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What drives *Eucalyptus globulus* natural establishment outside plantations? The relative importance of climate, plantation and site characteristics

Patrícia Fernandes · Cristina Máguas · Otília Correia ·
Pablo González-Moreno

Abstract *Eucalyptus globulus* has great economic importance in the Iberian Peninsula and is now the most widespread tree species on the Portuguese mainland. We aimed to evaluate the establishment capacity of *E. globulus* from plantations into natural habitats and to understand its association with the climate, plantation characteristics and host site characteristics. We surveyed 50 *E. globulus* plantations across Portugal looking at the natural establishment (occurrence and density) of *E. globulus* in habitats adjacent to plantations. Eucalypts presence was only recorded in 8% of the plots. Site characteristics (such as habitat type, vegetation cover and disturbance) were the most important variables influencing the natural recruitment of *E. globulus* in comparison to climate or plantation variables. Forest and grassland were the most resistant habitats to eucalyptus invasion while highly disturbed areas can be considered hubs for eucalypt density. The high importance of site characteristics reflects that most of the variability in eucalypt establishment occurs at small spatial scales. Thus, monitoring and management efforts should focus on those sites with higher establishment probability (i.e. open areas) trying to promote native vegetation and reduce disturbance levels.

Keywords Non-native species ·
Forestry plantations · Portugal · Habitat suitability

P. Fernandes (✉) · C. Máguas · O. Correia
cE3c, Centre for Ecology, Evolution and Environmental
Changes, Faculdade de Ciências, Universidade de Lisboa,
FCUL, Campo Grande, Bloco C2, Piso 5, 1749 – 016
Lisbon, Portugal
e-mail: patfernandes@fc.ul.pt

P. González-Moreno
CABI, Bakeham Lane, Egham TW20 9TY, UK

P. González-Moreno
Estación Biológica de Doñana, Consejo Superior de
Investigaciones Científicas (EBD-CSIC), Av. Américo
Vespucio S/N, Isla de la Cartuja, 41092 Seville, Spain

Introduction

Forest plantations account for 264 million hectares globally (7% of the total forest area), of which approximately 25% consist of non-native species (FAO 2010). The use of non-native species in forest plantations (mostly pine and eucalypt) is primarily related to the wide range of ecological requirements of these species, their rapid growth and high productivity. In many countries, these species play a significant role towards the economy, particularly in areas where native species do not perform well (Dodet and Collet 2012; Richardson 1998). However, the prolific nature of the non-native tree species selected and their widespread use increases the risk of these species invading the natural and semi-natural habitats surrounding a plantation (Dodet and Collet 2012; Essl et al. 2010; Richardson 1998; Richardson and Rejmánek 2011; Van Der Meer et al. 1999).

Forest plantations are one of the main sources of plant invaders worldwide and the expansion of non-native trees into habitats outside plantations is a relevant concern for managers and conservationists (Dodet and Collet 2012; Richardson 1998). In order to manage forest plantations sustainably (minimizing ecological risks and maintaining economical productivity) it is important to study the main factors driving the natural establishment of non-native plant species and determine the capacity of a species to colonize outside the planted areas (Richardson and Rejmánek 2011).

Eucalyptus species are among the most cultivated forest species worldwide. They are mainly planted in temperate, tropical and subtropical regions, where they cover approximately 20 million ha (Rejmánek and Richardson 2011). *Eucalyptus globulus* Labill. (Tasmanian blue gum), native to southeast Australia, is currently one of the most important tree species planted worldwide, with the majority of plantations occurring in the Iberian Peninsula. *Eucalyptus globulus* was first introduced into Portugal in the mid-19th century and its use was dramatically promoted by the pulp and paper industries (Alves et al. 2007). Today, *E. globulus* is the most widespread tree species on the Portuguese mainland, representing 26% of its forest cover (ICNF 2013) with great economic importance to the western region (Potts et al. 2004).

Based on the Australian Weed Risk Assessment (WRA), *E. globulus* has been reported as a species with "high" invasion risk (Daehler et al. 2004; Gassó et al. 2009; Gordon et al. 2012; Marchante et al. 2014), and is a particular problem in seven regions globally: North, Central and South America, Europe, New Zealand, Pacific Islands and Indian Oceans Islands (Rejmánek and Richardson 2013). WRAs are based upon biological traits and expert knowledge of the species (Pheloung et al. 1999), with most risk assessments considering the history of invasiveness elsewhere (e.g. its distribution in areas where introduced). WRAs are rarely based solely on quantitative information collected from the field and, in this instance, several quantitative field studies have not found eucalypts to be invasive (Callaham et al. 2013; da Silva et al. 2011; Fernandes et al. 2016; Larcombe et al. 2013; Lorentz and Minogue 2015). In general, *Eucalyptus* have rarely spread considerable distances from planting sites, their regeneration is sporadic (Callaham et al. 2013; Fernandes et al. 2016;

Larcombe et al. 2013; Rejmánek and Richardson 2011) and seedlings have a high rate of mortality (Calviño-Cancela and Rubido-Bará 2013; da Silva et al. 2011; Lorentz and Minogue 2015; Rejmánek and Richardson 2011). These factors all contribute to the limited invasiveness of *Eucalyptus* species (Rejmánek and Richardson 2011). Studies on *Pinus* and *Acacia* have found that species invasiveness is related to repeated introductions, planting intensity and a long residence time (Gibson et al. 2011; Procheş et al. 2012; Wilson et al. 2009), which are however, the characteristics of many *Eucalyptus* species (including *E. globulus* in Portugal). In general, *Eucalyptus* are viewed as less invasive than several other widely cultivated trees such as pines and acacias (Rejmánek and Richardson 2011) but a paper by Rejmánek and Richardson (2011) opened with the question: "Are eucalyptus inherently less invasive, or are they just a ticking time bomb?". Understanding the factors driving the natural establishment of *E. globulus* should help to evaluate the invasive potential of this species (Richardson and Rejmánek 2011).

