Table S1), but this relationship was not statistically significant across the entire aridity gradient. As part of the SEM, reduced fire activity enabled greater accumulation of aboveground biomass (Fig. 2), probably due to the likelihood of longer intervals between disturbances. To add to this, we found a negative effect of consecutive disturbances on the resprouting success (i.e., survival) in the field (Supplementary Table S9; Fig 4). These findings support existing evidence that short intervals between disturbances reduce a plant's resprouting capacity (Canadell and López-Soria, 1998; Paula and Ojeda, 2006; 2009; Enright *et al.*, 2011). Resprouting exhaustion may occur due to depleted NSC reserves (insufficient time to build up reserves between disturbances) (Canadell and López-Soria, 1998; Enright *et al.*, 2011; Paula and Ojeda, 2011) or depleted bud bank reserves (Bell and Pate, 1996). While we experimentally simulated a very short disturbance interval, large fires in Mediterranean ecosystems are becoming more frequent (Pausas and Millán, 2019), as are compound disturbances like consecutive fires and droughts (Kane *et al.*, 2017; Nolan *et al.*, 2021), making this a critical concern. In our study, we did not find significant interactions between these factors; however, aridity, soil nitrogen availability, and fire activity are often interconnected, with their dynamics expected to shift considerably in the future. Increased aridity is expected to reduce total nitrogen availability in soils (lower plant cover and thus reduced litter decomposition and N fixation) which could impair plant nutrient uptake and decrease net primary production (Delgado-Baquerizo *et al.*, 2013). Low soil fertility has been positively correlated with increased fire activity, as nutrient-poor soils tend to promote vegetation flammability (Paula *et al.*, 2024). However, this effect may be less relevant in high-aridity, fuel-limited sites.

To disentangle the role of local adaptation from environmental legacies, we tested resprouting responses under controlled conditions in a common garden experiment. We found no significant effects of climate at seed provenance on pre-disturbance plant size, resprouting success, or resprouting vigour (Table 3), suggesting local adaptation does not determine resprouting response. Thus, the observed (albeit small) variability in resprouting success among field populations may instead reflect the cumulative legacy effects of long-term ecological processes, and possibly phenotypic plasticity (de Villemereuil *et al.*, 2022). In the common garden, there was also a relatively high degree of among individual variability (Supplementary Table S11), and the importance of pre-disturbance plant condition for resprouting response was maintained (Table 3; Fig. 5). However, in contrast to the field experiment, resprouting response in the common garden was highly dependent on immediate water availability (Table 3; Fig. 5). This likely reflects ontogenetic differences, as these plants lacked the extensive root systems of older field plants, making them more sensitive to water variation. In fact, ontogenetic differences in drought resistance are an important source of intraspecific variability within populations (Tautenhahn *et al.*, 2019; Barton, 2024). Notably, if young plants are more vulnerable, facultative resprouters could become functionally obligate resprouters in a drier world with more disturbances. This is especially relevant given our species are not always strong resprouters, and thus such a shift could result in pronounced demographic consequences.

Conclusion

Intraspecific variability of resprouting response was highest among individuals and pre-disturbance plant condition was the most important determinant of resprouting response. This underscores the importance of individual plant history, including age, historical small-scale disturbances (herbivory, insects, and drought), small-scale variability in soil conditions, and ontogenetic differences in drought resistance. At the broader, among-population level, legacy effects from long-term environmental variables that influence the characteristics of plants' belowground system, such as aridity, soil nitrogen content, and historical fire frequency, have an indirect and secondary role in the ability for plants to resprout. Additionally, our results demonstrate that consecutive disturbances in a short interval, such as increased fire frequency or possibly compound disturbances of fire and drought, will have negative impacts on resprouting response. Finally, the growth and resprouting response of young plants was strongly related to the amount of water, likely due to their lack of a well-developed belowground system. This suggests that for facultative resprouters, a key component of Mediterranean biodiversity, adult plants are more resilient to disturbance under low levels of water availability than younger individuals, which may increase the demographic importance of resprouting in a drier world with more frequent disturbances.

