



# The role of fire in the germination of invasive plants in Mediterranean environments: A meta-analysis

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## ABSTRACT

Fire is a key trigger for the germination of serotinous plants in Mediterranean environments. Despite the availability of ample investigations into how fire contributes to plant fitness and germination patterns in pyriscent plants, there is no published content on how fire and associated heat and smoke factors influence germination of the group of plants successfully invading a particular biome. In this meta-analytic study, 29 studies were collated regarding the effects on germination of the temperature range corresponding to Mediterranean subsoil fire temperatures (50–99 °C), and a further 29 experiments were used to reveal the effects on germination of soil surface temperatures (100–120 °C) during Mediterranean fires. 24 studies were selected to investigate the effects of smoke during a shorter and longer exposure duration to reveal the boundaries of imbibition and toxicity associated with fire smoke. The chosen experiments performed heat shocks or smoke treatments on the invasive species found in the Mediterranean biome- a part of the globe that experiences periodic, extensive fire regimes. These experiments were then subsequently categorized into herbaceous or ligneous plants to study whether type of serotiny is associated with morphology life history. The results showed that generally, soil fire temperatures have a positive effect on the germination rate of invasive plants but only significantly in the case of invasive ligneous plants. Additionally, subsoil fire temperatures trigger invasive plant germination significantly, whereas soil surface fire temperatures do not. Only short exposure periods (c.a. 5 min) to smoke produced a positive effect in the germination of invasive plants. Longer exposures can be toxic and prevent germination. Herbaceous invasive plants responded positively to smoke treatments and ligneous invasive plants responded positively to heat shock. Our results highlight the importance of fire components (high temperature and smoke) in the success of many invasive plant species in Mediterranean environments.

## 1. Introduction

Temperature and precipitation are often referred to as the main determinants of vegetational variation seen across the world's major biomes (Holdridge, 1947). Fire has more recently been acknowledged as a salient factor in shaping biome distributions and plant communities (Bond et al., 2005; Pausas and Ribeiro, 2017), with ecological communities and landscapes having been subjected to extensive fire regimes as early as the carboniferous period (Scott, 2000). Today, the Mediterranean biome is one such area exposed to periodic fires that forms pyro-climax communities. Just in the Mediterranean basin there are over 478,900 ha burnt per year (San-Miguel-Ayanz et al., 2012). Previous remote sensing studies showed that post-fire land surface

temperature is a valuable indicator of soil burn severity in Mediterranean fire-prone ecosystems (Quintano et al., 2015; Marcos et al., 2018). Pyro-climax communities are often largely comprised of species with resprouting or serotinous adaptations. Resprouting involves post-fire regrowth from dormant buds (Clarke et al., 2013). Serotiny is the activation of germination after the storage of seeds for one or more years via an environmental shift, whereas pyriscence refers exclusively to fire-mediated serotiny (Lamont et al., 1991). However, the terms are often used interchangeably (Causley et al., 2016).

Here, the focus will be on serotinous traits that trigger the germination of seeds in response to fire. The seeds that react this way are called serotinous refractory seeds, and the stimulus can be that of heat shock or smoke induced germination (Keeley, 1995). Serotinous seeds

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exhibit “innate” dormancy, which is maintained through a hard seed coat that prevents imbibition by water or gases (Keeley, 1995). The most important and studied components of fire that can affect seed germination are heat and smoke (Hodges et al., 2021; Moreira et al., 2010; Zironi et al., 2019). Refractory seeds that respond to heat shock are dormant and unresponsive to light and nutrient alterations (De la Cuadra, 1993). Through elevated temperature, scarification creates permeability to water which allows the end of dormancy, promoting germination (Keeley and Fotheringham, 2000). Seeds that experience smoke triggered germination are often latent, viable seeds that would respond to nutrient or light alterations even without smoke exposure (De la Cuadra, 1993). Smoke sensitive seeds can be generally characterized by possessing a comparatively weak outer cuticle, lacking extensive cutinization, whereas seeds stimulated by heat shock have a thick outer cuticle that is impermeable to water (Keeley and Keeley, 1987).

The smoke induced germination mechanism functions principally through acidity shifts created during burning or oxidizing gases in smoke that end dormancy (Keeley and Fotheringham, 1998). However, there are 5 mechanisms generally accepted with regards to smoke. These are: change in solute permeability of the cuticle permitting the germinative action of ions, the change in solute permeability allowing for the leaching out of endogenous inhibitors, the germinative action of nitrates, the pH shift caused by the acids present in smoke, or the stimulation of germination by smoke provoked enzymatic disinhibition (Keeley and Fotheringham, 1998). The group of chemicals identified as the main provokers of smoke germination are the “Karrakins”, which are butanolides created upon burning cellulose (Keeley and Pausas, 2018). Other chemicals present in smoke that can favor seed germination are nitrogen oxides and cyanohydrin (Keeley and Pausas, 2018). Herbaceous plants have a greater proportion of cellulose than ligneous plants (trees, shrubs). The type of dormancy or latency in smoke responsive seeds exhibited depends on the mechanism responsible. It has been discovered that many species respond to chemical breakdowns of smoke because of mechanisms that respond to soil nutrient quantity, that have evolved in areas historically devoid of fire (Keeley and Pausas, 2018). Coincidentally, these nutrient detection systems also respond to the chemicals in smoke, creating in many species a two-fold system that detects the amelioration of environmental conditions.

Additionally, some species utilize serotinous cones for heat and flame protection, where a resin is melted to allow for seed release after the passing of a fire (Beaufait, 1960). These serotinous cones have

non-refractory seeds; seed dormancy is not broken by direct effects on the seed coat, but rather the surrounding cone (Keeley, 1995). These forms of serotiny contrast with non-serotinous seeds or cones that are resistant to fire, but because of thick protective layers and not a fire-mediated germination mechanism (Michaletz et al., 2013). Seeds are stored either in soil seed banks or in aerial seed banks (Goubitz, Werger and Ne’eman, 2003). Serotinous cones reside in aerial seed banks where they risk faster senescence and seed predation, in order to maximize nutrient provision to seeds (Keeley, 1995). Refractory seeds are stored in the soil seed bank, where they are safer from seed predation, but compromise their seed size and nutrient provision for secondary succession (Keeley, 1995).

Post-fire environments can be favorable because disturbance provides opportune conditions for settlement (Causley et al., 2016). The passing of fire burns existing vegetational structures to ashes, leaving nutrient rich soils with a greater solar exposure (Keeley and Fotheringham, 2000). This temporarily reduces competition for resources and discourages the presence of herbivores and other forms of predation (Keeley and Fotheringham, 2000). Additionally, the burning of vegetative mass disables the functioning of allelopathy in the burnt area- which is known to control seed germination (Keeley et al., 1985). Once simultaneous seedling establishment occurs, predator and herbivore satiation maintain favorable conditions in the post-fire environment- a low risk of mortality (O’Dowd and Gill, 1984).

