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Fire as driver of the expansion of *Paraserianthes lophantha* (Willd.) I. C. Nielsen in SW Europe

J. García-Duro · O. Cruz · M. Casal · O. Reyes

Área de Ecología, Dpto. de Biología Funcional, Facultad de Biología, Universidade de Santiago de Compostela, Campus Vida, 15783 Santiago de Compostela, Spain
e-mail: juan.garcia.duro@usc.es

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Abstract *Paraserianthes lophantha* (Willd.) I. C. Nielsen is a plant species native to SW Australia that has recently invaded temperate ecosystems in Europe and other areas in the world. Since it has been found in burnt areas and its expansion could be promoted by forest fires, the germination response of seeds to fire factors (heat, smoke, ash and charcoal) was analyzed. Furthermore, stochastic post-fire invasion models were developed to check the impact of one-off and repeated forest fires. The spreading pattern after fire was modeled to provide accurate forecasts for future fires. The model was parameterized using data recorded after the 2013 forest fire in the Natura 2000 site Monte Pindo. Germination response is mainly modified by heat, which breaks seed dormancy at moderate temperature and kills seeds at high temperatures. Smoke, ash and charcoal did not have relevant influence on seed germination except large amounts of ash, which prevented seed germination. Neither charcoal origin (from native or from exotic species) had a significant effect on *P. lophantha* germination. The invasion model demonstrated the significant role of forest fires promoting *P. lophantha* spreading. Recurrent fires promote the spreading of invasive species, threatening natural plant communities. However, the expansion of the species was not exclusively linked to forest fires: anthropic systems, edges of agricultural areas and old fields were particularly affected by *P. lophantha* expansion. Some control methods based on the reproductive behavior and spreading pattern of *P. lophantha* were proposed in order to prevent new invasions and manage invaded areas.

Introduction

Forest fires are one of the main disturbances in ecosystems across the world and particularly in Mediterranean areas. They modify plant's reproductive success of many species (Cavallero and Raffaele 2010). The intensity of fire through the different

effects detected on ecosystems (heat, smoke, charcoal, ash) can modulate the reproductive behaviour of alien and native plant species (Reyes and Casal 2004, 2008; Reyes and Trabaud 2009; Aran et al. 2013; Reyes et al. 2015a, b) and their success after disturbance as well.

However, since the germination is the most critical phase in the life cycle of plants (Reyes et al. 1997), the success in colonizing new areas critically depends on it. It is known that plant reproductive attributes have a major impact on community structure over time (Herrera 1986; Smith-Ramirez and Armesto 1994).

Disturbances such as forest fires, no matter where, also promote the proliferation of invasive alien species in native plant communities (Richardson et al. 1990; D'Antonio and Meyerson 2002; Didham et al. 2007; Pauchard et al. 2008; Masocha et al. 2011). Many alien plant species are better competitors than native species (Heger and Trepl 2003), take advantage of resources in rich post disturbance environments and are able to exclude them for long periods of time (Davis et al. 2000) altering many ecological processes (D'Antonio and Meyerson 2002; Gassó et al. 2009; Mandle et al. 2011), triggering the reduction of diversity through competition, predation and habitat modification (Rascher et al. 2011). Alien invasive species are a growing threat to the persistence of native assemblages and natural communities. Indeed, a number of authors have demonstrated the feed-back between the recurrence of fire and the entrance of invasive species (Pauchard et al. 2008; Mandle et al. 2011; Masocha et al. 2011).

Paraserianthes lophantha (Willd.) I. C. Nielsen is a leguminous plant species native to coastal areas in SW Australia (Adair 2008) that has invaded other areas in Australia and other regions and countries across the world such as New Zealand, Indonesia, South Africa, Bolivia, Chile, Colombia, Ecuador, Venezuela, USA, Portugal, France, Italy and Spain, according to the Global Biodiversity Information Facility (2017). Galicia (NW Spain) is one of the main entrance gates for *P. lophantha* in Southern Europe. It is also one of the areas in Europe with the highest incidence of fire (Rodríguez de Sancho 2006) despite the dominance of Atlantic climate and vegetation. According to official data of the Regional Fire Service (Xunta de Galicia 2017), 90,222 fires were detected between 2001 and 2015. 380,773 ha were burnt within that period, which makes up 18% of the forested area. Fire incidence in Galicia is somehow the result of its location in SW Europe, on the edge of Atlantic and Mediterranean climatic areas, where the quick accumulation of biomass in ecosystems combines with occasional summer droughts. At the same time, Galicia has a very high species diversity compared to other regions

in Atlantic Europe (Ramil Rego 2001; Muñoz et al. 2012) and fire has a relevant role in the management of such diversity (Muñoz et al. 2014) but the often associated proliferation of alien invasive species is seriously threatening ecosystems' diversity.