Acknowledgements

We thank CIDE field technician Guillermo Benítez López for his essential role throughout the years of field data collection, and Beatriz López Gurillo, Asier, Nico, Irene Moreno, Leticia, Rubén, and Martín for their assistance in the field. We are also grateful to Eugenia Gimeno García for facilitating the soil nutrient analyses and providing guidance, and to Elisabeth Barrachina for conducting the soil laboratory work. We thank Jorge Prieto and Susana Paula for their valuable comments on earlier versions of the manuscript. Fire maps were made available through the support of Generalitat Valenciana, Junta de Andalucía, and Generalitat de Catalunya.

Author Contributions

Maya A. Zomer: Conceptualization; investigation; methodology; formal analysis; writing – original draft; writing – review and editing. Bruno Moreira: Conceptualization; methodology; formal analysis; writing – review and editing. Juli G. Pausas: Funding acquisition; resources; conceptualization; methodology; formal analysis; writing – review and editing.

Conflict of Interest

No conflict of interest declared

Funding

This work was supported by the Generalitat Valenciana through the program Santiago Grisolia (GRISOLIAP/2017/176) and projects FOCSEC (PROMETEO/2016/021) and FOCSCALES (PROMETEO/2021/040). CIDE is a joint institute of the Spanish National Research Council (CSIC), the University of Valencia, and the regional government of Valencia (Generalitat Valenciana).

Data Availability Statement

All primary data to support the findings of this study are openly available in the Figshare digital repository at https://doi.org/10.6084/m9.figshare.29037134 (Zomer et al. 2025).

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Table 1. Decomposition of variation, total and proportional (the latter in brackets), of plant biomass and resprouting response across three nested levels for the field experiment. Levels include between species, among populations within species, and among individuals within-populations within species. Variation is calculated for plant biomass before cut 1 (pre-disturbance size; dry biomass g) and before cut 2 (i.e., resprouting vigour; dry biomass g); and resprouting success (yes/no) after cut 1 and 2. N is the number of plants. In bold are the largest (scaled) variation across nested levels.

Variable (N)	**Between-species**	**Among-populations**	**Among-individuals**
Pre-biomass (378)	1334 (0.235)	819 (0.144)	3523 (**0.620**)
Resprout success cut 1 (378)	~ 0 (~ 0)	0.0146 (0.132)	0.0959 (**0.868**)
Resprout vigour (312)	71(0.029)	861 (0.350)	1529 (**0.621**)
Resprout success cut 2 (284)	0.003 (0.035)	0.006 (0.061)	0.084 (**0.903**)

Table 2. Summary of multigroup SEM for resprouting response (success and vigour) of adult populations in the field in relation to historical aridity, fire activity, soil nitrogen, and pre-disturbance plant biomass. Species was included as a grouping variable; thus, results are presented separately for *A. cytisoides* and *G. alypum*. A global effect is constrained to the model-wide estimate and standard estimate, (i.e., the interaction with grouping variable species was not significant) and is signified by a 'c'. A local effect, (i.e., a significant interaction with species) allows estimates and standard estimates to vary between species. Statistically significant ($P<0.05$) differences are highlighted in bold. Variable units and transformation are as follows: pre-disturbance biomass (g, log-transformed, scaled and centred); resprout success (yes/no); resprout vigour (g, log-transformed, scaled and centred); aridity (scaled and centred); fire activity (scaled and centred): mean annual burned area in buffer (ha); and soil nitrogen (%, scaled and centred). Causal model is displayed in Fig. 2.