Invasive species are historically exotic species that have a large impact on the ecosystems they invade (Davis and Thompson, 2000). They are now of relevance due to the economic and environmental costs they impose. Invasive species cost Europe over 12.5 billion euros per year (Kettunen et al., 2008). Invasive species are becoming increasingly common because of human globalization of trade, species introductions in pest control and an increase in anthropogenic caused disturbance such as fire (Seebens et al., 2017). Fire frequency and intensity are increasing in the Mediterranean basin due to land use alterations and climate warming (Turco et al., 2018). Short-interval fire regimes are thought to encourage invasiveness (Vilà-Cabrera, Saura-Mas and Lloret, 2008). The increase in the severity of fires has also been related to the invasion success of many species in Mediterranean ecosystems (Arianoutsou and Vilà, 2012; Grenz and Clements, 2023; Reilly et al., 2020). Most alien species do not become “invasive”, but there is a tendency for invasiveness in the Mediterranean biome (Arianoutsou and Vilà, 2012). Besides, the amelioration of an environment via

**Table 1**

A summary of the metanalytical results taken from the forest plots. The “Independent factor” is the treatment investigated, the “Group” is the plant type according to the classification, “Heterogeneity” is measured using  $\tau^2$  (between-study variance) with the Mantel Haenszel method, the “Odds ratio” is the overall effect score for the random effects model with the 95 % confidence Intervals (CI), the “Effect on germination” shows whether for each treatment germination increased= stimulation, did not change= neutral, or decreased= Inhibition, the “significance of the effect” represents whether the odds ratio was deemed a significant increase or decrease of germination, and the FSN values (Fail-Safe Number) show the number of missing studies with a treatment effect equal to zero, needed to render those independent factors with significant effects non-significant. The asterisks (\*) indicate a robust FSN, i.e.,  $FSN > 5n+10$ , where  $n$  is the number of studies.

Independent Factor	Vegetation Group	Number of studies (n)	Heterogeneity ( $I^2$ )	Odds Ratio [95 %-CI]	Effect on Germination	Significance of the Effect	FSN Values
Global Heat Shock (50–120 °C)	Herbaceous+Ligneous	58	94 % (High)	2.38 [1.25; 4.55]	Stimulation	Yes	759*
	Herbaceous	21	94 % (High)	1.00 [0.48; 2.05]	Neutral	No	-
	Ligneous	37	94 % (High)	4.26 [1.69; 10.75]	Stimulation	Yes	616*
Higher Heat Shock (100–120 °C)	Herbaceous+Ligneous	29	96 % (High)	1.81 [0.62; 5.31]	Stimulation	No	-
	Herbaceous+Ligneous	29	88 % (High)	3.01[1.59; 5.71]	Stimulation	Yes	449*
Global Smoke (5–10 mins)	Herbaceous+Ligneous	48	84 % (High)	1.59 [1.13; 2.22]	Stimulation	Yes	191
	Herbaceous	22	89 % (High)	2.91 [1.60; 5.29]	Stimulation	Yes	414*
	Ligneous	26	50 % (Relatively Low)	0.88 [0.71; 1.08]	Inhibition	No	-
Longer Smoke (10-mins)	Herbaceous+Ligneous	24	84 % (High)	1.49 [0.90; 2.46]	Stimulation	No	-
Shorter Smoke (5-mins)	Herbaceous+Ligneous	24	85 % (High)	1.70 [1.07; 2.69]	Stimulation	Yes	91

eutrophication or disturbance creates enhanced invasibility (Davis and Thompson, 2000). Resource availability, physical environment suitability (including niche availability) and the enemy release hypothesis account for the prominence of invasive species in disturbed areas (Shea and Chesson, 2002).

The Mediterranean *matorral* found throughout the five corresponding fire-prone regions can be broadly classed as herbaceous species or ligneous species (Du Rietz, G. E, 1931). This distinction arises from ligneous species demonstrating a lignin-based central stem or trunk structure existing as bushes, sub-bushes, shrubs, or trees as perennials (Du Rietz, G. E, 1931). On the other hand, herbaceous species do not present this characteristic feature and are instead grasses, rushes and other annuals that do not live long enough to warrant the ligneous investment (Du Rietz, G. E, 1931). Because of differing life history strategies, one would expect them to differ in reproductive strategy too. Herbaceous annuals favor immediate reproduction ignoring individual long-term investment in protective features and accumulate a large permanent soil seedbank (Abedi et al., 2018). Contrastingly, ligneous perennials should show morphologies and reproductive strategies that invest resources to enhance individual survivorship and delayed reproduction (Abedi et al., 2018). In a study conducted on the germination rates of autochthonous plants of the Mediterranean basin, herbaceous annuals were more responsive to smoke treatments than herbaceous

perennials or woody plants (Çatav et al., 2018). Smoke is linked to nutrient detection systems making herbaceous species (often annuals) germinate more easily- which is to be expected in annuals (Abedi et al., 2018). Following these ideas, herbaceous invasive species should be more responsive to smoke chemicals. Ligneous species (perennials) would not be expected to respond to smoke as readily as herbaceous species, due to generally more impermeable seeds. Therefore, ligneous species may be more readily associated with fire resistance, resprouting or heat shock.

There has been a lot of research on seed germination of individual species in response to elevated temperatures or charred wood, with a great proportion investigating the effects of heat shock and smoke treatments in conjunction with forms of serotiny. This study aims to provide novel insight into how invasive species as a category cope with fire within the biome of the Mediterranean. The objective of this meta-analysis was to investigate the effect of fire temperature and smoke exposure duration on the germination of the invasive species of the Mediterranean biome. The data set was then subsequently categorized to provide insight into how herbaceous and ligneous seeds deal with these fire factors. We explored the temperature and smoke components of fire exposure, but not the indirect fire-related effects on germination rates, such as light, soil nutrient content or allelopathy.

Given that a higher density of seeds of a soil seed bank is found at the

**Table 2**

Information on each selected invasive species associated taxonomic family, assigned group (Herbaceous or Ligneous; Du Rietz, G.E., 1931), geographic origin and relevant responses to heat and smoke factors. “Europe” mainly refers to the Mediterranean but not exclusively. The following symbology is used: + (positive), - (negative), NS (not significant), NA (not available) and the study reference number is in brackets i.e. (3). L: Ligneous; H: Herbaceous.

