



# *Hakea decurrens* invasion increases fire hazard at the landscape scale

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**Abstract** *Hakea decurrens* subsp. *physocarpa* is an invasive fire-adapted shrub of Australian origin that is quickly expanding in Portugal with potential impacts on fire behavior and fire regime. In this study we examined the effects of *H. decurrens* on fire hazard by assessing fire behavior indicators at the landscape scale, using a modeling and simulation approach. Six fuel models for *H. decurrens* were developed through fuel characterization and experimental fires. The fuel models correspond to combinations of developmental stages of *H. decurrens* populations (Early, Intermediate and Mature) and management (Standing and Slashed fuels). These combinations were used with three levels of

*H. decurrens* invasion, corresponding to 25%, 50% and 75% of cover of the landscape, applied to five real landscapes in northern Portugal (replicates) under three fuel moisture conditions (Low, Medium and High), used as surrogates of weather severity. Fire behavior simulations were conducted with FlamMap software. The relationships between fire behavior indicators (flame length, rate of spread and burn probability) at the landscape level and the four factors tested were analyzed using Generalized Linear Mixed Models. Standing fuels were found to be more hazardous than slashed fuels. Fire-hazard increased with *H. decurrens* stand maturity and

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slash, regardless of moisture conditions. The results of this study indicate that *H. decurrens* expansion might negatively affect the fire regime in the north of Portugal. Our findings add to other known negative impacts of the species on native ecosystems, calling for the need to reinforce its control.

**Keywords** Fire behavior · Fire hazard · FlamMap · Fuel models · Plant invasions

## Introduction

Invasive alien plant species (IAPS) and wildfires are two of the most serious economic and environmental threats to terrestrial ecosystems in the world (Rai and Singh 2020), often related to human activities (McNeely 2001). Invasive alien plant species can cause ecological impacts at several levels, including effects on individuals, populations (genetics and dynamics), communities (composition and structure), and landscapes (changes in structure and function) and in the supply of ecosystem services (Ehrenfeld 2003; Bradley et al. 2019; Pyšek et al. 2020). The two topics, plant invasions and wildfires, are often interrelated. The effect of fire on plant invasions has been thoroughly studied by several authors. Fire is an important promotor of plant invasions due to the changes it causes on community structure, altering patterns of coexistence and competition (Brooks et al. 2004; Yelenik and D'Antonio 2013). Wildfires and prescribed fires can promote IAPS (Alba et al. 2015) by increasing light availability in the soil, supplying nutrients in a short burst, leaving the soil bare or disturbed, causing plant death, and stimulating germination, seed release or resprouting (Brooks and Lusk 2008; Alcañiz et al. 2018, Ojeda et al. 2019; Nunes et al. 2020). These changes create opportunities for new species to colonize and existing invasive species to dominate areas disturbed by fire, and limit the regeneration processes in native communities favoring their definitive replacement by communities dominated by alien species (Yelenik and D'Antonio 2013). These effects can vary depending on the species and site conditions, but also on differences in the way fire occurs or is applied, such as in terms of seasonality or intensity (Stone and Andreu 2022). Some IAPS can be managed using prescribed fire, applied at the right time of year or plant life stage

and considering the side-effects on non-target species and on the ecosystem (Gaertner et al. 2014). While fire-IAPS interactions complicate the management of invaded areas and can dramatically alter ecosystem functions and composition, not all IAPS interact with fire in the same manner (Stone and Andreu 2022).

While there is plenty of information on the effect of fire on plant invasions, the effect of plant invasions on fire has been much less studied, mainly due to the difficulty to carry out field experiments testing this relationship and to the difficulty to gather expertise in two very distinct scientific fields: invasion ecology and fire behavior. The establishment and spreading of IAPS can alter fire behavior by changing fuel load, moisture content, flammability, continuity or structure in ecosystems and landscapes (Brooks et al. 2004; Davies and Nafus 2013). Moreover, the interaction between IAPS and fire can cause a feedback loop that alters the fire regime which increases the abundance of invasive species, creating an invasive plant-fire regime cycle (D'Antonio and Vitousek 1992; Brooks et al. 2004). Although there is widespread recognition that IAPS can modify the fire regime in the regions they colonize (Brooks et al. 2004), there is a paucity of scientific information regarding the fuel characteristics of these newly formed ecosystems. The initial hypothesis suggesting that IAPS might increase fire hazard does not necessarily hold true (Mandle et al. 2011), but few studies have specifically addressed this question. This lack of knowledge on the effects of plant invasions on the fire regime, calls for the development of studies on individual species, to broaden the range of studied taxa and of world regions. Developing fuel models for IAPS and simulating fire behavior across an invaded landscape is an approach that can deliver a sound assessment on this effect. However, this approach has been seldom used, probably because of the aforementioned difficulties.

One fire-adapted taxa of major concern due to its impacts in Portugal, South Africa and New Zealand is the genus *Hakea*, native from Australia. In the present study we focused on *Hakea decurrens* subsp. *physocarpa* WR Barker (Proteaceae), initially mistakenly identified in Portugal as *Hakea sericea* Schrad. & J.C. Wendl (Barker 1996; Paiva 1997; Jacobson et al. 2023; van Valkenburg et al. 2024). This species causes significant impacts on several ecosystems and landscapes and has been claimed to promote changes in fire behavior (Martins et al. 2016; Silva et al.