Response	**Predictor**	**Estimate**	***p***	**std Estimate**
A. cytisoides				
SEM 1 (a):				
pre-disturbance plant biomass	aridity	0.821	**0.016*c**	0.836
pre-disturbance plant biomass	fire activity	-0.899	**0.011*c**	-0.906
pre-disturbance plant biomass	soil nitrogen	1.048	**0.001 *c**	1.062
resprout success after cut 1	pre-disturbance plant biomass	-0.039	0.829	
SEM 2 (b):				
pre-disturbance plant biomass	aridity	0.573	**0.0205*c**	0.610
pre-disturbance plant biomass	fire activity	-0.636	**0.0147 *c**	-0.574
pre-disturbance plant biomass	soil nitrogen	0.618	**0.0164 *c**	0.626
resprout vigour	pre-disturbance plant biomass	0.530	**0.000***c**	0.530
resprout vigour	aridity	-0.365	0.6106	-0.150
resprout success cut 2	resprout vigour	0.947	**0.0004 ***c**	
G. alpyum				
SEM 1 (a):				
pre-disturbance plant biomass	aridity	0.821	**0.016*c**	0.836
pre-disturbance plant biomass	fire activity	-0.899	**0.011*c**	-0.906
pre-disturbance plant biomass	soil nitrogen	1.048	**0.001 *c**	1.062
resprout success cut 1	pre-disturbance plant biomass	-0.039	0.829	
SEM 2 (b):				
pre-disturbance plant biomass	aridity	0.573	**0.0205*c**	0.610
pre-disturbance plant biomass	fire activity	-0.636	**0.0147 *c**	-0.574
pre-disturbance plant biomass	soil nitrogen	0.618	**0.0164 *c**	0.626
resprout vigour	pre-disturbance plant biomass	0.530	**0.000***c**	0.530
resprout vigour	aridity	0.342	**0.0101**	0.384
resprout success cut 2	resprout vigour	0.947	**0.0004 ***c**	

(a) N= 378 plants. Fisher's C= 13.04 with P-value = 0.04 and on 6 degrees of freedom; AIC: 31.04, BIC: 66.453, Individual R^2 conditional: 0.68 (pre-disturbance plant biomass), 0.10 (resprout success cut 1)

(b) N= 312 (biomass and vigour) and N= 284 (resprout success cut 2). Fisher's C= 19.30 with P-value 0.08 and on 12 degrees of freedom; AIC: 32.95, BIC: 84.04, Individual R^2 conditional: 0.49 (pre-disturbance plant biomass), 0.52 (resprout vigour), 0.12 (resprout success cut 2)

Table 3. Summary of SEM for resprouting response (success and vigour) of seedlings in the common garden experiment in relation to water treatment, climate at seed provenance, and pre-disturbance plant biomass. Note that for categorical and binomial response variables, the significance test from the ANOVA is reported in the row corresponding to the group effect, and if significant, marginal means are reported for each level of the grouping factor. There are no standardized estimates for either the ANOVA effect or marginal means, because these are not linear coefficients. Statistically significant (P<0.05) differences are highlighted in bold. Variable units and transformation are as follows: resprout success (yes/no); resprout vigour (g); pre-disturbance biomass (g); water treatment (Drought/Watered); climate at seed provenance (High aridity/ Low aridity). Causal model is displayed in Fig. 5.

Response	**Predictor**	**Estimate**	***P***	**std Estimate**
SEM 1 (^{a}):				
pre-disturbance plant biomass	water treatment		**0.000** ***	
pre-disturbance plant biomass	water (drought)	32.59	**0.000** ***	
pre-disturbance plant biomass	water (watered)	47.62	**0.000** ***	
pre-disturbance plant biomass	climate seed provenance		0.988	
resprout success cut 1	pre-disturbance plant biomass	0.23	**0.015** *	
resprout success cut 1	water treatment		0.269	
resprout success cut 1	climate seed provenance		0.988	
SEM 2 (^{b}):				
pre-disturbance plant biomass	water treatment		**0.000** ***	
pre-disturbance plant biomass	water (drought)	33.88	**0.000** ***	
pre-disturbance plant biomass	water (watered)	48.70	**0.000** ***	
pre-disturbance plant biomass	climate seed provenance		0.528	
resprout vigour	pre-disturbance plant biomass	0.24	0.061	0.206
resprout vigour	water treatment		**0.000** ***	
resprout vigour	water (drought)	16.23	**0.000** ***	
resprout vigour	water (watered)	34.38	**0.000** ***	
resprout vigour	climate seed provenance		0.596	
resprout success cut 2	water treatment		**0.032** *	
resprout success cut 2	water (drought)	0.23	0.566	
resprout success cut 2	water (watered)	1.71	**0.002** **	
resprout success cut 2	climate seed provenance		0.291	