SPECIES	FAMILY	Group (L/H)	Origin	Heatshock		Smoke	
				High	Low	Long	Short
<i>Daucus carota</i>	Apiaceae	H	Eurasia	-	NS	NS	NS
<i>Coryza canadensis</i>	Asteraceae	H	N. America	NA	NA	+	+
<i>Crotalaria juncea</i>	Asteraceae	H	Europe	+	+	NA	NA
<i>Helichrysum foetidum</i>	Asteraceae	H	S. Africa	-	NS	NS	NS
<i>Scolymus hispanicus</i>	Asteraceae	H	Europe	NS	NS	NA	NA
<i>Echium plantagineum</i>	Boraginaceae	H	Europe	-	NS	NA	NA
<i>Spergula arvensis</i>	Brassicaceae	H	Europe	NA	NA	NS	NS
<i>Cistus ladanifer</i>	Cistaceae	L	W. Europe	+	+	NA	NA
<i>Cistus monspeliensis</i>	Cistaceae	L	W. Europe/NW. Africa	NA	NA	NS	NS
<i>Cistus salvifolius</i>	Cistaceae	L	Europe/N.Africa	+	+	NA	NA
<i>Spartium junceum</i>	Fabaceae	H	Eurasia/ N. Africa	NA	NA	-	NS
<i>Acacia dealbata</i>	Fabaceae	L	Australia	+	+	-	NS
<i>Acacia longifolia</i>	Fabaceae	L	Australia	-	+	NS	-
<i>Acacia mearnsii</i>	Fabaceae	L	Australia	+	+	NS	NS
<i>Acacia melanoxylon</i>	Fabaceae	L	Australia	-	+	NS	NS
<i>Acacia saligna</i>	Fabaceae	L	Australia	+	+	NA	NA
<i>Cystisus striatus</i>	Fabaceae	L	W. Europe/N. Africa	+	+	NA	NA
<i>Cytisus scoparius</i>	Fabaceae	L	W. Europe	NS	+	NA	NA
<i>Paraserianthes lapantha</i>	Fabaceae	L	Australia	+	+	NS	NS
<i>Robinia pseudoacacia</i>	Fabaceae	L	N. America	+	+	NS	NS
<i>Teline monspessulana</i>	Fabaceae	L	Europe	+	+	NA	NA
<i>Pharlaris paradoxa</i>	GramineaePoaceae	H	Europe	NA	NA	+	+
<i>Salvia verbenaca</i>	Lamiaceae	H	Europe	-	-	NA	NA
<i>Rosmarinus officinalis</i>	Lamiaceae	L	Europe	NA	NA	NS	NS
<i>Vitex agnuscastus</i>	Lamiaceae	L	Europe	+	+	NA	NA
<i>Malva arborea</i>	Malvaceae	L	Europe	NS	NS	NA	NA
<i>Eucalyptus cinerea</i>	Myrtaceae	L	Australia	NS	NS	NA	NA
<i>Eucalyptus globulus</i>	Myrtaceae	L	Australia	NS	-	-	NS
<i>Oenothera glazioviana</i>	Onagraceae	H	Hybridization	+	+	NS	+
<i>Pinus contorta</i>	Pinaceae	L	N. America	NS	NS	NA	NA
<i>Pinus radiata</i>	Pinaceae	L	N. America (California)	NA	NS	NS	NS
<i>Alopecurus myosuroides</i>	Poaceae	H	N. America	NA	NA	+	NS
<i>Avena sterilis</i>	Poaceae	H	Eurasia	NA	NA	+	+
<i>Bromus diandrus</i>	Poaceae	H	Eurasia/N. Africa	NA	NA	NS	NS
<i>Sorghum halepense</i>	Poaceae	H	Hybridization	NA	NA	+	+
<i>Fallopia convolvulus</i>	Polygonaceae	H	Eurasia/ N. Africa	NA	NA	NS	NS
<i>Reseda lutea</i>	Resedaceae	H	Eurasia/N. Africa	+	NS	NA	NA
<i>Reseda luteola</i>	Resedaceae	H	Eurasia/N. Africa	NS	NS	NA	NA
<i>Rhamnus alaternus</i>	Rhamnaceae	L	Europe	NA	NA	NS	NS
<i>Ailanthus altissima</i>	Simaroubaceae	L	Asia (China)	-	NS	NS	+
<i>Nicotiana glauca</i>	Solanaceae	L	Argentina	-	NS	NA	NA

1 cm depth below the surface (Santana et al., 2012), most seeds are expected to be more adapted to, and thus their germination more favored by, the lower temperature bracket associated with subsoil fire temperature, than by the bracket of higher surface temperatures. In addition, this is compounded by the fact that soil acts as a protective barrier to the extreme surface temperatures that are lethal for most seeds (Tangney et al., 2020). Smoke imbibition requirements and toxicity limits could be associated with either exposure duration, or with neither, but considering the toxicity limit (Keeley and Fotheringham, 1997) the shorter duration seems more plausible to stimulate seed germination. Altogether, the results of this study allow conclusions on the types of traits found in the invasive community of Mediterranean biome fire-prone regions. This information is essential to guide prevention strategies of invasive plants in high-risk areas of fire, as well as control and management plans in burned areas.

## 2. Methods

Using a range of experimental results, a meta-analysis was conducted using the PRISMA method (Moher et al., 2015). The search engine “Web of Science” was used on January 17th of 2022, implementing the string of words “Fire” AND “Germination” AND “Mediterranean” AND “invasive”. A second search with a reduced string of the same words without “invasive” was also conducted, and then subsequently scanned for invasive species relevance. The third search substituted the word “fire” for the phrase “heat shock”, and the fourth search used “smoke” instead of “fire”. A minimum of the year 2000 was used to ensure the topicality of the invasive species investigated. The first search resulted in 37 results, the second search gave 536 results, the third search gave 84 results and the fourth 108 results. These results were then used by the corresponding author in conjunction with snowball sampling (in the reference sections of the relevant articles) and finally scanned as the PRISMA method (Moher et al., 2015) for relevance to the aims of this study using the following additional criteria:

(1) The experiments in the articles were only deemed adequate if they were original, peer-

reviewed, fire-induced seed germination laboratory experiments; (2) Many studies needed to be ignored on the premise that they did not actually perform the germination experiments on seeds but instead their protective, serotinous cones; (3) We only considered articles studying invasive species in Mediterranean biome, which include invasive species in five regions of the world: California, central Chile, the Mediterranean Basin (all the countries surrounding the Mediterranean Sea), the Cape Region of South Africa, and southwestern Australia (Rundel et al., 2016). We used the word “Mediterranean” during the search to include all the different terms referring to the Mediterranean biome, such as Mediterranean-type ecosystems, environments, or regions; (4) For studies that performed fire treatments on invasive and native species, further examination was required to determine which of the species experimented on were the invasive ones; (5) Studies that did not explicitly describe a species as invasive but used similar terms such as “exotic” were short listed to require posterior confirmation of their status as invasive in a Mediterranean area. Another Web of Science, Google Scholar or CABI (CABI, 2022) search using the Latin name of the species and the word “invasive” allowed for the confirmation of the species status as “invasive”. The status was considered conclusive if the scientific articles from this search referred to the species as “invasive”, or if it was present in the “DAISIE” GBIF dataset (GBIF, 2022). We found during our investigation that some species cited in the papers as invasive are not actually identified as such in the invasive databases previously mentioned, but as allochthonous or exotic. Therefore, these species were excluded from the study.