Among the abiotic factors that determine biological invasions, the effect of climate is probably the most studied (Thuiller et al. 2005) and is considered to be the main driver of plant distribution from continental to regional scales (Milbau et al. 2009; Pearson et al. 2004). For example, summer droughts in the Mediterranean limits plant performance and prevents the establishment success of many non-native plants (Chytrý et al. 2008b). Although *E. globulus* is tolerant to a wide range of environmental conditions, water availability and low temperatures (mainly occurrence of temperatures below 0 °C) are the main climatic factors limiting its growth in Portugal (Almeida et al. 1994; Alves et al. 2012; Catry et al. 2015). Thus, given the Mediterranean character of most of the Portuguese territory (with associated drought stress during summer months), we hypothesize that *E. globulus* establishment is primarily affected by precipitation.

The establishment success of a non-native species depends on the characteristics of the species itself, the host community and the interaction between them (Lonsdale 1999; Rejmánek et al. 2005; Richardson and Pyšek 2006). However our knowledge about the potential natural establishment of *E. globulus* in different habitats is still scarce. Understanding why

some sites are more susceptible to the establishment of a given plant species than others has been a central topic in biological invasion research (Chytrý et al. 2008b). In turn, the susceptibility of the receiving community can change in function of competitive and facilitative interactions, nutrient availability, or disturbance levels (e.g. Davis and Pelsor 2001; Davis et al. 2000; Traveset and Richardson 2014). The role of disturbance has been long recognized as an important driver of biological invasions (Elton 1958) and many studies have observed that disturbance, specifically the removal of native vegetation, favours the establishment of non-native plants (e.g. Alston and Richardson 2006; Davis and Pelsor 2001; Davis et al. 2000; Higgins and Richardson 1998; Mitchell et al. 2006). Disturbance has also been suggested to be a prerequisite for the establishment of eucalyptus (da Silva et al. 2011; Lorentz and Minogue 2015; Wevill and Read 2010).

The number of propagules arriving in a new environment has also been observed as one of the mechanisms that strongly contributes to the success of a non-native species colonizing an area (e.g. Catford et al. 2011, 2009; Krivánek et al. 2006; Lockwood et al. 2009; Pyšek et al. 2009; Rouget and Richardson 2003) and this is also true for *Eucalyptus* populations (Gordon et al. 2012; Rejmánek and Richardson 2011). For forestry species, the expansion and the intensity of the planted area determines the magnitude of the propagule pressure. The propagule pressure of eucalypts has the potential to be very high considering the quantity of trees planted, the distribution and area in which plantations occupy and the prolific seed production (Rejmánek and Richardson 2011). There is however, evidence to suggest that reproductive output is highly variable in *E. globulus* plantations (Barbour et al. 2008; Larcombe et al. 2014).

Nevertheless, the importance of propagule pressure on establishment success can vary depending on the local conditions (i.e. characteristics of host community). For instance, a small number of propagules can be sufficient to colonize a community with low resistance (a highly disturbed area), whereas a greater number of propagules may be necessary in locations with highly resistant communities (areas with intense competition and harsh abiotic conditions) (Krivánek et al. 2006; Lockwood et al. 2009; Pyšek et al. 2009; Rouget and Richardson 2003).

Similarly, residence time (the time since a species was first introduced into a region) can also influence the success of non-native species (Dawson et al. 2009; Pyšek et al. 2009). Considering that data on these aspects is rarely available for most introduced species, the existence of detailed records of planting history for forestry species offers an opportunity to assess the relative importance of potential surrogates for propagule pressure and residence time in explaining the success of non-native species in colonizing an area.

Recently, Catry et al. (2015) studied the effect of abiotic factors on the natural establishment of *E. globulus* along roadside transects adjacent to eucalypt plantations in continental Portugal. However, the study did not consider the characteristics of surveyed plantations and other important site variables, such as vegetation cover and disturbance level. In addition, roadsides result from anthropogenic disturbances which are difficult to transpose to other habitat types. As a result, there is still the requirement to study the importance of propagule pressure, residence time and the characteristics of the host community on the natural establishment of *E. globulus*. In this study, we evaluated how climatic factors, plantation characteristics (i.e. age, size, productivity and fire recurrence of the plantation) and host site characteristics (i.e. habitat type, soil type, aspect, disturbance level and vegetation cover) are associated with the establishment of *E. globulus* into natural habitats. This study comprises of two specific questions: (1) what is the relative importance of site characteristics; plantation characteristics; and climate, for the natural establishment of *Eucalyptus globulus* from plantations? (2) once *Eucalyptus globulus* has established, which factors are associated with their abundance? We assessed the natural colonization of *E. globulus* in several habitat types adjacent to 50 plantations across mainland Portugal (~ 450 km). A close collaboration with plantation owners offered access to detailed information about *E. globulus* plantation (e.g. age of the stand, fire history, plantation history) and produced a unique database to estimate the importance of plantation characteristics in forestry species invasions.