Since *P. lophantha* is currently in an initial stage of spreading in South Europe (Herrero-Borgoñón 2007; Derkx et al. 2015), where forest fires burn natural ecosystems so often (Reyes et al. 2000; Moreira et al. 2001), it is particularly necessary to get to know the role of fire in its expansion process and to design tools for the control of the species (Pauchard et al. 2008).

Paraserianthes lophantha in its original distribution area is an obligate seeder shrub or small tree that forms permanent soil seed banks (Bell et al. 1995). It is a fast-growing species which, once seedlings become established, can outcompete native vegetation (Weber 2003).

Little is known about the germination of this species in absence of fire (Cavanagh and Langkamp 1987; Weber 2003) and we are not aware of any other study analyzing the effects of fire upon the viability or the germination response of seeds in invaded areas. The spreading process after fire has not been modelled either. Modelling alien species spreading after fire will provide tools to predict their expansion in environments under high recurrence of fire, which is extremely useful for decision-making. Knowing the spreading rate and the reproductive behavior in relation to fire is essential to design management tools when dealing with invasive alien species in areas with high recurrence of fire; particularly coastal areas, which are often entrance ways to new areas for exotic invasive species (Chytrý et al. 2009; Gassó et al. 2009; Rascher et al. 2011).

Thus, we designed this study with the overall objective of knowing the role of fire in the spreading of *P. lophantha* in a temperate coastal area and to propose control management measures. The underlying objectives were: a) to know the effect of the fire factors upon the germination and viability of seeds of this species, b) to assess the spreading of *P. lophantha* under high fire recurrence through a spatially explicit invasion model specifically developed for this purpose. In this way, we have identified some of the most invasion-prone environments and proposed control management tools.

Materials and methods

Study area

The site Carnota-Monte Pindo (NW Spain, SW Europe), a 4700 ha coastal area in Galicia included within the EU Natura 2000 Network, was chosen as the study area. Mild temperatures, close to 13.8 °C, the rainy conditions, about 1050 mm per year, and seasonality, with a moderate summer drought and less than 125 mm during summer (Fick and Hijmans 2017) and underdeveloped acidic soils characterize this coastal site. Flat areas with deeper soils here have traditionally been converted to croplands; however, the remaining areas, occupied by natural ecosystems, are still managed by tree logging, grazing, heathland cutting and cultural burnings. The abandonment of agriculture and the traditional management after the mid 1950's led to strong changes in ecosystems, and wildfires are the main disturbance nowadays.

Monte Pindo is also among the areas of high risk of fire in Galicia (DOGA 2007) and its ecosystems endured repeated forest fires throughout recent history: the SE sector was burned in 2000 and forest fires in 2005 and 2013 burned nearly the whole of Monte Pindo. The last fire burnt 2323 ha in 2013, setting the boundaries of the study area.

The typical vegetation show low nutrient requirements. The most representative vegetation within burnt areas was sparse pine (*Pinus pinaster* Aiton) forest. The poor regeneration of *P. pinaster* and the quick post-fire recovery of the understory vegetation resulted in the consolidation of several types of plant communities in some areas, mainly heathlands, broomlands, gorselands and other communities with high cover of non-native species, particularly *Eucalyptus globulus* Labill., *P. lophantha* and *Acacia melanoxylon* R. Br.

The first plants of *P. lophantha* were introduced in populated areas of Monte Pindo with ornamental purposes a few years before 2005, according to the local people. This species grows rapidly in Monte Pindo (4 m high in 3 years) and by the third year produces many seeds relatively large (about 6700 seeds/m² with an average maximum length of 4.52 mm, unpublished data). Some compact stands started to develop after the 2005 fire and the number and size of patches increased considerably after the fire of 2013.