(6) For the temperature based investigation, selected experimental investigations needed to expose the seeds to the heat shock for between 5 and 15 minutes, as this is how long these temperatures last during the passage of fire in Mediterranean environments (Riveiro et al., 2019).

The search results were separated into two categories based on temperature range which correspond to different soil depths. The higher temperature category (100–120 °C) corresponds to canopy and soil surface temperatures, whilst the lower temperature category refers to subsurface soil temperatures during a fire. The subsoil category encompasses those temperatures from 50 to 99 °C. Seed dormancy is suggested to be broken by summer temperatures in some species and by fire temperatures in others. The maximum summer soil temperatures in the Mediterranean generally do not surpass 50 °C (Zupo et al., 2016). Seeds that exhibit dormancy in Mediterranean fire-prone areas are known to be unresponsive to summer temperatures (Moreira and Pausas, 2012) and so temperatures below 50 °C were excluded. The maximum temperature that is normally seen in Mediterranean fires 1 cm below the surface (the highest density of seeds in soil seed banks are found at 1 cm depth) (Santana et al., 2012) is 99 °C, so this was used as the maximum temperature for the subsoil category. Mediterranean fires can reach very high temperatures of 400 °C above the surface (Baeza et al., 2002). However, very few species experience increased germination after seed exposure to heat shock of 120 °C and exposure of 150 °C is virtually always lethal (Reyes and Trabaud, 2009). These high temperatures often crack hard seed coats or melt waxy coverings (Tarrega et al., 1992), so we decided to exclude this data from the metanalysis. In addition, in this study we were interested in a range of temperatures that can cause a variable effect on the germination of different species, not in temperatures that are lethal for most seeds. The method used to heat shock the seeds could be a source of variation in the results, but most of the studies reviewed used the same method: dry heat with an oven.

(7) The procedure for the second line of investigation on smoke, included experiments that exposed the seeds to a smoke treatment or a chemical breakdown of smoke, representative of the types of molecules that are resultant from Mediterranean biome fires (nitrogen oxides, glyceronitrile or karrakin; Keeley and Pausas, 2018). The concentrations of the smoke and the chemicals used varied, so they needed to justify their representativity of burnt vegetation to be included. The search results were separated into two categories based on smoke exposure duration, which indicate relative imbibition requirements for germination and toxicity levels for inhibition of germination. A shorter duration of smoke exposure for triggering germination represents a greater sensitivity to smoke signals and a longer duration is indicative of a lower sensitivity. Sensitivity can also be interpreted as tolerance but is not necessarily a direct relationship. Smoke exposure times in natural Mediterranean fires vary enormously; studies have revealed that most seeds can tolerate up to 10 minutes direct exposure and up to 4 hours of indirect exposure (Keeley and Fotheringham, 1997). To reduce potential variation because of this distinction, experiments were only selected if they used direct treatments. As a result of the general intolerance to >10 minutes direct exposure to smoke there are less experiments conducted on 15-minute exposure available from the initial search- which is the reason that 5- and 10-minute durations were chosen as the two categories. A 15 plus minute exposure tends to result in toxicity for some species without increasing the rate of germination in tolerant species- designating it surplus for this general study (Keeley and Fotheringham, 1997). Although it is difficult to separate the serotinous smoke mechanisms from the nutrient or light detection systems to inform of seed types and dormancy patterns without individual study, this metanalysis will still inform on the adaptability of invasive species to smoke related factors, even if the morphology has an indirect evolutionary relation.

After this process of refinement, 29 relevant studies were found for the 1 cm depth temperature bracket, and 29 relevant studies were utilized for the surface temperature bracket (see appendix S1 and appendix S2). For the smoke subsection, 24 studies were used for the shorter 5-minute smoke exposure, and 24 studies were used for the longer 10-minute smoke exposure category (see appendix S3 and appendix S4). This means that following screening, 53 studies were selected from the original 765 search engine results. Studies that performed more than one heat shock of relevance falling within a single temperature bracket (i.e.,

100 °C & 110 °C) were taken as a single entry for 110 °C.

For the secondary objectives of this meta-analysis, the above studies were then separated based upon a vegetative distinction of ligneous or herbaceous. The degree of lignification of the aerial structures of a mature plant is a classical paradigm distinction for plants (Du Rietz, G. E, 1931). The original classification describes three types of plant based on the degree of lignification: Woody/ligneous (holoxyles: trees, shrubs, half-shrubs, woody cushion plants and woody lianas), semi-woody (tall and dwarf half-shrubs) and herbaceous (chthonic, epiphytic, parasitic and herbaceous lianas). To simplify this paradigm and assess fire related germination as a product of lignification presence or absence, it has been reduced to the dichotomous ligneous (wood and semi-woody) or herbaceous plants.

From each study the following information was extracted: species name, treatment type and intensity, total number of seeds in the study and the number of seeds that germinated after treatment. The relevant data was extracted either from the article text or from tables and graphs. Where raw data was not available in numerical form, the germination rates were estimated from the graphs. Due to many studies choosing to represent their data using germination percentages, the number of repeats was noted for each respective experiment to calculate the number of seeds that successfully germinated for the control and after treatment. Any study that did not provide calculable data in this format was not included because of incompatibility with the meta-analytic PRISMA method (Moher et al., 2015).

A meta-analysis relies upon the calculation of an effect size for the collated studies to be comparable. Odds ratio was determined as the suitable quantifier of effect size (Koricheva et al., 2013; Szumilas, 2010; Traveset and Verdú, 2002; Verdú and Traveset, 2004) for the experiments to show if the two groups differed in terms of an event happening or not, in this case germination (binary outcomes). Odds ratio effect sizes are considered useful when comparing the probability of seed germination under different conditions (Koricheva et al., 2013; Verdú and Traveset, 2004). The data was inserted into excel spreadsheet using headings specific to the *metabin* function in the *meta* package (Balduzzi et al., 2019). These were:

- *Event.e*: the number of successful germinations for the treatment.
- *N.e*: the total number of seeds subjected to the heat shock treatment.
- *Event.c*: the number of successful germinations for the control.
- *N.c*: the total number of seeds subjected to the control.