(a) N= 57 plants. Fisher's C= 0 with P-value = 1 and on 0 degrees of freedom; AIC: 20.00, BIC: 40.43; Individual R^2 conditional: 0.41 (pre-disturbance plant biomass), 0.54 (resprout success cut 1)

(b) N= 50 plants. Fisher's C= 0 with P-value = 1 and on 0 degrees of freedom; AIC: 30.00, BIC: 58.68; Individual R^2 conditional: 0.47 (pre-disturbance plant biomass), 0.73 (resprout vigour), 0.12 (resprout success cut 2)

Figure 1. Location of the study area (boxed region in inset map) in the Iberian Peninsula, showing the gradient of historical aridity (lower aridity index values are indicative of less aridity); location of field populations (left map) of *A. cytisoides* (*n* = 6, brown circles) and *G. alypum* (*n* = 10, teal triangles); and location of common garden seed provenances (right map) of *A. cytisoides* (*n* = 4) in Low aridity (blue circles) and High aridity (red circles) areas. Borders in the inset map are countries, and in main maps are provinces.

Figure 2. Multigroup SEM depict relationships among environmental drivers (historical aridity, fire activity, soil nitrogen (N); brown), pre-disturbance plant biomass and resprouting responses (green) in a two-stage field experiment following the temporal sequence of cuts (dotted black arrows). SEM 1, encompassing all plants, depicts pathways from environmental drivers to pre-disturbance biomass and to resprout success after cut 1; SEM 2, restricted to plants that resprouted after cut 1, depicts pathways from environmental drivers and pre-disturbance biomass to resprout vigour after cut 1 and to resprout success after cut 2. Solid arrows denote significant global effects shared across species (*A. cytisoides* and *G. alypum*), dashed arrows denote significant species-specific interactions (the effect is significant for the species indicated), and plus (+)/minus (–) signs indicate effect direction. Standardized path coefficients beside arrows indicate relative effect strength (not available for binomial outcomes). See Table 2 for full statistical results.

Figure 3. Differences in starch and total soluble sugar (SS) concentrations in roots (g 100 g^{-1} dry material) for *A. cytisoides* (ACY) and *G. alypum* (GAL) (panels A and B, respectively) under contrasting aridity conditions. Root samples were collected from one High aridity and one Low aridity site (*n* = 8 per species per site). Lower-case letters indicate comparisons between aridity levels for starch in ACY (non-significant), and upper-case letters indicate statistically significant differences in SS concentrations based on species and aridity. See Supplementary Table S8 for model results.

Figure 4. Probability of resprouting success following cut 1 and cut 2 (panels A and B, respectively) in relation to log-transformed pre-disturbance biomass for *A. cytisoides* (ACY) and *G. alypum* (GAL) in the field. For cut 1 (*N = 378)*, biomass refers to initial pre-disturbance biomass; for cut 2 (*N = 284)*, biomass corresponds to resprout vigour (i.e., pre-disturbance biomass before cut 2). Lines show predicted probabilities from a binomial GLMM; shaded ribbons represent 95% confidence intervals.

Points represent observed binary resprouting outcomes for individual plants (success = 1, failure = 0). See Supplementary Table S9 for full statistical results.