2019). The species' ability to expand at the landscape scale is a testament to its remarkable adaptability and reproductive strategies. The plant's success lies not only in its traits, but also in its interaction with fire, which facilitates its spread over vast areas. As fires sweep through landscapes of Portugal, the fire-related dryness triggers the release of *H. decurrens* seeds, resulting in increasing invaded areas (Wilson et al. 2020). The aftermath of the fire, with its nutrient-enriched soil and reduced competition, provides an ideal setting for the establishment and proliferation of this invasive shrub (El-Ahmir 2015). One of the key factors driving the landscape-scale expansion of *H. decurrens* is its capacity to outcompete native vegetation (Martins et al. 2016). The shrub's fast growth and adaptability to a range of environmental conditions allow it to thrive in diverse habitats, from open woodlands to disturbed areas and grasslands (Brunel et al. 2010). This adaptability grants *H. decurrens* a formidable advantage in Mediterranean ecosystems. Understanding the interactions between *H. decurrens* and fire and their effects on the structure and functioning of invaded ecosystems and landscapes provides fundamental inputs for its management (Silva and Marchante 2012; Alvarez-Taboada et al. 2017; Morais et al. 2021). Furthermore, understanding how *H. decurrens* affects fire behavior and how weather conditions and management influence these effects, is essential for a comprehensive assessment of invasion impacts and for the design of efficient fire management programs. However, despite a notable study conducted on a close species, *Hakea sericea*, in South Africa, concluded that fires in the native fynbos could potentially be more intense than in invaded areas (by van Wilgen and Richardson 1985), the effect (potential and actual) of *H. decurrens* expansion on fire behavior and regime in Portugal has not been studied.

In this context, here we present a study on the effect of *H. decurrens* expansion at the landscape scale in a specific region in Portugal. In particular, we address the following research question: does *H. decurrens* invasion increase fire hazard at the landscape scale in northern Portugal? Additionally, we address the role of shrub developmental stage, vegetation slashing, and fuel moisture conditions on fire behavior. To assess these effects, we used a modeling and simulation approach with fire behavior indicators as dependent variables, and scenarios made of factorial combinations of a) shrub developmental stage, b)

vegetation slashing, c) fuel moisture and d) proportion of invaded landscape, as independent variables.

## Methods

### Experimental design

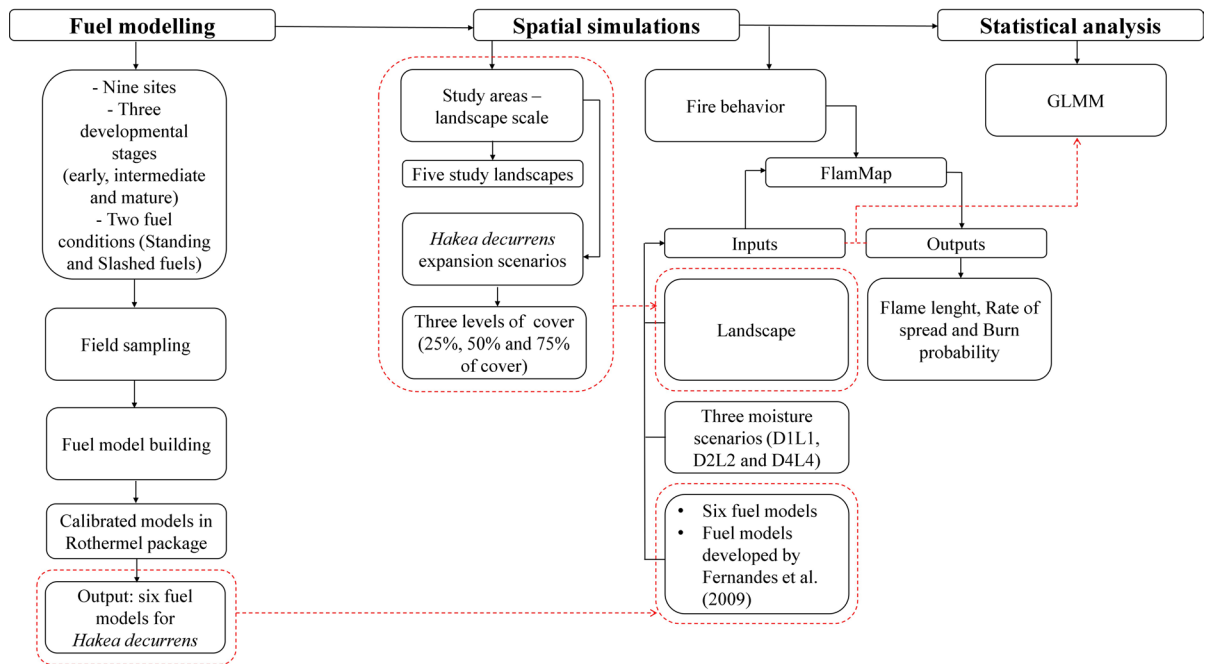
The study consisted of two steps (Fig. 1). In the first, we developed fuel models for areas dominated by *H. decurrens* at different developmental stages considering standing and slashed fuels. This step involved the collection of fuels in nine locations in the center and north of Portugal (Fig. 2), processing of fuel samples in the laboratory, and the calculation of the fuel parameters of each fuel model. The six fuel models corresponded to combinations of three developmental stages (Early, Intermediate and Mature) and two fuel conditions (Standing and Slashed fuels). In the second step we used the models developed in the first step to test spatially, at the landscape scale in five study areas (Fig. 3), the effects of *H. decurrens* invasion on fire behavior under three scenarios of *H. decurrens* expansion (25%, 50% and 75% cover of invaded landscape) and three fuel moisture scenarios (Low, Medium and High).

### Fuel modelling

#### Field sampling

To characterize the fuel complex and build fuel models of *H. decurrens* populations in Portugal, we collected a total of 18 fuel samples in populations in three developmental stages, totaling six samples for each stage (Fig. 2). Developmental stages represent age and growth of *H. decurrens* populations and were assessed using the average height of plants as proxy. Three developmental stages were established: Early (plant height  $\leq 1$  m), Intermediate (plant height  $> 1$  m  $\leq 2.5$  m), and Mature (plant height  $> 2.5$  m).