Each excel sheet was transformed to a tab-delimited file and imported into R studio (R Studio Team, 2019), where the *meta* package (Balduzzi et al., 2019) with the *metabin* function was run to produce separate forest plots and heterogeneity plots/ L'Abbé plots (L'Abbé et al., 1987). The *metabin* function adds 0.5 to the cells with a value of 0 when calculating the odds ratio to remove numerical error when dividing by 0.

Random effects model values higher than 1 indicate positive effect of the treatment on germination rates while values lower than 1 indicate negative effect. If the 95 % confidence interval passes through the line of no effect, indicate an insignificant effect. The effect is significant if the 95 % confidence interval does not pass through the line of no effect.

Heterogeneity is often taken as a key indicator of study reliability and whether a quantitative review is too broad in its scope (Hoaglin, 2016). The heterogeneity was measured using the  $I^2$  index which determines the percentage of variability that is due to between study variability rather than individual study sampling error (Huedo-Medina et al., 2006). Fixed effect sizes are used when meta-analysis study heterogeneity is believed to be due to chance and sampling error; one true effect underlies all studies (Schmidt et al., 2009). For this meta-analysis the random effects model was appropriate. This is because the temperature intervals were random within the selected temperature range as were the smoke concentrations; each study effect was from a distribution of study effects (Schmidt et al., 2009; Hak et al., 2016).

In line with using random effects-models we sought to calculate for each category a Fail-Safe Number (FSN) using Rosenberg's methodology (Rosenberg, 2005), instead of Rosenthal's original methodology (Rosenthal, 1979) that is used for fixed-effect studies and is often considered outdated (Rosenberg, 2005). This statistic indicates the number of missing studies with treatment effects of zero, needed to render the logarithmic odds ratio results non-significant. "A fail-safe number is often considered robust if it is greater than  $5n + 10$ , where  $n$  is the original number of studies" (Rosenthal 1991 as cited in Rosenberg, 2005). If the FSN is lower than the threshold, the results are arguably not robust in the presence of publication bias. This threshold has also been highly controversial (Rosenberg, 2005; Rothstein et al., 2005), but the FSN nonetheless still sheds light on the susceptibility of the meta-analysis to undiscovered publication bias and contributes valuable information to understanding the robustness of the results (Aguilar et al., 2006). The FSN was calculated for those independent variables with significant odds ratio results (Table 1) in R-Studio (R Studio Team, 2019), using the *metafor* package (Viechtbauer, 2010) with the *fsn* function.

### 3. Results

Overall (Table 1), lower temperature heat shock (50–99 °C) significantly increased the germination of invasive plant species, and the higher temperature heat shock was insignificant. The shorter smoke exposure significantly increased the germination of invasive plant species, whereas the longer smoke exposure was insignificant. Heat shock significantly increased germination in ligneous seeds, and smoke significantly increased germination in herbaceous seeds. Heat shock on herbaceous species had no overall effect and smoke exposure to ligneous seeds was insignificant. Table 2 shows the results found for each invasive plant species considered.

#### 3.1. Heterogeneity ( $I^2$ )

The overall temperature heterogeneity was high (94 %), as well as that of both temperature groupings, 96 % in 100°C-120°C and 88 % in 50°C-99°C. Heterogeneity of smoke treatments was c.a. 84 %. For the pooled effects of smoke and the pooled effects of heat shock on herbaceous species the heterogeneity was 89 % and 94 %, respectively. A high heterogeneity was also observed for the pooled effects of heat shock on ligneous species (94 %). Remarkably, the pooled smoke effect on ligneous species was more homogenous (50 %). The smoke tolerance is much more uniform than the heat shock tolerance for ligneous species. In all cases, the high variation in response to heat shock and smoke indicates that there is a great deal of between study variability: the invasive species of Mediterranean environments show variability in germinative responses to heat shock and to smoke treatments. The heterogeneity plots/ L'Abbé plots (L'Abbé et al., 1987) are available upon request.

#### 3.2. Effect sizes, confidence intervals and FSNs

##### 3.2.1. Heat shock

3.2.1.1. *Global temperature effect.* Heat shock of the collated data set using both sets of temperature ranges significantly increased the germination rate of the invasive species investigated in an analysis of 58 studies (odds ratio = 2.38; Table 1; S1). The FSN value of 759 is much larger than the threshold of 300 and the results are therefore considered robust in the presence of undetected publication bias.

3.2.1.2. *High temperature range.* Heat shock of the temperature range 100–120 °C had mixed effects on the germination of invasive species in an analysis of 29 studies. 1 study did not show a difference between

control and treatment and therefore appears vacant of data (study 14; S2). 62% of studies responded negatively, and 27.58% of studies showed significantly negative rates; three of them have a 95% confidence interval that passes through the line of no effect (Studies 9, 17 & 21; S2) representing a nonsignificant result. 44.83% of the studies showed significantly increased germination rates in response to the 100–120 °C heat shock when compared to controls. Overall, the random effects model value of 1.81 indicates a positive response but it was not significant (Table 1; S2).

**3.2.1.3. Low temperature range.** Heat shock of the temperature range 50–99 °C significantly increased the germination rate of the invasive species investigated (Odd ratio = 3.01; Table 1; S3). 2 studies appear as empty data cells because the treatment did not change the germination rate from the control rate. 22 of the 29 individual studies showed increased germination in reaction to heat shock (S3) and 15 individual studies demonstrate significant increases in germination in response to these temperatures. Only 1 of the 5 inhibited species was a significant inhibition of germination (Study 10, S3). The FSN value of 449 is much larger than the threshold of 155 and the results are therefore considered robust in the presence of undetected publication bias.

### 3.2.2. Smoke

**3.2.2.1. Global smoke effect.** The global smoke effect using both sets of smoke treatment durations significantly increased the germination rate of the invasive species investigated in an analysis of 48 studies (Table 1, S4). The collated results had an odd ratio of 1.59 which supports a weakly positive effect, indicating a significant effect. The FSN value of 191 is smaller than the threshold of 250 and the results are therefore not considered robust in the presence of undetected publication bias.