Figure 5. SEM depict relationships among water treatment (blue), pre-disturbance plant biomass and resprouting responses (green) in a two-stage common-garden experiment following the temporal sequence of cuts (dotted black arrows). SEM 1, encompassing all plants, depicts pathways from water treatment to pre-disturbance biomass and to resprout success after cut 1; SEM 2, restricted to plants that resprouted after cut 1, depicts pathways from water treatment and pre-disturbance biomass to resprout vigour after cut 1 and to resprout success after cut 2. Solid arrows denote significant effects, dashed grey arrows denote marginal effects (p = 0.06), and plus (+) signs indicate effect direction. Standardized path coefficients beside arrows indicate relative effect strength (not available for categorical predictors or binomial outcomes). See Table 3 for full statistical results.

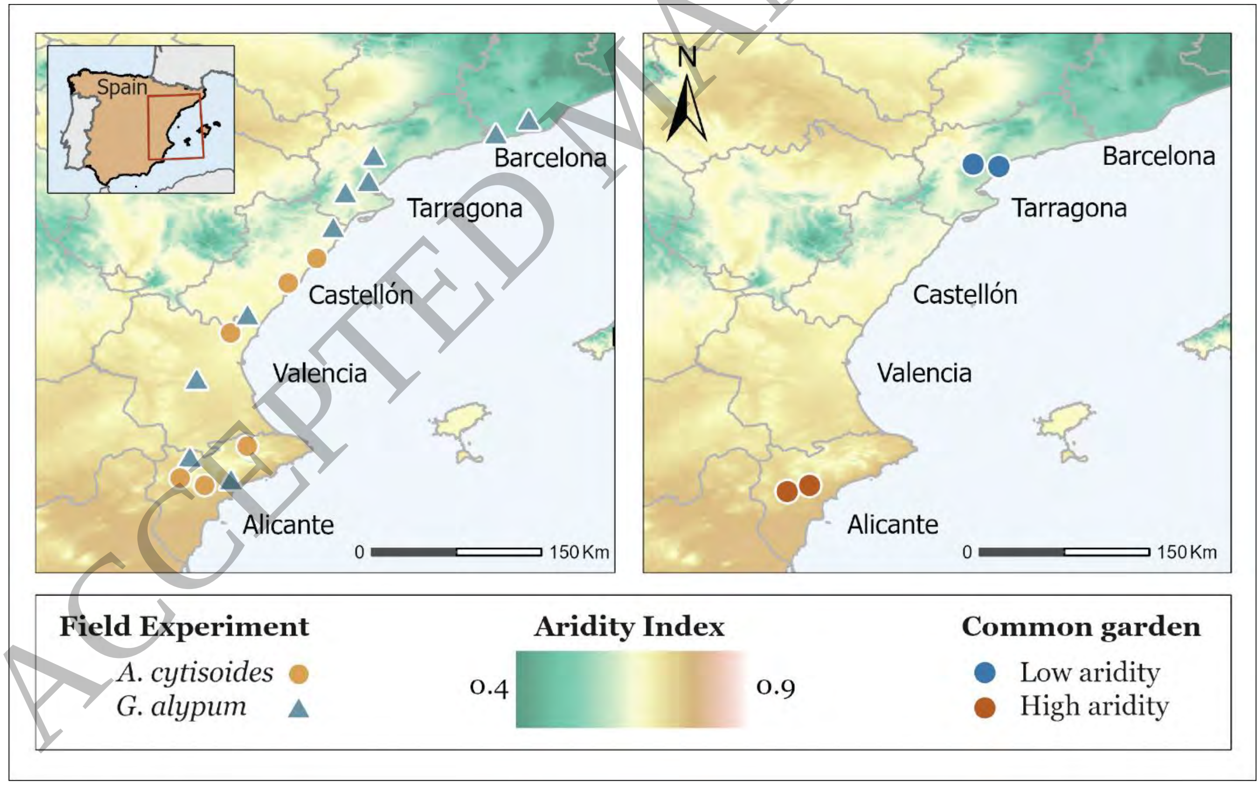

Figure 1
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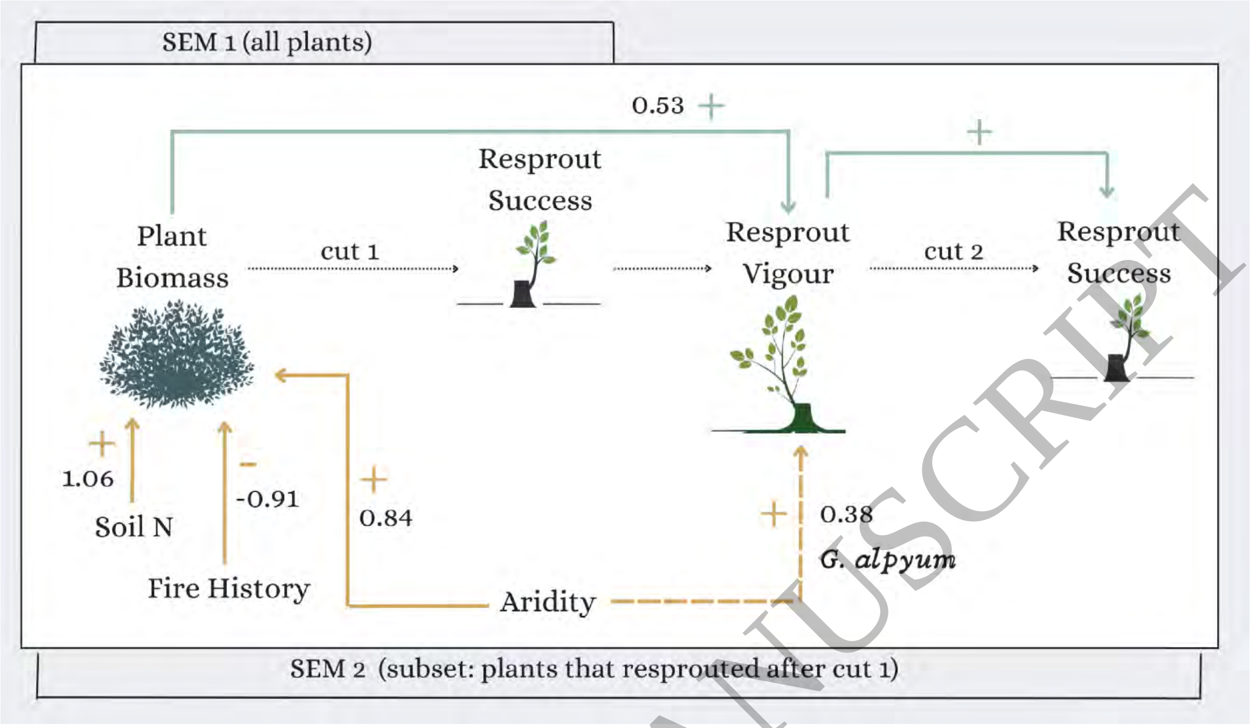