Paraserianthes lophantha germination and response to fire factors

The seeds used in germination and viability test were collected on July 2015 and July 2016. The germination response of *P. lophantha* seeds in control conditions and under the effects of fire factors was studied following the procedures in previous studies (Arán et al. 2013; Reyes et al. 2015a). In order to determine the role of fire intensity factors on germination, different levels of heat, smoke, ash and charcoal were applied to seeds collected on July 2015 from unburnt plants. The seeds were heated in a forced air oven at 80 °C, 110 °C, 150 °C and 200 °C, for 5 and 10 min for thermal treatments. These temperatures and exposure times correspond to those measured at different soil depths during forest fires and experimental burns by DeBano et al. (1977) in California chaparral, Trabaud (1979) in French garriges, by Auld and O'Connell (1991) and Bradstock and Auld (1995) in Mediterranean ecosystems of SE Australia and by Díaz-Fierros et al. (1990) in shrublands of SW Europe. Seeds in smoke treatments were settled in a smoke-saturated chamber for 5, 10 and 15 min resulting in 3 levels of smoke exposure. Ash addition treatments were Ash1 (0.027 g/replicate, 43.5 kg/ha), Ash2 (0.055 g/replicate, 87 kg/ha), Ash3 (0.11 g/replicate, 174 kg/ha), Ash4 (0.275 g/replicate, 435 kg/ha) and Ash5 (0.55 g/replicate, 870 kg/ha). These quantities of ash correspond to multiples of the values recorded by Soto et al. (1997) after experimental burns on an Atlantic shrubland in SW Europe. The seeds were sown in Petri dishes in presence of the corresponding quantity of ash. Two charcoal treatments, evaluating native or exotic origin of charcoal, were performed, one treatment with *P. lophantha* charcoal (exotic charcoal) and the other with charcoal of *Ulex europaeus* L. (native charcoal), the most abundant native shrub species in the area (Reyes et al. 2000; Puentes et al. 2016). The amount of charcoal used per replicate was 0.26 g (411 kg/ha). This quantity is the same as that taken by Ohlson and Tryterud (2000) in boreal forest fires of Scandinavia and with the quantities used in other studies (Reyes and Casal 2006; Reyes et al. 2015b). Afterwards, both the ash and the charcoal were put in Petri dishes. A factorial design, with the different intensity levels nested within each Fire factor was carried out.

Every treatment was composed of 5 replicates of 25 seeds each that were put in 9 cm Petri dishes over cellulose filter paper. Seeds were kept at 24 °C in light conditions for 16 h and 8 h in darkness at 16 °C during the experiment and the germination was monitored three times every week until the germination ended, 104 days after sowing (Arán et al. 2013; Reyes and Casal 2006; Reyes et al. 2015a).

Tetrazolium viability tests were conducted with control seeds from the 2015 and 2016 collections. Viability tests were performed with heated seeds from 2016, following the thermal treatments. Seed viability was also determined using 5 replicates of 25 seeds per treatment.

Differences in germination percentage and viability among the control treatments and fire treatments were tested using generalized linear models with binomial distribution. T_{50} data were analyzed by generalized linear models with Poisson distribution; however, treatments with fewer than three replicates with germination events were not included in the analyses. Tukey Contrasts were used as a post hoc test for multiple comparisons of means. All these analyses were performed in R (R Core Team 2016) with packages arm (Gelman and Su 2016) and multcomp (Hothorn et al. 2008).

Paraserianthes lophantha expansion and Modelling

Field sampling

The study area, the whole 2240 ha burned area, was partitioned into sectors 2.5 years after the 2013 fire in relation to built structures, roads and natural features in the landscape. Sectors and high-cover *P. lophantha* stands within each sector were edged and positioned with a sub-metric GPS and the features were post-processed. The pre and post-fire overall cover of *P. lophantha* within each stand was estimated visually.

Together with the sectored *P. lophantha* cover data we used the Land Occupation Information System of Spain, SIOSE (<http://www.siose.es>), to determine the relative abundance and rate of spreading of *P. lophantha* on different land cover classes and to identify the main environments threatened by the expansion of *P. lophantha*. The cover categories in the SIOSE system were classified into five groups: Artificial –populations and infrastructures–, Agricultural

lands –croplands, pastures and grasslands–, Forested areas –forests and plantations–, Shrublands and low cover Natural systems –rocky areas, bare soil areas, littoral sandy areas, water sheets... –.