In each of the nine sampling areas, fuel management consisting of cutting the vegetation using brushcutters was established, side by side with a reference plot with uncut fuels. Both treatments (hereafter Slashed and Standing fuels) were contained within  $5 \times 5$  m squares. Fuel sampling consisted of the collection of dead and live shrub (woody) vegetation in one  $1 \times 1$  m sub-plot



**Fig. 1** Flowchart of the research methodology involving collection of fuel material and development of fuel models for *Hakea decurrens* populations (left), simulation of fire behavior

at the landscape scale (middle), and statistical analysis (right). Black arrows indicate workflow, whereas dotted arrows indicate data input

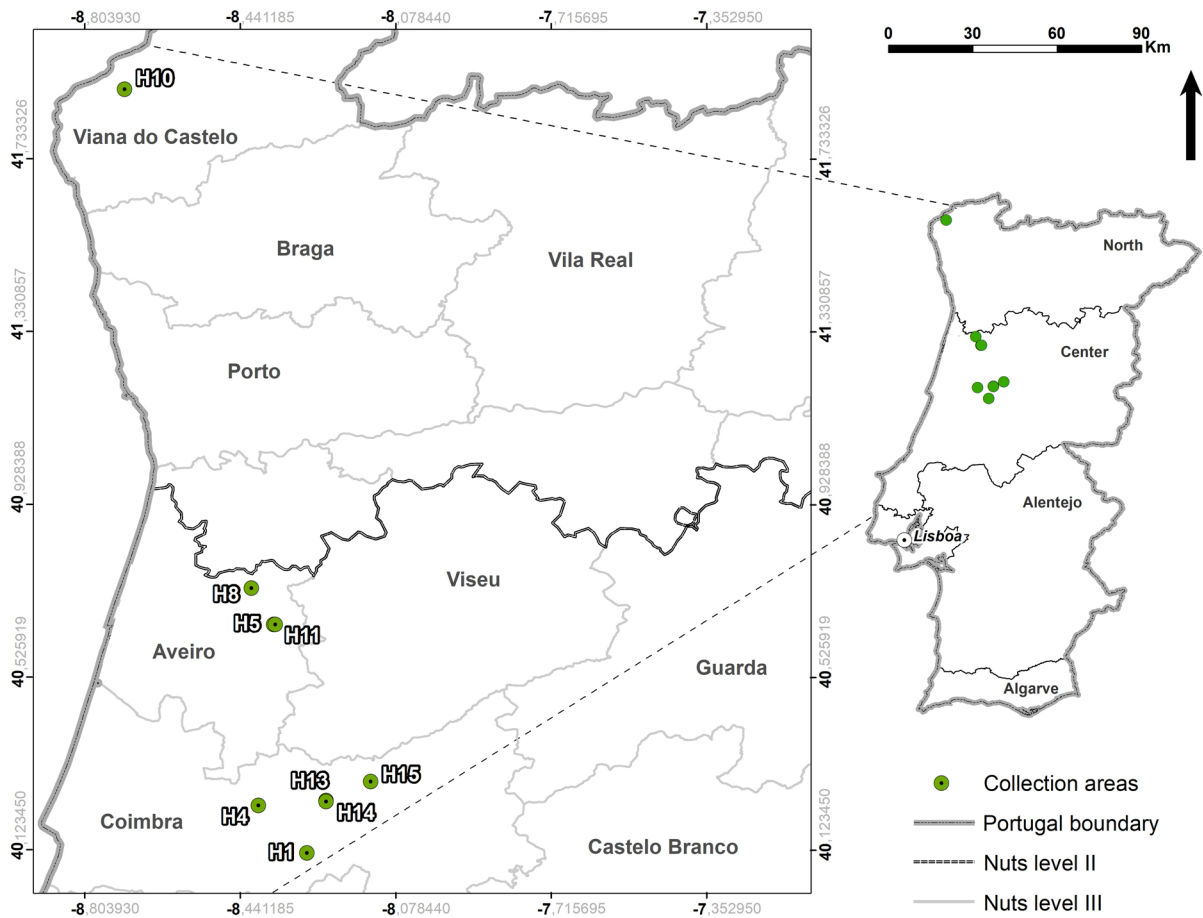
at the center of each  $5 \times 5$  m plot. Litter was collected in a  $0.5 \times 0.5$  m square in the center of each  $1 \times 1$  m plot. In the laboratory, fuels were separated according to fuel category (three time-lag classes for dead fuels, and live woody fuels) following the procedures of Deeming and Brown (1975). Due to the strong dominance of *H. decurrens*, no herbaceous fuels were found in the samples. The samples were dried in an oven at  $84^\circ\text{C}$  for 45 h for later determination of dry mass. The 100-h time-lag class fuel load corresponding to downed wood material was estimated using the line intersect method (van Wagner 1982). To estimate the total dry weight and dry weight of fine woody fuel of standing *H. decurrens* individuals, we measured the base diameter of four randomly selected individuals in each of the nine  $5 \times 5$  m plots, totaling 36 individuals, and used the allometric relationships provided by van Wilgen and Richardson (1985), where  $y$  is the mass (g) and  $x$  the diameter (cm)

$$\text{Total dry weight : } y = 100.76 x^{2.30} \quad (1)$$

$$\text{Dry weight of fine fuel : } y = 80.48 x^{1.83} \quad (2)$$

### Fuel model building

A fuel model is a set of parameters related to a certain type of vegetation referring to all combustible material available to burn that are used in a fire behavior model (Pyne 1984). Given the variability of these parameters, a model is a synthetic way of expressing and describing fuel properties, which are used to predict fire behavior (Rothermel 1972; Anderson 1982; Burgan and Rothermel 1984). We established six fuel models corresponding to combinations of developmental stage and fuel management (Standing and Slashed fuels) in the nine sampling areas. The fuel models combined data from the nine locations as follows: Early: models 250 and 253 (Locations: H13, H14 and H15); Intermediate: models 251 and 254 (Locations: H01, H05 and H10) and; Mature: models 252 and 255 (Locations: H04, H08 and H11) (Fig. 2). A proper use of a fuel model requires its calibration so that the fire behavior simulations are as close as possible to real-world fire behavior. The calibration process can be done manually through expert manipulation of the fuel model parameters, such as fuel load