Methods

Study species

In Portugal, most *Eucalyptus globulus* plantations are intensively managed through a coppice system (10–12 year rotations) and the wood is mainly used for pulp production (Soares et al. 2007). Plants reach sexual maturity after 3–4 years (Jordan et al. 1999) and each fruit (a woody capsule) contains approximately 6–25 viable seeds (Hardner and Potts 1995; Mimura et al. 2009). Seeds of *E. globulus* are small (but relatively large for eucalypts) with no specialized dispersal mechanism (Cremer 1977). Thus, seed dispersal distances are limited to 10–15 m from the edge of a plantation (Calviño-Cancela and Rubido-Bará 2013; Fernandes et al. 2016). Fruits are able to withstand fire which in turn triggers the dehiscence of seeds from the capsules (i.e. serotinous) (Reyes and Casal 2001). *E. globulus* seeds do not require a period of dormancy and germination is likely to take place within a year after seed release (Calviño-Cancela and Rubido-Bará 2013).

Study area

We sampled 50 *E. globulus* plantations in Portugal, conducting a country-wide field survey to document the establishment (natural regeneration) of *E. globulus* in natural habitats adjacent to the plantation (with at least one edge in contact) (Fig. 1). The average age of a plantation was 12-years-old, ranging from 8 to 26 years, (Table 1) and the average elevation was 216 m a.s.l (ranging from 14 m to 748 m). The climate is Mediterranean: cool rainy winters and hot dry summers; a mean annual temperature of 15 °C (ranging from 12 to 17 °C); and annual precipitation of 885 mm (ranging from 540 to 1438 mm) (Table 1). The major soil types found among sampled sites were cambisol, luvisol, podzol and lithosol (Table 1).

Survey method

Field surveys were conducted between May 2012 and May 2014, during Spring and Autumn. We performed a series of parallel plots of 50 m^2 (10 m × 5 m) to quantify the establishment *E. globulus* (i.e. number of plants) in the adjacent habitats of the managed forest plantations of *E. globulus* across Portugal (Fig. 1b, c). *Eucalyptus globulus* plants counted in this study corresponded to all *E. globulus* plants that had naturally established from planted trees irrespectively of size. The eucalypt seedlings registered in our study had in most of the cases less than 1.3 m. In total, 1579 plots were surveyed across the 50 plantations of the study area (Fig. 1a; Table 2).

The plots were established with the longer edge perpendicular to the plantation boundary (Fig. 1c). To calculate the confidence level of the survey (the probability of sampling *E. globulus*s at least once given a particular value of plots, β), we applied the following equation (Callaham et al. 2013; Green and Young 1993):