Additionally, the environments where *P. lophantha* seedlings grew vigorously and reached high cover were searched out to gather information on the structure of plants. An environmentally homogeneous plot about 150 m wide and 200 m long was selected and the plants were classified into three groups according to their location (stand kernel, stand edge and isolated). The maximum and minimum diameters of the projected crowns were measured for more than 50 plants randomly chosen 2.5 and 4 years after fire. The dimensions of plants before fire were also estimated inferring the projection of the pre-fire crown from the charred parts of plants.

The model: parameterization

A stochastic model was developed to reproduce the spreading of *P. lophantha* after fire by spatial point processes. Our model is similar to the model suggested by Mouillot et al. (2000) to simulate the spatial distribution of species based on aggregation–repulsion rules.

The model takes the post-processed polygons and the *P. lophantha* cover estimates recorded within the same area where the plant crowns had been measured 2.5 years after fire. It also takes the probability density function of the projected area of crowns of measured plants. The cover of *P. lophantha* within each polygon and a random sample from the crown areas distribution determined the number of plants within each polygon in the spatial model.

Plants before 2013 were generated from the center of polygons with burned plants. The cohorts after were generated from the position of plants in the previous cohorts. The spatial distribution of plants before 2013 and the distribution of new cohorts with respect to their mother plants were assumed to follow one of the following functions:

(a) the probability density function of the Gamma distributions:

$$g(x|k, \theta) \sim \frac{\theta^k x^{k-1} e^{-\theta x}}{\Gamma(k)} \quad \text{for } x > 0 \text{ and } k, \theta > 0 \quad (1)$$

(b) Truncated normal distributions, where the negative values of normal distributions were removed, so that

$$\psi(x|\mu, \sigma^2, 0) = \begin{cases} 0 & \text{if } x \leq 0 \\ \frac{\vartheta(x|\bar{\mu}, \bar{\sigma}^2)}{\Phi(x|\bar{\mu}, \bar{\sigma}^2)} & \text{otherwise.} \end{cases} \quad (2)$$

Here $\vartheta(x|\mu, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$ for $\mu, \sigma^2 > 0$ is the probability density function of the general normal distribution, $\Phi(\cdot)$ is the cumulative distribution function and the parameters $\bar{\mu}$ and $\bar{\sigma}^2$ are the mean and variance of the parent general normal probability density function; $\bar{\mu} = 0$.

(c) Uniform and truncated normal combined distributions

$$u(x|z, \mu, \sigma^2) \sim \begin{cases} \frac{p}{z} & \text{if } x < z \\ \frac{\vartheta(x|\bar{\mu}, \bar{\sigma}^2)}{\Phi(x|\bar{\mu}, \bar{\sigma}^2)} (1-p) & \text{otherwise,} \end{cases} \quad (3)$$

for $x > 0, z > 0$ and $\mu, \sigma^2 > 0$, being p the weighting parameter that makes overall probability equal to 1.

(d) T and negative exponential combined distributions for seed dispersal and density dependent effects, respectively (Beckman et al. 2012)

$$v(x|\alpha, \beta, \gamma) \sim \frac{1}{\pi e^\alpha \left(1 + \left(\frac{x}{e^\alpha}\right)^2\right)^2} - \beta \frac{2}{\pi \beta^2} e^{-2\frac{x}{\beta}} \quad (4)$$

for $x > 0$ and $\alpha, \beta, \gamma > 0$

Once the protocol was set, a minimum number of 250 simulations with randomized parameterization were run for each distribution to reproduce the allocation of plants in the area of interest 2.5 years after fire. The whole plot was split by Voronoi polygons and the projected area of each plant in the simulations was randomly taken from the crown area distribution according to the available space for each plant. Finally, the RSME of the cover of *P. lophantha* in each simulation regarding measured field cover was calculated and a curve or surface was fit by nonlinear least squares for each spatial distribution in order to select the distribution and parameters with lower deviation from field data.

The model: new rules for simulations and forecasts

Once the distribution and parameters that best fit field data were identified, 50 simulations were run to reproduce the occurrence of 4 consecutive fires in the same area: the fires in 2005 and 2013 plus another two additional fires. The initial conditions for the simulations were the same as indicated in the former section for parameterizing the model. However, since the total number of potential descendants followed a geometric progression, density dependent effects were assumed strong in the fires after 2013 and an external correction apart from the model was introduced in the simulations to reproduce post-recruitment mortality: a number of descendants in the fires after 2013 were removed in order to meet the distribution of crown areas at 2.5 and 4 years after fire. The protocol to remove plants based on the projected area of each simulated plant and the random selection of plants on overpopulated size classes. After assigning new areas to remaining plants after computing their available space through Voronoi polygons, the distribution of crown areas of simulated plants was checked against the theoretical distribution. The removed plants were definitively dismissed when the new distribution better fitted the theoretical distribution. This iterative process stopped after a number of iterations without improving the fit of the previous distribution.