Figure 2

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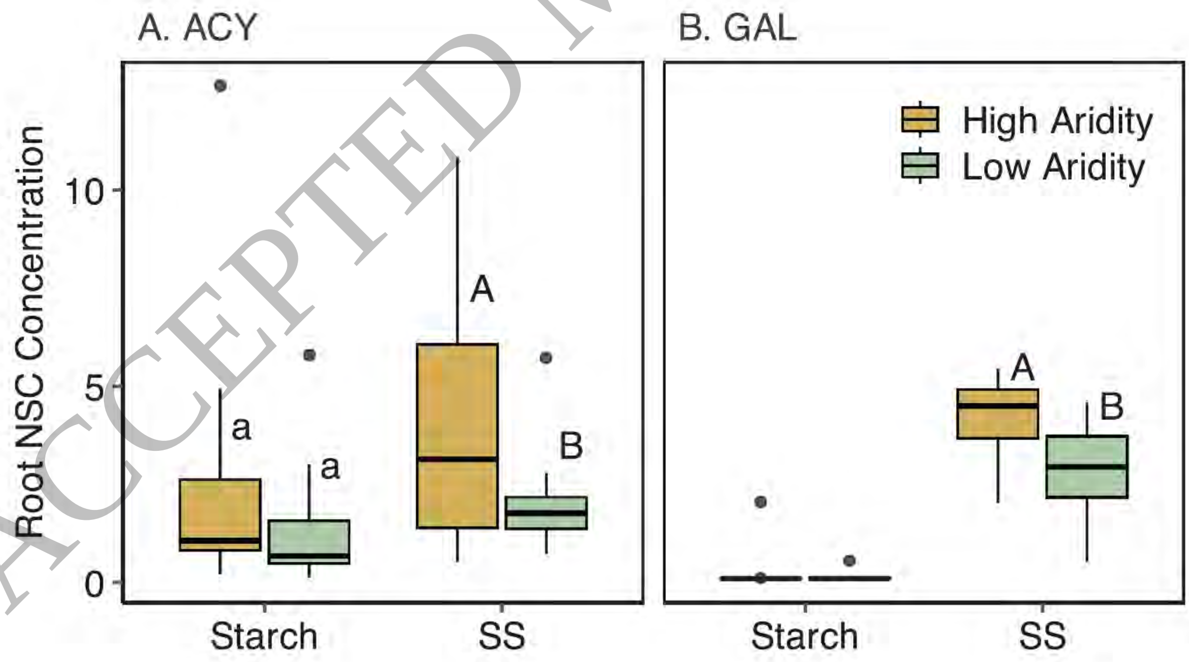

Figure 3

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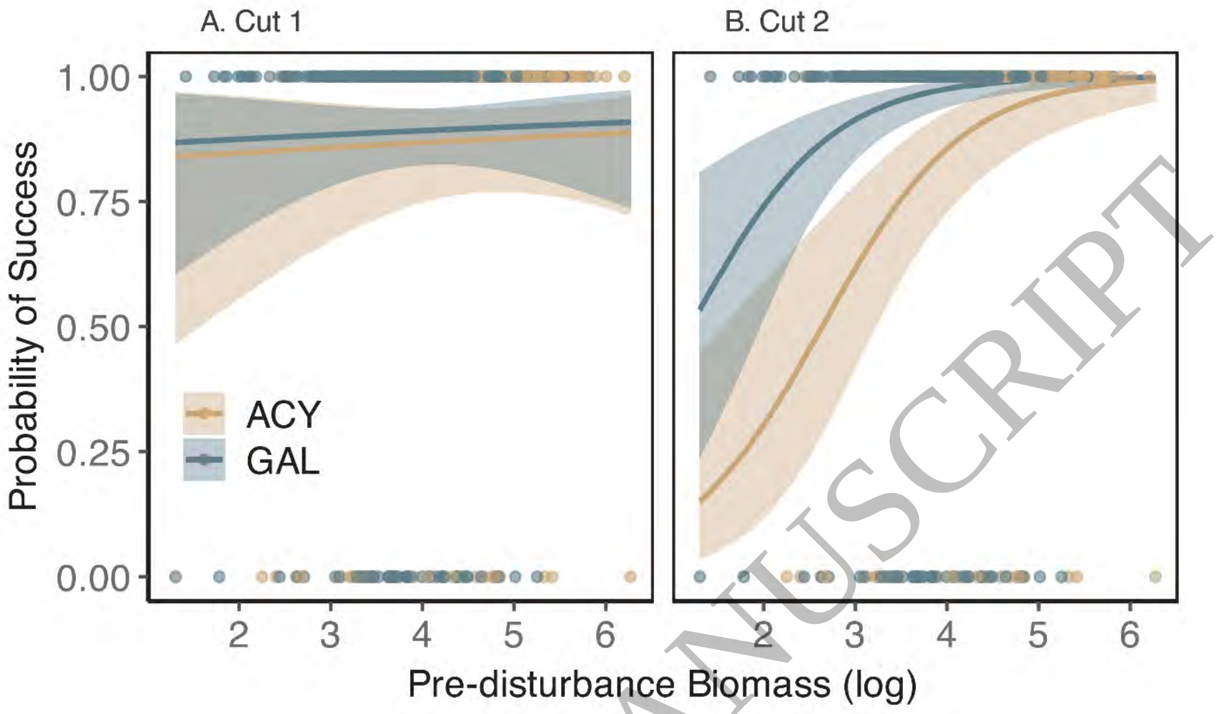