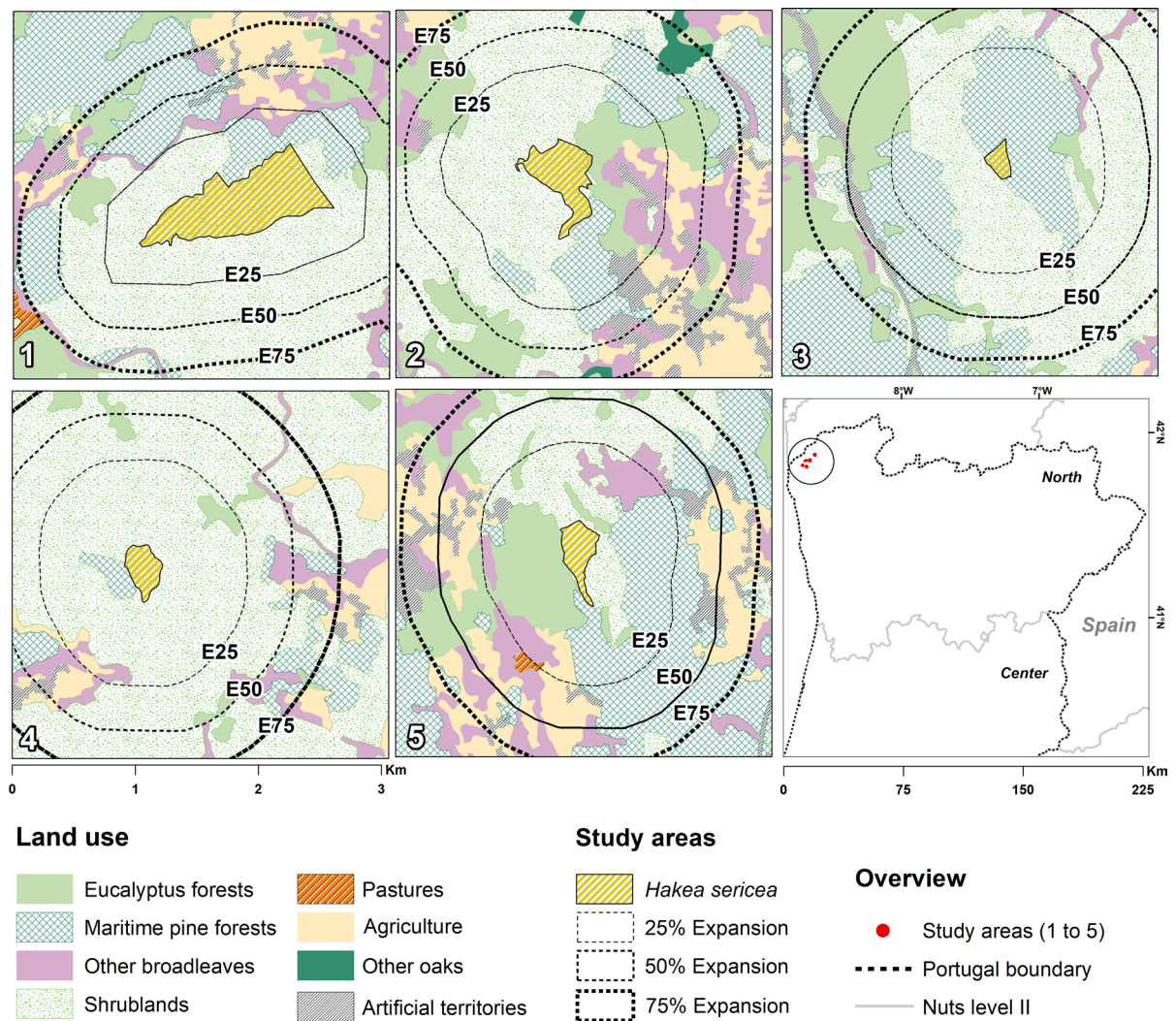


**Fig. 2** Location of the nine study areas in Portugal where samples were collected. Samples H13 and H14 and samples H5 and H11 overlap in the map due to the small dis-

tances between them (324 m and 321 m, respectively). NUTS (Nomenclature of Territorial Units for Statistics) are administrative divisions in European Union countries

and fuel depth, or it can be done using optimization processes. In this study calibration was performed using the Rothermel package for R (Vacchiano and Ascoli 2015). This package uses Genetic Algorithms, i.e., stochastic search algorithms, aimed at minimizing root mean square error (RMSE) of forward fire rate of spread predicted by the Rothermel model (Rothermel 1972) against observed data. For the fitting of the fuel models in the Rothermel package, we used the fuel models obtained for each location, and observed data from experimental fires conducted within the scope of the Aliens & Flames project (<http://fogoeinvasoras.isec.pt/>). In the standing fuel treatment, the plot was burned with the vegetation standing while in the slashed fuel treatment, vegetation was cut, left on the ground for 28

to 135 days, and then burned. Differences in time lag between cutting and burning were due to logistic constraints but provided variability in fuel moisture, useful for model calibration. The experimental fires were carried out under favorable meteorological conditions (63% relative humidity and 16 °C temperature, on average), resulting in an average flame length of  $1.23 \pm 0.63$  m, an average rate of spread of  $0.40 \pm 0.29$  m/min, and an average residence time of  $150 \pm 71$  s. Fuels were collected, before and after the experimental fire, in the same day. Fuel loadings were obtained from the field work sampling and the lab procedures previously described. Fuel Bed Depth was directly measured in the field and adjusted afterwards through the already described calibration process, using the Rothermel package.



**Fig. 3** Study areas (1–5) selected for fire behavior simulations at the landscape scale and their location in northern Portugal (bottom right). Each map includes information on Land use/

Land cover and the theoretical areas of 25%, 50% and 75% expansion of *Hakea decurrens*

Surface-area-to-volume ratio, Moisture of Extinction and Heat Content were obtained from van Wilgen and Richardson (1985).

#### Spatial simulations

Simulation of fire behavior at the landscape scale under expansion of *H. decurrens* in combination with fuel treatment, developmental stage and moisture levels, was conducted in five 3 km<sup>2</sup> areas in the north of Portugal, Minho region (Fig. 3), where *H. decurrens* is widely distributed. The selection of these areas

was based on the presence of *H. decurrens* populations and the existence of variable landscape patterns (composition and configuration), representative of the region of study.