Once all the simulations were run and the overall cover in each simulation was computed at 0, 2.5 and 4 years after fire, the trend of *P. lophantha* cover after fire was fitted to a biparametric exponential function. Differences in the cover among fires were compared using nonlinear mixed models.

The model: software

Algorithms and statistics were developed in R environment. Maptools (Bivand and Lewin-Koh 2016), rgeos (Bivand and Rundel 2016), rgdal (Bivand et al. 2016), raster (Hijmans 2016), nlme (Pinheiro et al. 2018) and deldir (Turner 2016) packages were used for the management of spatial features and statistics in R. *P. lophantha* polygons were post-processed with MobileMapper Office 4.7 software and data from the Spanish National Geodesic Network of GNSS Permanent Stations of Reference (2016).

Results

Reproductive behavior after fire

Germination percentage

The germination of *P. lophantha* without fire was scarce, just a 0.8% germination rate (Fig. 1). Moderate thermal shocks (80 °C 5 min, 80 °C 10 min and 110 °C 5 min) produced a strong stimulation of the germination: germination in the 80 °C 10 min treatment was 21 times larger than control germination. Instead, high thermal shocks tend to stop the germination completely. The analysis of variance detected highly significant differences among treatments ($P < 2.2e-16$) and Tukey's test detected significant differences between control and moderate thermal treatments. Smoke and charcoal treatments did not modify the germination. The origin of the charcoal did not modify the germination. Low concentrations of ash produced germination percentages close to control values, but the germination tended to decrease as concentration of ash increased, reaching 0% with ash 5.

T_{50}

The time needed to reach half of the final germination events, T_{50} , was 57 days in control conditions (Fig. 2); many treatments led to lower T_{50} values. There were significant differences among treatments ($P < 2.2e-16$). Furthermore, the general trend showed that the treatments that increased the

germination percentage tend to reduce the T_{50} and viceversa. For instance, the T_{50} of treatment 80 °C 10 min and treatments with higher temperature was lower than 20 days and T_{50} of *Ulex* charcoal treatment was 80 days. Smoke 10 min was significantly higher than 80 °C 10 min and 110 °C treatments, with values that were quite similar to germination in control conditions.

Viability

The viability of control seeds was close to 100%, either seeds from 2015 harvest or from 2016 harvest (Fig. 3). The treatments 80 °C 5 min and 80 °C 10 min did not change seed viability; thermal shocks over 110 °C 5 min reduced the viability and the negative effects of the treatments grew larger when raising the temperature or when increasing the exposure time to heat. As a result of thermal shocks, the viability was 83.2% under treatment 110 °C 10 min, 42.4% with 110 °C 10 min. The treatment 150 °C 5 min and the treatments above killed all the seeds. The analysis of variance detected highly significant differences between treatments ($P < 2.2e-16$) and Tukey's test found three groups. The first one consisted of four treatments: Control 2015, Control 2016, 80 °C 5 min and 80 °C 10 min; the next group was composed of 110 °C 5 min and the remaining group included 110 °C 10 min, 150 °C 5 min, 150 °C 10 min, 200 °C 5 min and 200 °C 10 min. Most of the seeds, dormant in control conditions and moderate thermal treatments, died with high thermal shocks.

Fig. 1 Mean and standard deviation of the germination percentage reached with the fire treatments and the control treatment. Labels at the top of the bars indicate significant differences with control