Figure 4

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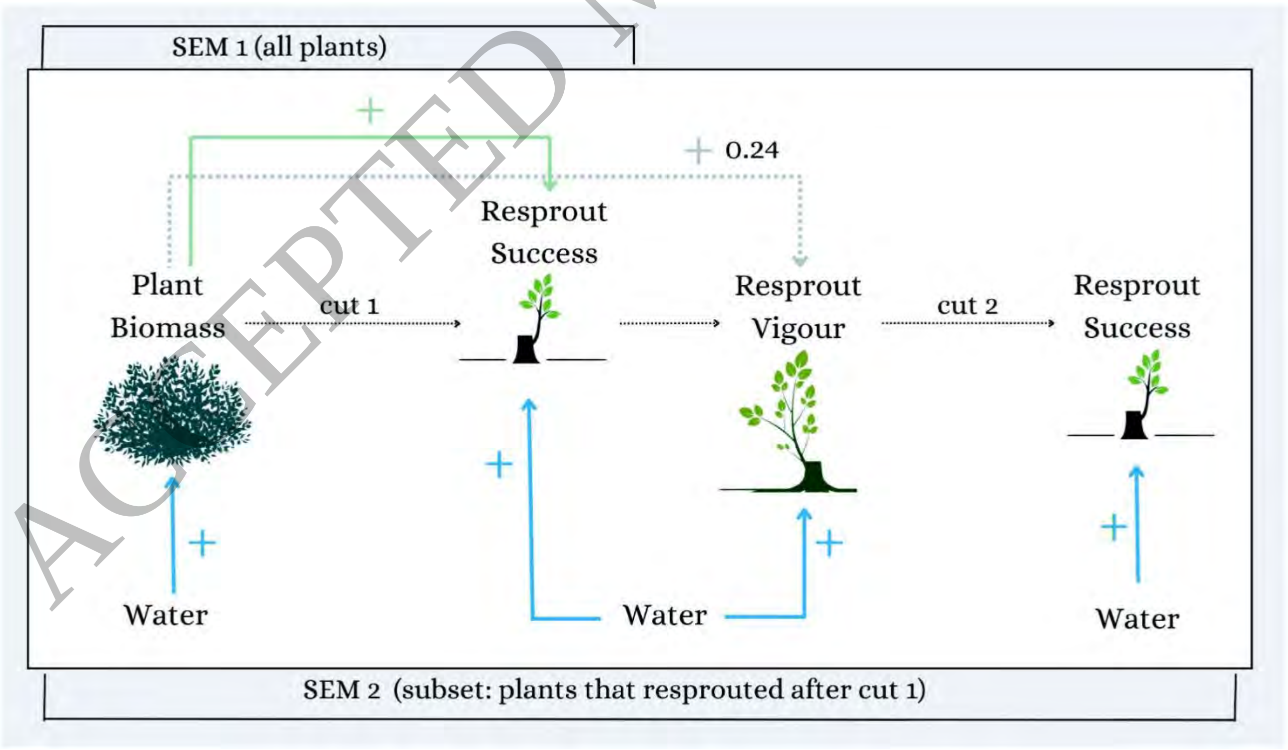

Figure 5