$$n = -\frac{1}{m} * (\log \beta),$$

where, in this study, n = the number of plots needed to detect *E. globulus* plants, m = the mean frequency of occurrence of eucalypt and β = confidence level of the estimate, in the terminology of Green and Young (1993). In practice, it is very difficult to determine m before the end of the sampling and therefore it must be defined a priori. We adopted $m = 0.1$ for the definition of "rare" (Green and Young 1993). Other studies used similar approaches to detect tree seedlings in the surrounding areas of the plantations (Callaham et al. 2013; Lavi et al. 2005). Before beginning the survey, we calculated that 30 plots per site would result in a confidence level of approximately 0.95. Therefore, the distance between plots at each plantation was determined by dividing the total length of the plantation boundary by 30. For very small plantations (when the plantation perimeter was less than 500 m) a distance of 15 m was used between plots. For larger stands, we sampled more than 30 transects in order to have the similar intensity sampling among plantations with different areas. Areas with very rough terrain such as boulders, ravines, or steep slopes were not considered in the study. Therefore, the number of plots at each site varied according to the size of the sampled plantation and the accessibility of adjacent habitat; the total number of plots ranged from 8 to 58 plots per plantation. Consequently, the values of β varied from site to site (β mean = 0.92 ± 0.09). This method was chosen because it allows a high level of detection of rare events (Green and Young 1993). The geographic
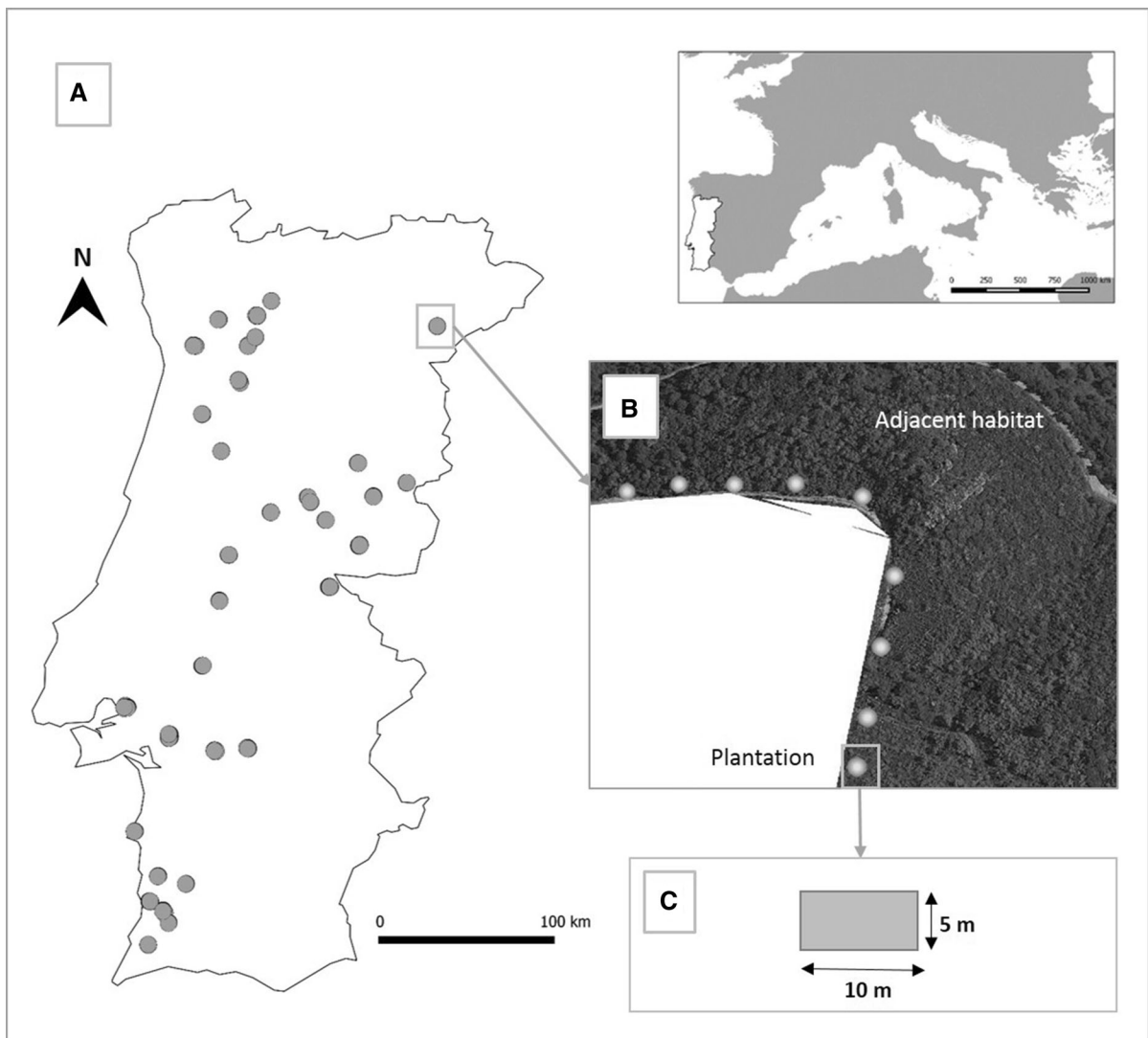
Fig. 1 a Location of the 50 studied *Eucalyptus globulus* plantations (grey circles) in continental Portugal. **b** Survey plots (grey circles) adjacent to the boundary edge of *Eucalyptus globulus* plantations. **c** Schematic diagram of the plot area (10 m × 5 m) which were established perpendicular to the plantation edge

coordinates of the centre of each plot was recorded using a hand-held GPS (Garmin, GPSMAP 76CSx).

Explanatory variables

We characterized each sampled plot with a broad range of variables as potential surrogates for biotic and abiotic conditions that can determine the susceptibility of the site for eucalypts establishment (Table 1). We used a 1 m² quadrat to calculate the percentage cover of vegetation (herbs and shrubs) and tree canopy cover (estimated as the sum of the

projected crown area inside the plot limits) and used this to calculate the percentage of non-bare ground in each plot. Within each plot we visually classified the disturbance level into three categories: undisturbed or low disturbed (intact vegetation structure with low animal trampling); medium (sporadic to moderate debris or moderate animal/human trampling); and highly disturbed (high human trampling and accumulation of debris, dumping, logging and high soil erosion). We recorded the aspect of the plantation edge for each plot. To facilitate interpretation and decrease the complexity of the models, we

Table 1 Variables used as predictors for the occurrence and density of *E. globulus* in natural habitats adjacent to forest plantations

Variable	Description	Mean (SD)	Range
Site characteristics			
Habitat type[a]	Three habitats types: forest, shrubland and grassland	–	–
Soil type[a]	Major soil type (5 *cat.*): cambisol, lithosol, luvisol, podzol and others	–	–
Aspect[a]	Aspect (2 *cat.*): unfavourable (SE, S and SW aspects) and favourable (remaining aspects)	–	–
Disturbance[a]	Categorical range of 3 levels: (1) undisturbed—low; (2) medium; (3) high	–	–
Shrubs cover (%)		51.24 (27.88)	0–100
Herbs cover (%)		16.27 (25.67)	0–100
Canopy cover (%)[a]		12.98 (23.76)	0–90
Non-bare ground cover (%)[a]		74.34 (18.36)	10–100
Plantation characteristics			
Plantation age (years)[a]		11.57 (2.62)	8–26
Residence time (years)[a]		29.63 (14.02)	15–68
Plantation area (ha)[a]		9.29 (10.36)	0.45–45.18
Productivity region[a]	Categorical range of 3 levels: (1) low; (2) medium; (3) high	–	–
Fire occurrence[a]	2 cat.: 1 (yes), or 0 (no)	0.36 (0.48)	0–1
Climate[b]			
Mean annual temperature (°C)		15.23 (1.44)	11.6–17
Temperature seasonality[a]		4734.11 (582)	3816–5914
Mean minimum temperature (°C January)		5.45 (1.95)	1.8–8.4
Mean maximum temperature (°C July)		28.54 (1.75)	25.1–32
Annual precipitation (mm)[a]		884.83 (273.7)	540–1438
Precipitation seasonality		57.28 (5.15)	49–67
Summer precipitation (mm)		56.67 (28.43)	21–108

cat. categories

[a] Variables included in the final analysis to avoid collinearity among continuous variables