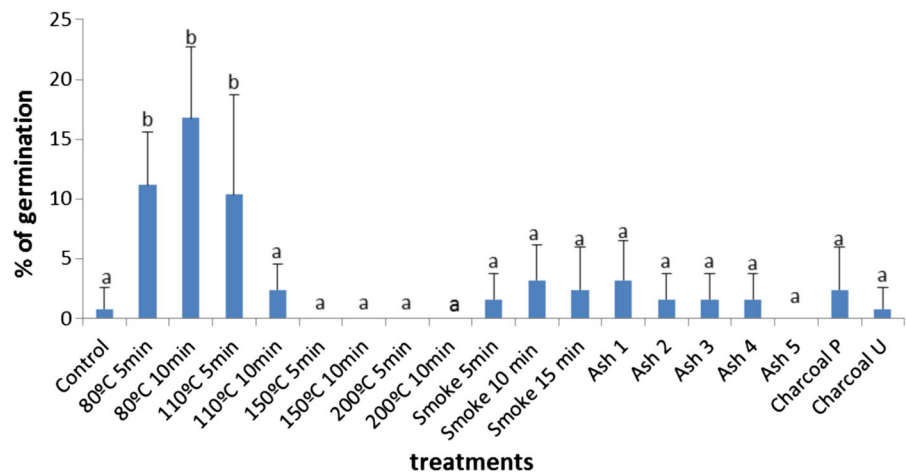


Fig. 2 Mean and standard deviation T_{50} reached with the fire treatments. Labels at the top of the bars indicate significant differences among treatments. Treatments without labels did not reach enough replicates with germination events and they were not included in the analyses

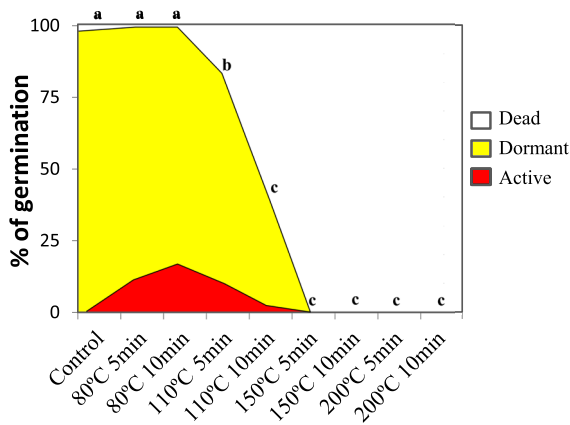
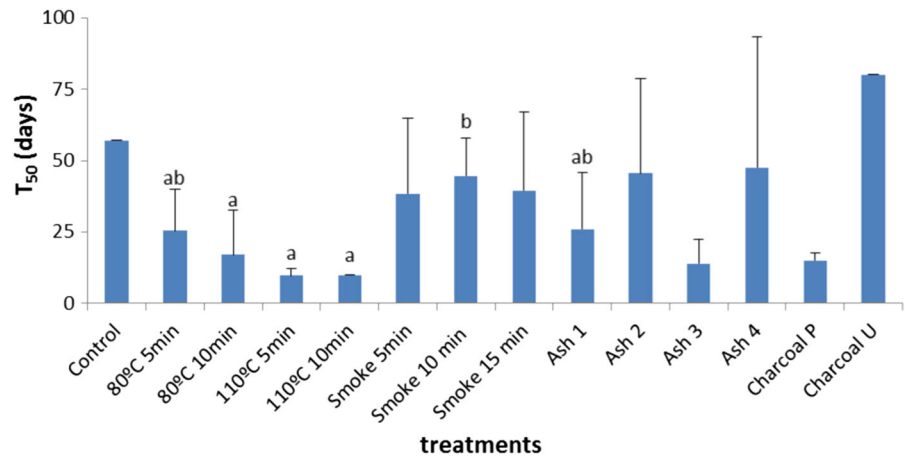


Fig. 3 Active seeds, dormant seeds and dead seeds in control conditions and after thermal treatments. Labels indicate differences in the viability percentage of *P. lophantha* seeds after thermal treatments

Paraserianthes lophantha spreading and modelling

Shrublands and Low-cover natural systems occupied about the 87% of the study area, Forested areas about 9% and Agricultural lands and low-cover Natural systems about 2.5% and 1.6%, respectively, according to the SIOSE system.

Paraserianthes lophantha stands were widely distributed across Monte Pindo, but some environments such as uncontrolled inert waste landfills were highly susceptible to invasion by *P. lophantha* and many other alien species. These environments were the first being invaded, reaching high cover before 2005 and they were the invasion source for new areas. *P. lophantha* also tend to be near road systems and forest tracks.

Besides, edges of agricultural areas and oldfields were particularly affected by *P. lophantha*. Instead, well preserved natural ecosystems with high cover of vegetation and areas with underdeveloped soils showed low presence and lower expansion of the species.