The climate of Minho region is temperate with rainy winters and dry and hot summers (Csb, according to the Köppen classification) (Deliège and Nicolay 2016). Average annual temperature is 15.2 °C, average annual rainfall is 1882.7 mm, and average moisture is 80% (Vila Nova de Cerveira weather station, IPMA (2023)). In terms of Land use/ Land cover (LULC), four out of the five study areas were

dominated by shrublands that can represent as much as 78% of the land (Area 4) (Table 1). The dominant forest species are Maritime pine (*Pinus pinaster*), *Eucalyptus* (*Eucalyptus globulus*), oaks (mostly *Quercus robur*), and other broadleaves.

### *Hakea decurrens* expansion scenarios

We simulated the spatial process of *H. decurrens* expansion using the Scenario Generator module of the InVEST model (Sharp et al. 2014). This module allows the projection of future landscape spatial scenarios based on landscape change processes, integrating multi-criteria evaluation methods, overlay analysis, and expert knowledge (Sharp et al. 2014). We established experimental scenarios in the five study areas considering three levels of expansion of *H. decurrens*: 25%, 50% and 75% of the area. These proportions were established based on the initial area of *H. decurrens* in each site (56.02 ha, 19.08 ha, 3.41 ha, 7.75 ha and 9.35 ha, for Areas 1–5, respectively) (Table 1). We assumed transition probabilities of LULC classes and land suitability factors constant since the purpose of the research was to test increasing levels of expansion of *H. decurrens*. The transition probability is a measure of the likelihood of a land parcel (pixel) changing from one LULC class to another. The expansion model of Shrub and Bush (32) (Anderson et al. 1976), is one of the different models made available by the InVEST program database. This model was used because it presents similar characteristics to the expansion of *H. decurrens*. The spatial extent of the other classes was assessed based on COS-2018 data (Direção-Geral do Território (2022), Table 2). Areas classified as Artificial territories were assigned a value of zero and were not considered in the fire behavior simulations.

### Fire behavior simulations

We used the computer program FlamMap (Finney et al. 2019) to spatially simulate fire behavior in the five study areas. FlamMap is a fire behavior mapping and analysis program that computes potential fire behavior descriptors (e.g., Flame length, Rate of spread, Fireline intensity) (Finney 2006). This software is well suited to make landscape comparisons to assess fire hazard according to fuel, topography and weather conditions, aimed to prioritize forest

fire management (Stratton 2004, 2006). Fire behavior simulations were performed considering the six fuel models developed for *H. decurrens* in maps representing expansion scenarios at the landscape scale. The remaining LULC classes in the five study areas (Table 2) were represented by fuel models developed by Fernandes and Loureiro (2021). The correspondence between fuel models and LULC classes was established following the guidelines by Fernandes and Loureiro (2021).

FlamMap uses a base input Landscape file (LCP) composed of five compulsory raster layers: slope, aspect, elevation, fuel models and canopy cover. Data for building landscape files for the five areas were obtained using ArcMap software. Final maps had a resolution of 25 m. To address variable weather severity conditions, we used three Fuel Moisture Scenarios (FMS) according to Scott and Burgan (2005): D1L1 (Very low dead fully cured herb), D2L2 (Low dead, 2/3 cured herb) and D4L4 (High dead, fully green herb). As for *H. decurrens* fuel models, we tested in each area the six models, representing combinations of developmental stage (Early, Intermediate and Mature) and management (Standing and Slashed fuels). Wind speed and direction and crown characteristics were held constant for all the simulations.

Fire simulations were performed using two distinct approaches: (a) the basic fire behavior that computes the maximum values of fire behavior parameters for each pixel of the landscape and (b) the Burn probability function that computes the probability of burning for each node of the spatial grid using in the Minimum Travel Time Fire Spread (MTT) algorithm. This algorithm computes fire paths and fire growth across an overlapped grid disposed over the landscape. We used 100 ignitions placed randomly across the landscape. For approach (a) we computed the average of fire behavior parameters Flame length and Rate of spread in the whole landscape. For approach (b) we used the average Burn probability for the whole Minimum Travel Time Fire Spread (MTT) grid. These fire behavior outputs were used as dependent variables in the statistical models. Overall, fire behavior simulations were conducted for three invasion scenarios, three FMS and six fuel models in five study areas, totaling 270 simulations.

**Table 1** Land use/Land cover in the five study areas with indication of the corresponding fuel model used in the fire simulations. The descriptors of each fuel model are presented in Tables 2 and 3. Data from COS 2018 (Direção-Geral do Território 2022)

Study area	Land use/land cover class	Area		Fuel model number
		(ha)	(%)	
1	Artificial territories	18.9	2.10	0
	<i>Eucalyptus</i> forests	87.99	9.78	211
	Other broadleaves	48.96	5.44	212
	Maritime pine forests	204.05	22.67	213
	Oaks	27.3	3.03	221
	Pastures	6.97	0.77	231
	Agriculture	62.04	6.89	232
	Shrublands	387.77	43.09	233
	<i>Hakea decurrens</i>	56.02	6.22	250–255
2	Artificial territories	58.17	6.46	0
	<i>Eucalyptus</i> forests	141.95	15.77	211
	Other broadleaves	102.51	11.39	212
	Maritime pine forests	113.31	12.59	213
	Oaks	15.62	1.74	221
	Agriculture	117.59	13.07	232
	Shrublands	331.77	36.86	233
	<i>Hakea decurrens</i>	19.08	2.12	250–255
	3	Artificial territories	6.89	0.77
<i>Eucalyptus</i> forests		164.03	18.23	211
Other broadleaves		19.85	2.21	212
Maritime pine forests		298.56	33.17	213
Oaks		4.02	0.45	221
Agriculture		8.46	0.94	232
Shrublands		393.78	43.75	233
<i>Hakea decurrens</i>		4.41	0.49	250–255
4		Artificial territories	11.61	1.29
	<i>Eucalyptus</i> forests	26.48	2.94	211
	Other broadleaves	37.32	4.15	212
	Maritime pine forests	56.34	6.26	213
	Oaks	16.73	1.86	221
	Agriculture	42.81	4.76	232
	Shrublands	700.96	77.88	233
	<i>Hakea decurrens</i>	7.75	0.86	250–255
	5	Artificial territories	45.35	5.00
<i>Eucalyptus</i> forests		133.6	14.90	211
Other broadleaves		88.11	9.83	212
Maritime pine forests		301.61	33.65	213
Oaks		22.18	2.47	221
Pastures		2.89	0.24	231
Agriculture		147.13	16.26	232
Shrublands		149.78	16.60	233
<i>Hakea decurrens</i>		9.35	1.04	250–255