[b] Data source: WorldClim (Hijmans et al. 2005)

transformed south-facing aspects into an unfavourable group where radiation and evapotranspiration are expected to be higher; the remaining aspects were classified as favourable (Beers et al. 1966; Kutiel and Lavee 1999). Plots were established in areas with moderate slope (i.e. 5% in average) in order to minimize the effect of slope in the relation of eucalypt density among sites. Slope and aspect could

Table 2 A summary of habitat types and the associated eucalypts sampled during the survey

Habitat type	Number of plots	Number of eucalypts	Number of plots with eucalypts	Proportion of plots with eucalypts
Forest	409	4	2	0.005[a]
Grassland	215	8	3	0.014[b]
Shrubland	955	468	115	0.120[c]
Total	1579	480	120	0.076

Letters indicate significant differences ($p > 0.05$) among habitat types according to post hoc test corrected for multiple hypothesis based on the best occurrence model selected by AICc criteria

interact to change radiation levels. However, as plots were established in sites with moderate topography, we regarded aspect as a sufficient indicator of light penetration (González-Moreno et al. 2013b). The habitat type of each sampling plot was recorded in the field: (a) forest, mainly small woods with *Quercus robur*, *Quercus pyrenaica* and *Quercus faginea*); (b) shrubland, Mediterranean garrigue composed by a mix of short and medium shrubs (maximum 2 m of height) as rockrose (*Cistus spp.*) and others *Cistaceae*, heather (genus *Erica* and *Calluna*), gorse (*Ulex* spp.), broom (*Cytisus* spp.) and many aromatic species (e.g. *Lavandula stoechas*, *Rosmarinus officinalis, Thymus vulgaris*); and (c) grassland occupied by rich annual herbaceous species. As a result of agricultural land abandonment, shrubland was the most dominant habitat type surrounding forest plantations, The soil type in each plot was calculated from the Portuguese Atlas of Environment (APA 2013; scale 1:1,100,000).

Using data obtained from plantation owners, we characterized plantations based on their age, residence time, area, productivity and fire history (Table 1). Plantation age was defined as the time (in years) since trees were first planted or the time since last harvest, to the date of survey. Residence time was calculated based on the number of plantation rotations and cycles (the first cycle corresponds to the establishment of trees for new plantings, including 2–4 rotations and the next cycles correspond to replanting after 2–4 rotations). The productivity of plantation was categorized into three levels (low, medium and high) based on climate and soil suitability for the growth of *E. globulus* (Soares et al. 2007; Tomé et al. 2001). Fire history was quantified as the presence or absence of large fire

events in the last decade (mostly corresponding to 2003 and 2005).

Finally, to account for climate influences, we selected seven variables that are ecologically most relevant for establishment success (i.e. plant growth and survival; Ibáñez et al. 2009) (Table 1). We selected mean annual temperature, mean minimum temperature of the coldest month, mean maximum temperature of the warmest month (the latter two to inform us about the temperature tolerance limits of *E. globulus*), temperature seasonality and precipitation seasonality (i.e. coefficient of variation in temperature/precipitation along the year), annual precipitation and mean precipitation of warmest quarter (which provides a proxy for dryness during summer months). Climatic data were downloaded from the WorldClim database and taken as averages from 1950 to 2000 (Hijmans et al. 2005). Each of the plot centre location was intersected with climate data at a 30 arcsec resolution (~ 1 km).

Data analysis

Considering the high number of zeros in the data, we used separate models to analyse occurrence (i.e. presence/absence of eucalypts) and density data (i.e. density models only used data from occupied plots). This approach solves the over-dispersion problem and the potential bias in parameter estimation when modelling zero-inflated data. Furthermore, the results of both models reflect the different stages of plant colonization and they are interpreted as two coupled process (Catford et al. 2011; González-Moreno et al. 2014; Ibáñez et al. 2009). Since there is no reason to expect factors to be of equal importance for both presence and density stages, the coupled modelling process ensures that factors that contribute to high

density could be identified regardless of whether sites are presently occupied by eucalypts (Catford et al. 2011). We analysed the association of the occurrence of eucalypts (i.e. presence/absence data in 1579 plots) and subsequent density (i.e. number of plants) with site characteristics, plantation characteristics and climate (Table 1) by multimodel inference (Burnham and Anderson 2002) and variance partitioning techniques (Mood 1969) based on generalized linear mixed models (GLMM) with the identification of plantation as a random effect to account for pseudoreplication. Due to the low number of plots with eucalypts present in grassland (n = 3) and forest (n = 2) habitats, habitat type was not considered in the density model. This approach facilitated model convergence and results were similar if data is restricted to the main habitat type (i.e. shrubland; See Appendix Table 4). The final density dataset has information from 120 plots. Occurrence was modelled by setting a binomial distribution for the response variable and a logit link (presence model) (Quinn and Keough 2002). The density was modelled using a negative binomial distribution, which is typically used for count data when over-dispersion occurs (Gelman and Hill 2007). Preliminary analysis using Moran´s Index, indicated no relevant spatial autocorrelation in the model´s residuals ($I < 0.4$) (see Appendix Fig. 4).