**3.2.2.2. Longer smoke treatment duration.** The smoke treatments of 10 minutes duration increased the germination rate of the invasive species investigated, but the effect was not significant (odd ratio = 1.49; Table 1; S5). 10 of the 24 individual studies showed increased germination, of which 5 are significant. There were 9 studies that experienced a deduction in seed germination rate in response to this smoke exposure, of which 3 were significant inhibitions of germination (Studies 3, 17 & 22; S5). Therefore, the rate of significant inhibition of seed germination by smoke was 12.5% of studies included, and the rate of significant stimulation of seed germination was almost 21% of the studies. The remaining 5 studies were either non-significant or showed no appreciable difference between treatment exposure and control.

**3.2.2.3. Shorter smoke treatment duration.** The smoke treatments of 5 minutes duration significantly increased the germination rate of the invasive species investigated (odd ratio = 1.70; Table 1; S6). 12 of the 24 individual studies showed increased germination in reaction to smoke which is 50% (S6) and 4 studies demonstrate significant increases in germination in response to 5 minutes smoke exposure (16%). There were 8 studies that experienced a deduction in seed germination rate in response to these temperatures (S6) and 1 was a significant inhibition of germination. The FSN value of 91 is smaller than the threshold of 130 and the results are therefore not considered robust in the presence of undetected publication bias.

### 3.2.3. Vegetation type: herbaceous

**3.2.3.1. Herbaceous heat shock.** General heat shock had no overall effect on the germination rate of the herbaceous invasive species investigated (Table 1; S7). 1 species did not change germination rate from control upon heat shock treatment and is blanked out. 11 of the 21 individual studies on herbaceous seeds showed increased germination in reaction to heat shock, but only 5 studies demonstrate significant increases in

germination in response to heat shock. There were 9 studies that experienced a deduction in seed germination rate in response to heat shock (S7), with effect sizes smaller than 1. 6 of these 9 were significant inhibitions of germination.

**3.2.3.2. Herbaceous smoke.** General smoke exposure significantly increased the germination rate of the herbaceous invasive species investigated (odd ratio = 2.91; Table 1; S8). 3 of the study's fall on the line of no effect with odds ratio scores of 1- designating no effect. 14 of the 22 individual studies showed increased germination in reaction to smoke and 10 of these studies demonstrate significant increases in germination in response to general smoke exposure. There were 5 studies that experienced a deduction in seed germination rate in response to these temperatures (S8), with effect sizes smaller than 1- but none were significant inhibitions. The FSN value of 414 is much larger than the threshold of 120 and the results are therefore considered robust in the presence of undetected publication bias.

### 3.2.4. Vegetation type: ligneous

**3.2.4.1. Ligneous heat shock.** General heat shock significantly increased the germination rate of the ligneous invasive species investigated (odd ratio = 4.26; Table 1; S9). Over 75% of 37 ligneous studies experienced promoted germination from heat shock when compared to controls. Of these, 23 studies demonstrate significant increases in germination in response to general heat shock. 4 of 7 negative responses were significant inhibitions of germination; the 95% confidence interval does not pass through the line of no effect (S9). The FSN value of 616 is much larger than the threshold of 195 and the results are therefore considered robust in the presence of undetected publication bias.

**3.2.4.2. Ligneous smoke.** Smoke decreased the germination rate of the ligneous invasive species investigated, but the effect was not significant (odd ratio = 0.88; Table 1; S10). 8 of 26 ligneous studies experienced promoted germination from smoke exposure when compared to controls, however only 1 species demonstrates a significant increase in germination. 4 of 26 ligneous studies had significant inhibitions of germination.

## 4. Discussion

The increase in germination of invasive plant species (mainly ligneous) subjected to low-grade heat shock confirms that serotinous features are advantageous in fire-prone environments. The serotinous species germinate in response to fire characteristics, permitting germination in a disturbed environment with limited competition (sunlight, water, nutrients etc.) and reduced chance of herbivory or predation (few predators/ herbivores are maintained post- fire) (Keeley and Fotheringham, 2000). These factors increase plant fitness and chance of reproductive success, making serotinous species more successful in the early stages of secondary succession after a fire (Keeley et al., 2011). This study highlights that many ligneous invasive species succeed in fire-prone Mediterranean ecosystems thanks to serotinous mechanisms, which is in line with the results of Santana et al. (2018) that confirmed that stimulated germination after fire is especially advantageous in Mediterranean climates.

Upon revision, our results show that most of the ligneous species that positively responded to heat shock come from Europe and Australia (Table 2). Conservation measures can consider these patterns to prevent the spread of these ligneous invasive species in the other Mediterranean ecosystems where they have been introduced. For instance, *Acacia* species, native to Australia, especially *Acacia mearnsii*, which is considered one of the world's most invasive species (Global Invasive Species Database, 2024), is present in South Africa, and some countries of Eurasia and America (CABI, 2024). Regarding those species

originating in the Mediterranean basin, measures are needed to control the invasiveness of *Cytisus scoparius*, an aggressive invasive species in Australia, America, and South Africa (CABI, 2024). In Chile, as in other Mediterranean-type ecosystems, the intensity of fires is increasing (Úbeda and Saricolea, 2016) and some native species are not well adapted to germinate after fire (Gómez-González et al., 2017), thus offering less competitiveness to invasive species like *Cytisus scoparius* or *Teline monspessulana* that germinate and resprout in response to fire temperatures (Pauchard et al., 2008).

Keeping with findings of previous studies (Carthey et al., 2018; Fichino et al., 2016), our results suggest that certain families are more stimulated by fire than others. For example, species from the Fabaceae and Cistaceae families (ligneous species), are generally stimulated by fire temperatures, while species from the Poaceae family (herbaceous species), are in general stimulated by smoke. Interestingly, the most homogenous response arose from ligneous species to smoke treatments (S20). It is seemingly more feasible for ligneous species to invest in individual survivorship and delayed reproduction, whilst not possessing a smoke-based germination mechanism. These invasive ligneous species invest in dormancy rather than latency. This is beneficial as smoke sensitive seeds tend to also respond to light and nutrient variations (Abedi et al., 2018) that can control gibberellin levels, increasing the probability of germination- something not desirable for ligneous plants. The respective advantages and disadvantages of seed type, size, mortality, dispersal and reproductive mechanism, as well as paradigm differences between refractory and non-refractory seeds, have been extensively written about (Greig, 1993; Moles et al., 2003; Martín-Sanz et al., 2017; Keeley, 1995; Fenner et al., 2005) and can help to theorize why some seed types may be favoured over others in particular habitats.