**Table 2** Fuel models for Land use/Land cover classes other than *Hakea decurrens*

Fuel model number	Fuel model code	Fuel loading (t ha <sup>-1</sup> )				Surface area to volume ratio (m <sup>-1</sup> )			Fuel bed depth (m)	Moisture of extinction (%)	Heat content (kJ kg <sup>-1</sup> )	
		1H	10H	100H	Live Herbaceous	Live Woody	1H	Live Herbaceous			Live Woody	Dead
211	F-EUC	4.63	2.96	1.27	0.00	1.12	4200	-	0.32	26	21000	21000
212	F-FOL	2.67	1.27	0.69	0.00	1.16	4500	-	0.15	25	20500	20500
213	F-PIN	6.50	1.50	0.00	0.00	0.00	5500	-	0.10	45	20500	20500
221	M-CAD	4.54	1.87	0.61	0.00	9.08	6000	-	0.63	30	20000	20000
231	V-Ha	0.65	0.15	0.00	2.35	0.40	4000	5500	0.60	24	19000	19000
232	V-Hb	0.30	0.00	0.00	1.20	0.00	6000	6000	0.35	24	19000	19000
233	V-MAa	9.50	2.50	0.00	0.00	14.50	3500	-	1.05	35	21000	21000

1H – 1-h timelag class fuel particles; 10H – 10-h timelag class fuel particles; 100H – 100-h timelag class fuel particles; F-models (litter predominance), M-models (litter and vegetation) and V-models (vegetation predominance); M-CAD: Deciduous forest with litter and understory; V-Ha: Tall herbs; V-Hb: Short herbs; V-MAa: Shrub spp. with dead fuel, high; F-FOL: Compact litter of deciduous or evergreen hardwoods; F-PIN: Litter of intermediate to long needle pines; F-EUC: Eucalypt litter. Source: (Fernandes and Loureiro 2021)

*Statistical Analysis*

The effect of *H. decurrens* invasion on fire behavior was assessed with Generalized Linear Mixed Models (GLMM) with a Gaussian error distribution and using *the study area* as a random effect. The GLMM were fit using the R package *lme4* (Bates et al. 2023; R Core Team 2022) following the model building procedures proposed by Zuur et al. (2009). The dependent variables were the fire behavior parameters described in the previous section (Rate of Spread, Flame length and average Burn probability) and the independent variables were: *H. decurrens* developmental stage (ordinal variable with three levels: early, intermediate; mature); management (factor with two levels: Standing fuels, Slashed fuels); The proportion of invaded landscape (numeric variable: 25; 50; 75%); Fuel Moisture Scenario (factor with three levels; D1L1 (Low), D2L2 (Medium); D4L4 (High)). The proportion of variance explained by each model was obtained using the procedures for computing pseudo-R<sup>2</sup> in GLMM proposed by Nakagawa and Schielzeth (2013).

**Results**

Fuel models

Based on field sampling of *Hakea decurrens* fuels, and the calibration performed using the Rothermel package, we obtained six fuel models that represent combinations of developmental stage (Early, Intermediate and Mature) and management (Standing and Slashed fuels) conditions (Table 3). The three Standing fuel models presented the expected variation across development stages, with dead and live fuel loadings and the fuel bed depth increasing from Early to Mature stands. This variation (only dead fuels) across development stages was also observed for Slashed fuels. Standing fuel models differed from Slashed ones because the latter lacked a live component, and also because fuel depth was naturally lower in slashed fuels.

**Table 3** Fuel models for *Hakea decurrens* populations at different stages of development and two management treatments

Fuel model number	Fuel model code	Fuel loading (t ha <sup>-1</sup> )				Surface area to volume ratio (m <sup>-1</sup> )				Fuel bed depth (m)	Moisture of extinction (%)	Heat content (kJ kg <sup>-1</sup> )	
		1H	10H	100H	Live Her-baceous	Live Woody	1H	Live Her-baceous	Live Woody			Dead	Live
250	Hd-St-early	2.44	0.00	0.00	0.00	6.74	7215	-	8450	0.50	34	18300	18300
251	Hd-St-intermediate	10.64	0.00	0.00	0.00	8.35	7215	-	8450	0.93	34	18300	18300
252	Hd-St-mature	20.38	0.17	0.00	0.00	28.08	7215	-	8450	0.98	34	18300	18300
253	Hd-Sl-early	6.80	3.54	0.00	0.00	0.00	7215	-	-	0.26	34	18300	18300
254	Hd-Sl-intermediate	12.50	5.74	0.00	0.00	0.00	7215	-	-	0.32	34	18300	18300
255	Hd-Sl-mature	21.78	6.81	0.00	0.00	0.00	7215	-	-	0.45	34	18300	18300

1H –1-h timelag class fuel particles; 10H –10-h timelag class fuel particles; 100H –100-h timelag class fuel particles; HC – Heat Content; Hd – *Hakea decurrens*; St–Standing fuels treatment; Sl–Slashed fuels treatment; early, intermediate and mature – stages of development

**Table 4** Generalized linear mixed model of the effect of *H. decurrens* developmental stage, control treatment, expansion and Fuel Moisture Scenario ( $n=270$ ) on Flame length (m). The table shows the coefficients of the model, standard errors, z statistics and associated probabilities: \*\* $p \leq 0.01$ ; \*\*\* $p \leq 0.001$ . The baseline factor levels are indicated in brackets