Prior to modelling we checked the explanatory variables for collinearity using pair-wise Pearson´s correlation test, excluding correlation values higher than 0.6 and then selected ones with best explanatory power (see Appendix Tables 5 and 6). With regard to site variables, shrub and herb cover were correlated with non-bare ground cover. For the final model, we used the percentage of non-bare ground cover and canopy cover site variables. We kept all plantation variables. Climate variables were highly correlated and thus we selected only two non-collinear variables: temperature seasonality and annual precipitation.

Multimodel inference, the model selection method used in this study, provides a framework to 'evaluate the relative strength of evidence in data for multiple hypotheses represented as models' (Hobbs and Hilborn 2006). This method provides two approaches to find the best models to use: model selection and model averaging. Thus, multimodel inference method allowed us to identify the best possible models and rank all explanatory variables according to their importance on eucalyptus occurrence and density (Burnham and Anderson 2002). We performed multimodel inference based on all-subsets selection of GLMMs using Akaike's information criterion corrected for a large number of predictors (AICc) (Burnham and Anderson 2002; González-Moreno et al. 2013a). First, for each group of predictors (site, plantation characteristics and climate) we selected the best model (smallest AICc). The same procedure was then performed combining the best variables of each group to establish the set of best candidate models. All models within four AICc units from the best model (delta < 4) were considered as the set of best models given the selected predictors. This threshold is within the limits adopted in other studies (González-Moreno et al. 2013a; Grueber et al. 2011). Within the best models subset we calculated the Akaike weight of evidence (w_i) for each candidate model to rank the predictors in order of importance in their relation to response variables. The w_i of each predictor was estimated as the sum of the model AICc weights across all models in which the selected predictor appeared. This means that the predictor with highest w_i (i.e. closest to one) gets the highest relative importance (compared to the rest of predictors) to explain the response variables within the given data (Burnham and Anderson 2002). In addition, multimodel inference was used to estimate regression coefficients and their confidence intervals (with adjusted standard error) within the best models subset ($\Delta < 4$). Coefficient of a given selected predictor was calculated as the sum of the predictor´s coefficient multiplied by the weight of evidence, across all possible models where the predictor is present (Burnham and Anderson 2002).

Variance partitioning techniques indicate the variability explained by the single and shared groups of variables (Mood 1969). We set up the best GLMMs selected in the previous approach for each dependent variable and incorporated site variables, plantation variables and climate variables individually before combining all three variables. Considering that deviance is a good measure of variability explained by a model, we used the deviance explained by each model to identify the pure and mixed effects by simple equation systems (Carrete et al. 2007; González-Moreno et al. 2013a). Following the same approach, we also partitioned the deviance of

eucalyptus presence and density accounted by site characteristics within three best site factors explaining each dependent variable. We performed the variance partitioning analysis with the two of the most important non-collinear variables of each group, in order to compare the differences between the results with all variables and with the same number of variables by group. The results did not show significant differences between these two approaches (see Appendix Fig. 5). We only present the results for all variables.

Statistical analysis was performed with the R-CRAN software (R Development Core Team 2009). We used the package MuMIn for some procedures of the multimodel inference method and the VEGAN package as the base code for deviance-partition.

Results

### Differences in *E. globulus* occurrence probability among habitat types

Eucalyptus globulus was recorded in 120 plots, representing 8% of the total plots assessed (Table 2).

The survey detected a total of 480 eucalypts (Table 2), ranging from 0 to 20 individuals per plot. Natural regeneration of eucalyptus occurred mainly in shrubland with eucalyptus being recorded in 12% (115 plots) of the plots sampled of this habitat type, accounting for a total of 468 plants (Table 2). Considering the best occurrence model (see Appendix Table 7), forest and grassland were the most resistant habitat to eucalyptus establishment (Table 2).

Partitioning the influence of climate, plantation and site characteristics on the natural regeneration of eucalyptus

The variability of both the occurrence and density of eucalyptus was predominantly explained by site variables, which had a very high single effect on eucalypts occurrence (57%; Fig. 2a-i). In contrast, climate and plantation characteristics had a very low single effect and its explanatory power was shared mainly with site variables (Fig. 2a-i). Considering site variables separately, deviance partitioning-analyses revealed that the percentage cover of non-bare ground of the areas surrounding plantations explained