Before fire the relative occupation was very low in all the land cover categories. Over the 0.035% on Agricultural lands and Artificial areas, about 0.015% on Forested areas and Shrublands and 0.006% on low-cover Natural systems. Four years after fire the cover of *P. lophantha* was 15 times higher on Forested areas, associated to the decline of pine forests which hardly endure the high recurrence of fire, 7 times higher on Shrublands, 5.6 on Agricultural lands, 4.9 on low-cover Natural systems and 3.4 on Artificial areas. However, the regular management, specific control measures and the decrease of suitable environments have limited the expansion of *P. lophantha* on Agricultural lands and Artificial areas.

The total area occupied by the projection of *P. lophantha* plants three years after fire, in 2017, was 1.99 ha; 7.5 times higher than pre-fire cover. *P. lophantha* formed dense stands after fire (over 95% cover), replacing native communities, where native species hardly exist (ESM_1). These stands were found in areas where the species was already present before fire or locations where huge amounts of seeds arrived from neighboring pre-fire stands. Isolated plants were usually found around dense post fire stands, scattered into native plant communities.

There were no large differences in the minimum RMSE of the four functions (ESM_2). The lesser fitted

RSME value (72.6) was given by function (2). The RSME of function (3) tends to approach the RSME of function (2) when parameter z approached 0, being 78.6 the lowest RSME with z value close to 0. Function (4) goodness of fit was somewhere in the middle of functions (2) and (3), and the minimum RSME was 75.2. Function (4) fitted the worst (90.1).

Besides the low RSME, the need for a low number of parameters led to the selection of function (2), which only needs one parameter, against the remaining functions, particularly function (4) which requires up to three parameters.

The forecasts of the model indicated an increase in the number of plants and cover of *P. lophantha* after each fire. The increase in the number of plants was also related to a strong increase of cover generation after generation (Fig. 4), fire after fire, until there was not enough space for more plants. The strongest increase in cover and number of plants was found between the first and the second fires; the cover after the 2013 fire was many times greater than after the fire of 2005, when a small number of plants invaded the area for the first time. Nevertheless, since most of the initial mother plants were located on one edge of the plot, this limited the post-fire cover in fires after 2013; the population could only spread in one direction after a few fires. The cover of *P. lophantha* also increased after each fire following a sigmoid curve. The strongest increases in cover were detected during the first 2 years after fire. The increase of cover after 2.5 years was low due to the competition among plants

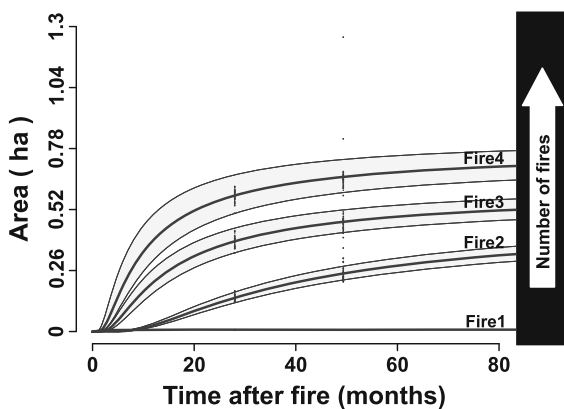


Fig. 4 Mean and 95% confidence interval of the post-fire cover of *P. lophantha* according to the fire expansion model after 4 forest fires in the invasion-prone area in Monte Pindo used to model *P. lophantha* spreading

within the stands and the decrease in the number of plants along time. The increase of cover after 4 years was particularly low after the latest fires (the 3rd and 4th fires), when most plants were part of big, dense stands.

Discussion

Fire factors, which often have an effect upon species germination, and the characteristics of post-fire environments tend to create favorable conditions for invasive species to spread. Both aspects are needed to get to know the expansion of alien invader species and to propose control management measures. In this regard, four years after fire *P. lophantha* cover was multiplied 7.5 times and their encroachment was closely related to some fire factors. It shows low germination in control conditions despite the high viability of seeds. The germination was stimulated by moderate thermal shocks, which fastened and stimulated it; so did native populations of *P. lophantha*, which also need heat to reach high germination values (Bell et al. 1995). Even though the germination percentages did not reach high values in our experiment, they were 21 times higher than those recorded under control conditions. The heat broke seed dormancy and triggered germination processes, as evidenced in other leguminous species (Rivas et al. 2006; Reyes and Trabaud 2009; Baeza and Roy 2008; Arán et al. 2017). As the temperature exceeded 100 °C the number of scarified seeds was increasingly higher; however, the percentage of seeds with damaged or killed embryos also increased. The increase of seed mortality with raising temperatures was noticeable over 110 °C 5 min and, in particular, over 110 °C 10 min. Intense thermal shocks, 150 °C 5 min or over, totally suppressed the germination. Fire factors such as smoke, ash and charcoal (native and exotic) did not change germination percentage because they couldn't break seed dormancy; nonetheless, there is the possibility that these factors (smoke, ash, charcoal) influence germination when they occur in combination with heat, as seen in other studies (Thomas et al. 2003; Arán et al. 2012). The only exception was high concentrations of ash, which inhibited seed germination probably as a result of the high difference in osmotic pressure in and out of the seed, preventing the entrance of water (González-Rabanal and Casal 1995).