Model parameters	Estimate	SE	z value	Pr(> z )
Intercept	0.194	0.116	1.680	***
<i>Stage (early)</i>				
Intermediate	0.578	0.042	13.683	***
Mature	0.755	0.042	17.852	***
<i>Treatment (slashed fuels)</i>				
Standing fuels	0.104	0.034	3.015	**
<i>Expansion (25%)</i>				
50%	0.151	0.042	3.561	**
75%	0.342	0.042	8.095	***
<i>Fuel moisture scenario (High)</i>				
Medium	0.435	0.042	10.298	***
Low	1.037	0.042	24.533	***

Effect of *H. decurrens* on fire behavior

Fire behavior showed similar trends for Flame length, Rate of spread and Burn probability in response to all independent variables. Standing fuels presented higher values of these variables than slashed fuels. All three fire behavior parameters increased from early to mature developmental stages, regardless of moisture conditions. Increasing proportions of invasion at the landscape level also led to higher values for the three fire behavior parameters. These relationships were tested using GLMM models. All two-way variable interactions were tested but none delivered significant results. The best-fit GLMM model for Flame length (Marginal  $R^2 = 69.5\%$ ; Conditional  $R^2 = 81.9\%$ ) showed that all predictors significantly affected this variable (Table 4). Standing fuels in relation to slashed control showed a higher Flame length ( $p \leq 0.01$ ). Developmental stage significantly ( $p < 0.001$ ) influenced fire behavior, i.e., the more advanced the developmental stage of *H. decurrens* populations the higher the Flame length. Also, expansion of *H. decurrens* at the landscape scale significantly increased Flame length. Flame length also increased under lower Fuel Moisture Scenarios due to low moisture content of the fuel material. The best

**Table 5** Generalized linear mixed model of the effect of *H. decurrens* developmental stage, control treatment, expansion and Fuel Moisture Scenarios ( $n=270$ ) on Rate of spread (m/min). The table shows the coefficients of the model, standard errors, z statistics and the associated probabilities: \* $p \leq 0.05$ ; \*\*\* $p \leq 0.001$ . The baseline factor levels are indicated in brackets

Model parameters	Estimate	SE	z value	Pr(> z )
Intercept	-0.055	0.210	-0.263	***
<i>Stage (early)</i>				
Intermediate	0.746	0.078	9.503	***
Mature	1.243	0.078	15.840	***
<i>Treatment (slashed fuels)</i>				
Standing fuels	0.124	0.064	1.939	*
<i>Expansion (25%)</i>				
50%	0.374	0.078	4.768	***
75%	0.770	0.078	9.810	***
<i>Fuel moisture scenario (High)</i>				
Medium	0.630	0.078	8.023	***
Low	1.933	0.078	24.630	***

**Table 6** Generalized linear mixed model of the effect of *H. decurrens* developmental stage, control treatment, expansion and Fuel Moisture Scenarios ( $n=270$ ) on Burn probability (%). The table shows the coefficients of the model, standard errors, z statistics and the associated probabilities: \*\* $p \leq 0.01$ ; \*\*\* $p \leq 0.001$ . The baseline factor levels are indicated in brackets

Model parameters	Estimate	SE	z value	Pr(> z )
Intercept	-0.216	0.059	-3.629	***
<i>Stage (early)</i>				
Intermediate	0.242	0.033	7.209	***
Mature	0.438	0.033	13.073	***
<i>Treatment (slashed fuels)</i>				
Standing fuels	0.120	0.027	4.393	***
<i>Expansion (25%)</i>				
50%	0.102	0.033	3.041	**
75%	0.221	0.033	6.596	***
<i>Fuel moisture scenario (High)</i>				
Medium	0.160	0.033	4.761	***
Low	0.654	0.033	19.496	***

GLMM obtained for Rate of spread also indicated a significant effect of all tested predictors (Table 5). Rate of spread increased with invasion proportion, being the highest when *H. decurrens* covered 75% of the landscape ( $p \leq 0.001$ ) (Table 5). Standing fuels resulted in higher Rate of spread ( $p \leq 0.05$ ) in comparison to slashed fuels treatment. *Hakea decurrens* populations at a mature stage of development showed the highest Rate of spread and Burn probability compared to populations at intermediate and early stages. The Marginal  $R^2$  was 69.0%, and the Conditional  $R^2$  was 81.2%, showing a high influence of the location of each landscape. Similarly to the previous dependent variables, the best-fit GLMM model for Burn probability (Marginal  $R^2 = 66.7\%$ ; Conditional  $R^2 = 72.3\%$ ) showed significant effects of all predictors on this variable (Table 6).

**Discussion**

Our work produced relevant information about how the expansion of a fire-adapted invasive species may affect fire behavior and fire hazard. Additionally, we have improved our understanding of how other factors may affect fire behavior at the landscape scale,

namely plant development stage, management, and fuel moisture, which provides guidance for landscape and fire management in invaded landscapes. Our results show that as *H. decurrens* expands on the landscape, the fire behavior variables related with fire hazard also increase. Also, higher Flame length, Rate of Spread and Burn probability were observed in the landscape when *H. decurrens* stands were not slashed (in opposition to standing) and when plants were at mature developmental stages. The same pattern was observed for decreasing moisture scenarios.

The reasons for these results are directly related to the fuel models used to simulate fire behavior (Table 3) and the fuel models used to represent the land use and land cover classes in the landscapes of study, together with the proportions of these models in the studied landscapes. The six fuel models developed for *H. decurrens* (Table 3) have, in general, much higher loadings, in particular 1 and 10 h loadings, compared to the seven fuel models that represent the original/ non-invaded landscape (Table 2). Also, fuel loadings increased with developmental stage of *H. decurrens*. Therefore, increasing proportion of *H. decurrens* fuel models in the landscape, particularly when corresponding to standing populations at a mature stage of development, increased the response

of fire indicators at the landscape level. In the case of moisture scenarios, decreasing moisture leads to an increase of fire behavior parameters, as expected (Rothermel 1972; Pyne 1984; Schunk et al. 2017). This is a trivial result, but moisture scenarios were included in the analysis in the expectation that the interaction with the other variables, e.g., *H. decurrens* expansion, would have been statistically significant. While this did not occur, it was to be expected as it is known that more severe weather scenarios lead to more homogeneous fire behavior, regardless of the fuel type (e.g., Nunes et al. 2005).