Fig. 2 Deviance partitioning of *E. globulus* presence (**a**) and density (**b**) using generalized linear mixed models **i** among climate, plantation and site characteristics predictors, and **ii** among the three best site factors explaining each dependent variable. Each circle corresponds to a group of variables. Numbers within circles are the proportion of deviance explained by each set of predictors alone (non-overlapping parts of circles) or shared. Residuals indicate the deviance not explained by the models
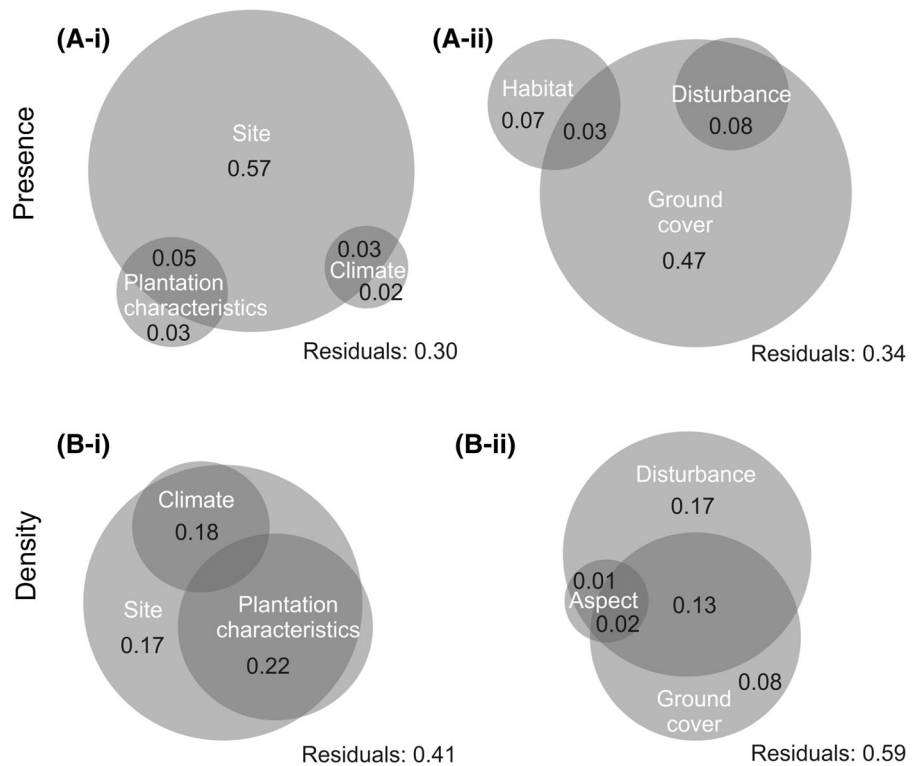
most of the deviance of eucalyptus occurrence (47%; Fig. 2a-ii). The explanatory power of habitat type was partially shared with percentage of non-bare ground cover (3%) and accounts for 7% of single effect. The effect of disturbance on the occurrence of eucalypts was shared with percentage of non-bare ground cover (Fig. 2a-ii).

Deviance partitioning indicates that a combined effect of plantation and site variables accounted for the largest proportion (22%) of variability of the eucalyptus density, followed by the combined effect of climate and site variables (18%). Site variables had the largest independent effect (17%) and the independent effect of the others two groups was practically inexistent (Fig. 2b-i). Considering site variables, the variability of eucalyptus density was mainly explained by the single effect of disturbance (17%), followed by the combined effect with non-bare ground cover (13%). The percentage of non-bare ground cover had a low single effect (8%) on eucalyptus density. The total amount of aspect effect was shared with disturbance and non-bare ground cover (Fig. 2b-ii).

The association of climate, plantation and site characteristics with the natural regeneration of eucalypts

The variables best explaining eucalyptus occurrence and density differed. In the case of density data analysis, climate and plantation variables were not selected (Tables 3 and see Appendix Table 8). The major correlates (i.e. higher weight of evidence) for eucalyptus presence were site factors: habitat type and non-bare ground cover. After site factors, productivity region (the best plantation predictor explaining eucalyptus occurrence) was the next in importance to model fit, followed by annual precipitation (the best climate factor) (Table 3). Specifically, we found a higher probability of eucalyptus occurring in shrubland than in forest habitat (Table 2). The probability of eucalyptus occurrence was lower at low productivity regions. Non-bare ground cover showed a significant negative association with eucalyptus occurrence. Finally, annual precipitation had a weak positive relation with eucalyptus occurrence (Table 3).

The variables best explaining eucalyptus density were disturbance and non-bare ground cover (Table 3). Considering the best density model (Table 8), eucalyptus density had a significant

Table 3 Multimodal inference results: weight of evidence, averaged coefficient estimates, adjusted standard error and confidence intervals (95% CI) of climate, plantation and site predictors for *E. globulus* occurrence in surrounding plantations habitats

Variable	Type	W	β averaged	Adjusted SE	Lower CI	Upper CI
Presence						
Intercept			− 12.191***	1.847	− 15.796	− 8.550
Habitat type	S	1.00				
Non-bare ground%	S	1.00	− 3.879***	0.433	− 4.726	− 3.029
Productivity region	P	0.84				
Annual precipitation	C	0.46	0.372	0.615	− 0.566	2.173
Density						
Intercept			1.173***	0.236	0.646	1.662
Disturbance	S	1.00				
Non-bare ground%	S	0.86	− 0.162*	0.073	− 0.304	− 0.020
Favourable aspect	S	0.69	0.374	0.207	− 0.032	0.781

Predictors of each model are sorted by importance according to the weight of evidence. Regression coefficients for the categorical variables habitat, productivity region and disturbance are not shown. Significance of averaged coefficients: *** $p < 0.001$; * $p < 0.05$. See Table 1 for a complete description of variables

Type of predictors: *S* site characteristics, *P* plantation characteristics, *C* climate. Habitat type was not considered in the Density model (see Methods)
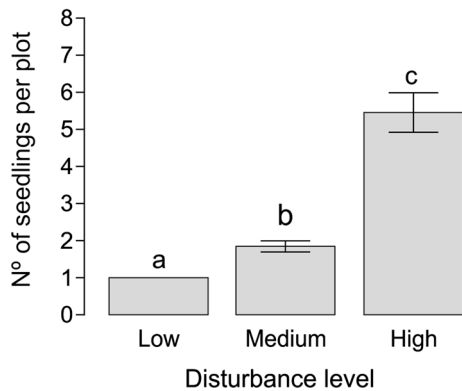
Fig. 3 Mean (± SE) eucalypts density (no of eucalypts/plot) for low (N = 2), medium (N = 46) and, high (N = 72) disturbance levels. Letters indicate significant differences ($p > 0.05$) between disturbance levels according to post hoc test corrected for multiple hypothesis based on the best density model selected by AICc criteria

negative association with non-bare ground cover and was significantly higher in the highly disturbed plots (Fig. 3). Aspect also had some importance explaining eucalyptus density, with slightly higher densities recorded in northern aspects, although this difference was not significant (Table 3).