Ligneous plants had a high heterogeneity in response to heat shock; not all ligneous species utilise heat for germination timing and therefore not all ligneous species use dormant serotinous refractory seeds. Perhaps, such species employ the dichotomous reproductive method, investing in dormant and viable seeds, or are resprouting geophytes. Herbaceous germination responses, to heat and to smoke, had high heterogeneity, showing that they are more diverse in the way they deal with fire factors- there are more herbaceous plants that use heat shock mechanisms, than ligneous that respond to smoke. This could be because the herbaceous classification was based on lignin content and potentially encompassed annuals, biannuals and perennials.

A high heterogeneity is repeatedly designated as a principal indicator of inconclusiveness and inconsistency (Fletcher, 2007). This would suggest that the meta-analytical results presented here are nonsignificant due to the high heterogeneity. However, it is also cautioned that the reliance on  $I^2$  as a measure for heterogeneity can be misleading; the measure is dependent on the number of studies included for effect pooling (Rücker et al., 2008). Although the heterogeneity results of this meta-analysis diminish the conclusiveness of the pooled effect size results, one could argue they do not render the odds ratio results useless. The evaluation of heterogeneity values is dependent on the study methodology and by no means universal (Higgins and Thompson, 2002). In this case, a high heterogeneity is expected and is arguably not clinically important as it would represent the plethora of different serotinous, and fire-resistant methods associated with these plants. The suspected utility of the analysis was to attempt to conclude on the potential existence of a preferential method for fire and smoke induced germination in invasive plant species of Mediterranean biome areas, rather than to observe an unanimously successful method of dealing with fire.

The stimulation of germination by fire subsoil temperatures and the lack of effect of germination by fire surface temperatures indicates that in general the invasive species of Mediterranean environments persist in soil seed banks rather than aerial seed banks and possess seed morphologies that can resist subsoil fire temperatures. This is confirmed by the list of species studied rarely possessing serotinous cone or non-serotinous cone reproductive methods (Appendix S7; Table 2).

Consequently, the characteristics for success of invasive species in these fire-prone environments can be determined. Those seeds that use soil seed banks and respond positively to subsoil temperature heat shock are characterized by possessing refractory seeds (Keeley, 1995). If these results are deemed significant, Mediterranean environments select more advantageously for invasive species with refractory seeds, as opposed to obligate seeders, facultative resprouters, obligate resprouters or serotinous cones-, which are less successful. This is not to suggest that these alternative methods of fire-resistance and serotiny are unsuccessful among invasive species, just less so than refractory seeds. From our results, we can extract that refractory seeds are successful in fire prone environments, but many species can also use other post-fire mechanisms, such as resprouting. For instance, *Acacia* species produce massive soil seed banks and profusely resprout after fire (Le Maitre et al., 2011).

Essentially, a trade-off exists between those seeds found in aerial seed banks (refractory and non-refractory seeds of serotinous and non-serotinous pines) and those found in soil seedbanks (refractory and non-refractory seeds with other fire adaptations). This compromise entails greater seed nutrition in large seeded species of aerial seedbanks and greater dispersal capabilities and defense from seed predation in small seeded species of soil seedbanks (Keeley, 1995). This distinction selects for aerial seed banks in areas of poorer soil quality with fewer seed predators, and soil seed banks in more nitrogen and phosphorus rich soils with more seed predators (Keeley, 1995; Lamont and Enright, 2000). Richer soils mean that a developing seed will not need an as nutritious endosperm energy store, whereas poor quality soils select for a more bountiful endosperm (Keeley, 1995).

The shorter duration smoke treatments significantly increased germination demonstrating a tendency for a requirement of 5-minute direct smoke exposure, and intolerance in some species to the 10-minute direct smoke exposure. This indicates that 5-minutes direct smoke exposure is optimal for proper imbibition of most invasive species in these environments. Seeds that are responsive to smoke tend to be latent and non-refractory, and not dormant like in heat shock responsive refractory seeds (De la Cuadra, 1993). However, this presents conflicting information, as both 5-minute smoke exposure and low heat shock were successful in stimulating germination. The only plausible explanation is a combination of majority low-level heat shock and smoke exposure resistance, and the remaining species, responding more positively to smoke and heat shock than vice versa. This is what was observed in the forest plots (S3 & 6). This would suggest refractory or semi-refractory seeds with thick cuticles to be able to resist the low heat shock and short duration smoke treatment. Those species that respond positively to smoke are likely to be more penetrable to smoke chemicals and likely to respond negatively to heat shock as a result. Those species that respond positively to heat shock must be refractory seeds that will likely not respond to smoke because of their thick cuticle. This trade-off is seen in all species investigated; no species experienced significant stimulation of germination by both smoke and heat shock factors.

It was predicted that herbaceous plants would invest in short-term reproductive strategies and sacrifice individual survivorship, prioritising a permanent extensive seedbank, recruitment, and environmentally sensitive latent seeds (Çatav et al., 2018). Conversely, ligneous would invest in long-term reproductive strategies and individual survivorship favouring a smaller seedbank of dormant refractory seeds or fire-resistant seeds (Martín-Sanz et al., 2017; Keeley, 1995). The meta-analysis confirmed this, showing how herbaceous plants are more responsive to smoke and had no net effect size when subjected to heat shock- indicating the herbaceous species have latent seeds that are triggered by amelioration of the environment or smoke signals. The ligneous plants were responsive to heat shock and had an insignificantly negative germinative response to smoke-indicating that ligneous species have dormant seeds that respond positively to a structural alteration. Furthermore, latent seeds are more easily germinable than dormant seeds (De la Cuadra, 1993), which compounds how herbaceous plants favour short-term reproduction and ligneous species long-term

reproduction- agreeing with their respective stereotypical anatomy.

Although, serotinous seed traits appear to be the most desirable means of guaranteeing plant fitness in fire disturbed habitats, a great deal of variation was observed as shown by the high heterogeneity values (Figures S1–20, Appendix S5 & S6). Those species that showed neither an increase nor a decrease in germinative capacity upon exposure to heat shock are likely to be fire-resistant seed species. Resprouters are not affected by surface fire temperatures as their subterranean organs administer provisions for survival (Clarke et al., 2013) and therefore must only survive subsurface temperatures. Resprouting from dormant buds is a highly effective way to deal with low-level fire disturbance (Minor et al., 2017), but in this meta-analysis a resprouter species would have resulted in inhibition of seed germination as the seeds generally lack strong fire-resistant traits (Clarke et al., 2013). A similar situation would be observed for non-serotinous and serotinous cone species, where the fire-resistance normally comes exclusively from the cone and not the seed itself (Fenner et al., 2005). This could account for those species that responded negatively to the lower bracket heat shock (S13). Resprouters, fire resistant seeds, non-serotinous and serotinous cone species may have skewed the data and minimised the overall effect sizes. Similarly, not all species use smoke sensitive mechanisms to thrive in Mediterranean environments: some species use heat-mediated serotiny, resprouting or rapid recruitment which diversify the statistical outcome. These species that employ alternative survival and reproductive strategies may have seen their germination inhibited in this metanalysis but can be just as successful and invasive as those species that had their germination triggered. In summary, there are diverse ways to capitalise on post-fire resource advantages, and invasive species in Mediterranean environments may not necessarily rely on refractory heat-sensitive seeds or smoke-sensitive mechanisms to maximise their chances of reproductive and invasive success (Clarke et al., 2013; Fenner et al., 2005).