The current literature shows contradictory results on the effect of invasive species on fire behavior, since this effect may depend on many factors (e.g., stage of development, population structure, management). Therefore, it cannot be generalized that invasive plants necessarily increase the potential for fire to spread. Mandle et al. (2011) reviewed the effect of woody plant invaders on fire and concluded that out of the 16 species analyzed, only eight have in fact increased the frequency or intensity of fire, five decreased these indicators of the fire regime and three had mixed effects. Experimental and modeling-based research has shown that invasive species, such as *Acacia dealbata*, *Acacia saligna* and *H. sericea* (very similar to *H. decurrens*) produce large amounts of highly flammable biomass, increasing the risk of fires during the dry season (van Wilgen and Richardson 1985; Gordon et al. 2017; Nunes et al. 2021). However, van Wilgen and Richardson (1985) found that invasion by *H. sericea* in the Fynbos Shrubland ecoregion, southwestern South Africa, resulted in reduced rates of fire spread because the fuel bed was so densely packed that combustion was inhibited, although there was an increase in fuel load by 60%. Nevertheless, the same authors, based on model simulations, concluded that fires can spread during extreme weather conditions, and increased fuel load can result in fires that are much more intense than in non-invaded locations. Fynbos landscapes and fuel types tested by van Wilgen and Richardson (1985) are different from those in our study areas and that may, at least partially, explain differences in the results.

The observed relationship between the expansion of *H. decurrens* and fire behavior indicates that in invaded areas changes in fire regime can occur in the near future. In some of the study areas fire regimes dominated by frequent small and low severity fires

(Pereira et al. 2022; Oliveira and Fernandes 2023) might be replaced by large and intense fires in the future. Although our study was not established to analyze fire regimes, the results regarding the effects of the invasion of *H. decurrens* on the rate of spread and flame length indicate that progressive expansion of the species can lead to more intense and larger fires, considering the increasing size of invaded areas. This increased fire hazard in larger invaded areas can lead to a fire-invasion cycle, similar to the widely reported grass-fire cycle in California and elsewhere (D'Antonio et al. 1992). In fact, given the fire-adaptation of *H. decurrens*, higher fire hazard may lead to higher fire frequency, which represents more opportunities for *H. decurrens* plants to reproduce and expand, leading to higher fire hazard and so-forth. This potential for the development of a *H. decurrens*-based fire cycle may have dramatic consequences from a landscape management perspective, given the strong dominance of *H. decurrens* stands over the native plant communities. On the other hand, since *H. decurrens* decreases the attractiveness of the landscape to activities that rely on and promote low-intensity frequent fires (such as grazing), the absence or exclusion of such activities can result in further expansion of invaded areas and larger fires. However, there is no empirical evidence of the relationship between *H. decurrens* invasion and fire behavior at the landscape scale. This is a relevant topic in invasive species research agendas in Portugal and elsewhere.

From a management perspective it is relevant to acknowledge the effect of slash and age of plants on fire behavior. It could be expected that applying the slash treatment to control *H. decurrens* could increase fire hazard, as this practice increases the amount of dead material (Silva et al. 2023). However, this was not observed in the simulations, where standing fuels have led to higher values of the fire variables analyzed. This can be partially explained by the greater depth and porosity (lower compaction) of the standing fuel. This suggests that slashing *H. decurrens* can be a better option to reduce fire hazard in the landscape.

In terms of plant development stage, the results indicate that flame length, rate of spread and burn probability increase with age of plants (Lusk et al. 2010; Falster et al. 2017). Therefore, preventing *H. decurrens* stands to reach mature developmental

stages should be a priority to reduce fire hazard at the landscape level.

The fuel models and simulations of fire behavior at the landscape scale presented here suggest a trend towards an increase in fire hazard in the study areas with increasing expansion level and maturity of plants and decreasing moisture level of *H. decurrens*. While fuel moisture is not possible to manage, it is possible to prevent (or delay) the expansion of existing *H. decurrens* populations. In already invaded landscapes, the control of *H. decurrens* can be determinant in fire prevention and risk management, especially in regions with an advanced stage of invasion and the results of this study should be taken into consideration. Accordingly, in particular where fire is a concern, practices to reduce landscape fire hazard can be directed either to maintaining *H. decurrens* at initial stages of development or to the application of slash treatments. The latter practice should be followed by prescribed fire in order to avoid proliferation of plants originating from seeds released during and after the cutting (Silva and Marchante 2012; Silva et al. 2023). Despite the importance of these practices, prevention through early-detection & rapid response are known to be the most cost-effective measures to manage invasions (Davies and Sheley 2007) and that should be a priority in land planning and management in the north and center of Portugal.

This work aims to be a contribution for a better knowledge of the relationships between fire and plant invasions. Although it is clear that not all invasive plant species lead to an increase in fire hazard, the case of *H. decurrens* does seem to confirm that at least some species may have this effect. In an evolutionary perspective it makes sense that a species that strongly benefits from fire for its reproduction and expansion, should also be highly fire-prone, as it seems to be the case. Although much research needs to be done on other species and in other world regions and ecosystems, the Mutch hypothesis (Mutch 1970) seems to apply well to *H. decurrens* in the sense that fire-adapted plants can also be highly fire-prone. The topic of plant invasions has however been seldom coupled with the topic of fire behavior, calling for other research initiatives that help shedding light on the role of fire-adapted invasive plant species on fire hazard.

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#### Declarations

**Conflicts of interest** All authors declare that they have no conflicts of interest.

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