Another invasive species in Europe, *Acacia melanoxylon* R. Br., also exhibited the same behavior regarding the origin of charcoal (Cruz et al. 2017).

The overall balance between seed coat breakage and embryo mortality resulted in a germination response to heat common to other leguminous and non-leguminous species in fire prone environments (Reyes and Casal 2008; Arán et al. 2013).

Despite many native species have a strong positive response to fire (Reyes and Casal 2008), forest fires promote *P. lophantha* spreading because fire has a double effect, stimulating seed germination, as indicated above, and reducing the competitive resistance of the native vegetation. Both effects also have a very significant positive effect on seedling recruitment of other leguminous, obligate seeder species (Baeza and Roy 2008; Pauchard et al. 2008). The recruitment of new plants mostly occurs the first months after fire and, later, the increase of cover relies on plant growth. Fire after fire, *P. lophantha* is able to colonize new areas following a temporary discontinuous spreading model where the expansion of the species is strongly linked to forest fires as the model developed herein demonstrates.

In addition, the highest initial levels of invasion usually occur for agricultural, urban and industrial land-cover classes (Chytrý et al. 2009). Alien species are often first introduced to urban areas, so they are often hotspots for invasions (McLean et al. 2017) that harbor significant populations of plant taxa that are able to spread to surrounding natural areas to launch invasions (McLean et al. 2017). Invasion prone environments were associated to human landscapes; particularly environments with high availability of resources such as abandoned agricultural lands and disturbed environments, often associated with the decline of native ecosystems. *Paraserianthes lophantha* rarely invaded unproductive environments and undisturbed natural ecosystems. The regular management, specific control measures and the availability of new suitable environments limit the expansion of *P. lophantha* on Agricultural lands and Artificial areas.

Despite *P. lophantha* seeds lacking specific structures for dispersal, they spread to other areas. Barochory, the dispersal by gravity alone, is probably the main dispersal type and the density of the heavy seeds decreases rapidly beyond the limits of the canopy, but other types such as zoochory or pod dispersal by wind cannot be disregarded. Indeed, seed dispersal by water

has already worked for some populations, as Weber (2003) found in other geographical areas. The importance of such methods is that they can disperse seeds a long distance away. These punctual events, if they succeed, trigger new invasion processes, threatening natural and managed ecosystems, particularly under recurrent fires. Thus, even if rare, they have very significant ecological consequences.

In any case, the spread of *P. lophantha* is often associated to human activity either by being introduced, dispersed or promoted through the creation of suitable conditions for recruitment and permanence. Such conditions are usually met in artificial and managed environments (Davis et al. 2000; Chytrý et al. 2009; Masocha et al. 2011; McLean et al. 2017).

Management proposals

P. lophantha is an obligate seeder (Bell et al. 1995) that cannot survive after clear-cutting. Thus, cutting the stand before the 3rd year after emergence (approximately 4 m tall) is an appropriate method to prevent the accumulation of new seeds in the soil seed bank. Seedling emergence and recruitment needs to be controlled after forest fires and controlled burns by cutting or removing plants because heat scarifies seeds and promotes germination.

Preventing seedlings' early growth and establishment is the key to control *P. lophantha*, and the early post-fire recovery of native vegetation will help to prevent the recolonization of burned areas and the invasion of new ones. Sowing seeds of highly resilient native species that germinate early and recover well on burned areas will contribute to this purpose. In Atlantic areas of SW Europe this role could be played by *U. europaeus* and *Cytisus scoparius* (L.) Link. Both species germinate early and intensely after fire, grow quickly and form such compact stands that sunlight hardly passes through the canopy, preventing the development of *P. lophantha* seedlings.

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