High frequency fire perturbed environments, create more openings for invasive species and deplete autochthonous species seedbanks (Vilà-Cabrera, Saura-Mas and Lloret, 2008). In addition, frequent fires reduce matorral mass and favor fast growing herbs (Keeley, 2000), changing the landscape of Mediterranean environments (already the case in California). If fires are too frequent, ligneous species do not have time to develop their ligneous protective layers or develop their soil seedbanks (Del Cacho and Lloret, 2012), leading to a potential shift towards herbaceous species dominance (Keeley, 2000). As a result, fire regimes should be controlled, modifying fire frequency, intensity, and treatments to favor ligneous species and deter herbaceous species, to maintain ecosystem balance.

In general, due to the invasive species of this study responding positively to both smoke and heat shock, prescribed fires, widely used for invasion management (Brancatelli et al., 2024), need to be used with caution in Mediterranean ecosystems to minimize invasive species prevalence and associated damage. This damage is compounded by invasive species increasing in biomass and therefore increasing fire severity to which they positively react (Shuman et al., 2017). This is not only true because of the adaptive strategies displayed in the results, but also because perturbed areas are of a higher invasibility (Davis and Thompson, 2000). The increase in fire frequency associated with climate change in Mediterranean environments would also increase the possibility of colonization and success of invasive species (Turco et al., 2018; Grenz and Clements, 2023; Davis and Thompson, 2000).

Prescribed burning techniques are already widely used to stop devastating fires from destroying entire ecosystems (Marino et al., 2011) - but these tactical fires could be favoring invasive species. In Mediterranean areas without the presence of invasive species with serotinous mechanisms and where the native species are pyriscent, fire should not be a problem. A previous evaluation would be beneficial to identify the presence of invasive species that could be favored by fire. In this case, prescribed burning at temperatures lower than 100 °C would be unadvisable. It is important to note that in this case, this does not mean that

one should prescribe fires of a higher temperature than 100°C; this should be evaluated case by case. The present study is a valuable guide to rapidly check for these fire-prone invasive species.

Alternatively, in areas where pyriscent invasive species grow in monocultures, prescribed burning can be used to strategically kill adult plants and stimulate seed germination, which will weaken the soil seed bank, and then the emerging seedlings can be removed using other methods, such as cutting or solarization with polyethylene mulching (Cohen et al., 2015; Sanhueza and Zalba, 2012). In addition, in these areas, where invasive species are densely populated, fires reaching temperatures higher than 120 °C can be lethal for plants and seeds of the undesirable invasive species (Reyes and Trabaud, 2009).

Depending on the objective of a restoration or conservation project in an area of the Mediterranean biome, the plan can be modified using the information presented in this study. Fire can only be advisable in Mediterranean ecosystems where native species can be favored, and invasive species negatively affected or at least not promoted. Smoke and heat shock seed treatments should be considered for promoting, herbaceous and ligneous species, respectively, in their native areas and should be avoided if such species are undesirable in non-native ecosystems. The smoke-herbaceous and heat shock-ligneous paradigms hold for native plants, and smoke treatments have already successfully been used in agricultural practices (Çatav et al., 2018). If such treatments are employed, managers can also take into account the information collected here and experiment with temperature ranges and exposure times that do not favour invasive species. For instance, a heat shock treatment higher than 99 °C and a direct smoke treatment longer than 5 minutes could be used to favour a known native species without excessive encouragement of invasive species. Additionally, conservation efforts using these results should also consider the likely effect on autochthonous species and on the environmental characteristics of the ecosystem.

The heat shock effects indicate that serotinous refractory seeds or heat resistant seeds can be favoured in Mediterranean ecosystems more than serotinous cones, resprouters, or colonizers without serotinous or heat resistant seeds. This has two implications. Firstly, the fact that fire exposed Mediterranean environments select for subsoil seed bank life cycles means that these types of species can be prioritised in ecological restoration efforts in their native areas to increase the probability of reproductive success and ecological community maturation. Secondly, this means that some invasive species are effectively using these methods to propagate effectively in Mediterranean ecosystems, and therefore, invasive species' elimination efforts should be concentrated to reduce the profitability of the soil seed bank for these invasive species. Successfully combining these superficially contradicting restoration efforts, would lead to healthier Mediterranean biome ecosystems.

## 5. Conclusions

From this meta-analysis, we can conclude that, globally, heat shock and smoke exposure treatments both increase germination of invasive species suggesting the presence of serotinous germinative mechanisms. This has important implications for fire regime management in the control of invasive species. The effect of heat shock and smoke differed, the former mainly promoting germination of ligneous species and the latter promoting the germination of herbaceous species. This information can be used in restoration efforts to help selectively promote or inhibit certain plant species and life histories within the target Mediterranean biome ecosystem community. In addition, only gentle heat shocks, with temperatures reached in the subsoil during fires (50–99 °C) and brief smoke exposures (less than 5 min) are more effective at increasing germination of Mediterranean invasive species. Therefore, when using prescribed fires, land managers should avoid these temperatures and exposure times in areas where the invasive species can be favoured. Alternatively, these temperatures can be used to deplete soil seed banks of invasive species and then kill the seedlings with

mechanical, chemical, or physical methods. Higher fire temperatures (>150 °C) are usually lethal for seeds and can be used to eradicate some invasive species and help restore an ecosystem with native species. The information found here can also be used to favour the germination of invasive species in their native areas.

### CRedit authorship contribution statement

**M. Esther Pérez Corona:** Writing – review & editing, Validation, Supervision, Conceptualization. **Samuel Suarez-Ronay:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Silvia Medina Villar:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Conceptualization.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

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Samuel Suarez-Ronay: Conceptualization, methodology, formal analysis, data curation, visualization, writing-original draft, writing-review and editing. Silvia Medina: Conceptualization, supervision, writing- review and editing. Esther Perez: Conceptualization, supervision, writing- review and editing. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.122168](https://doi.org/10.1016/j.foreco.2024.122168).

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