Discussion

Conceptual models to explain the establishment of non-native plants have suggested that a combination of having a large enough propagule pressure and a suitable biotic and abiotic environment favour establishment (Catford et al. 2009; Chytrý et al. 2008a). In this study, climate was used to estimate abiotic suitability (Walther et al. 2009), while site characteristics (including habitat type, vegetation cover and disturbance) represented the main characteristics of the host community (biotic and abiotic suitability) (Rejmánek et al. 2005). Among these variables, we found site characteristics to be the most important group of variables influencing the establishment of *E. globulus* (occurrence and density) outside planted areas in comparison to climate and plantation characteristics. This pattern reflects that most of the variability in *E. globulus* establishment occurs at a small spatial scale (site scale; < 1 km) (Milbau et al. 2009). Factors affecting species distribution most likely do so in a hierarchical manner, with different

ecological factors affecting plant establishment success more strongly at different spatial scales (Milbau et al. 2009). For example, a study by Pearson et al. (2004) on the impact of climate and land cover changes on species distributions in Britain reported a dominant effect of climate measured at the European scale over land-cover data at the British scale. In accordance with this, climate and plantation characteristics might control variability in the establishment of *E. globulus* among plantations (regional scale: 2000–200 km), whilst site characteristics influence the establishment of *E. globulus* within a plantation (site scale: 10–1000 m). At larger scales, such as continental, climate would probably have a more important role in shaping the natural establishment of *E. globulus* (Catry et al. 2015; Larcombe et al. 2013). Despite the scale of our study, we found a relatively high importance of annual precipitation as a climate predictor and, as such, *E. globulus* was more likely to be present in areas with high annual precipitation. This finding has also been identified in previous studies (Águas et al. 2014; Catry et al. 2015; Larcombe et al. 2013). For example, Catry et al. (2015) found that the density of eucalypts was lowest below c. 600–700 mm of annual precipitation and sharply increased up to around 1500 mm. They also found that eucalypts density reached the lowest values above 2400 mm. The maximum annual precipitation sampled in our study was 1438 mm with an average of 885 mm and therefore, optimal conditions for the establishment of eucalypts.

Habitat type and the percentage of non-bare ground cover were the most important factors explaining the occurrence of eucalypts. Previous studies have also found habitat type to be the foremost factor explaining differences in plant invasions (Chytrý et al. 2008a; Gassó et al. 2012). Moreover, it has been suggested that invasive species traits related to successful establishment are habitat dependent (González-Moreno et al. 2013b; Lake and Leishman 2004; Lloret et al. 2005). The probability of *Eucalyptus* occurrence was higher in shrubland than in forest and grassland. Shrubs can have a nurse effect on seedlings of eucalypts, protecting them from harsh environmental conditions (Gómez-Aparicio et al. 2008). Shrubland may also provide greater light availability during later stages of seedling development. *E. globulus* are classified as shade-intolerant species, requiring a high light regime to

develop (Correia et al. 1989). Native forests dominated by pedunculated oak, as other broad leaved trees, have low light irradiance regimes at ground level compared to the open vegetation of shrubland (Barbier et al. 2008). Therefore, the lowest probability of eucalypts occurrence found in forest patches is likely to be caused by a negative shading effect. A study by Calviño-Cancela and Rubido-Bará (2013) reported lower *E. globulus* seedling emergence under native forest patches (pedunculated oak) than in shrubland. This species is also reported as highly sensitive to drought, particularly at the seedling stage (Stoneman 1994). Eucalypts produce large quantities of seeds which are very small with no obvious endosperm. Thus, the newly emerged seedlings (sustained by cotyledon photosynthesis) need their roots to penetrate a suitable wet substrate very quickly in order to survive (Rejmánek and Richardson 2011). Grasslands normally show high seasonal fluctuation in water soil and nutrients availability (Rundel et al. 2014) which could negatively affect seedling survival (Rejmánek and Richardson 2011). High mortality during the initial phase of seedling growth, due to unsuitable environmental conditions or competition with other plants, has been recognized as one of the most important factors limiting eucalypts colonization (Callaham et al. 2013; da Silva et al. 2011; Rejmánek and Richardson 2011).

The survival of *Eucalyptus* seedlings is generally low in dense vegetation sites (Rejmánek and Richardson 2011). This is in agreement with the significant negative association found in our study between percentage non-bare ground cover (mainly determined by understory vegetation cover) and the probability of eucalypts occurrence and density. Non-bare ground cover alone explained 47% of the variability in eucalypts occurrence. Therefore, the higher probability of eucalypts establishment is mainly related to the horizontal structure of the community. Vegetation structure could be the responsible of the low establishment rate found in comparison to other studies. In Catry et al. (2015), eucalypts presence was found in 60% of the roadside transects adjacent to eucalypt plantations. On the contrary, *E. globulus* had established in only 8% of the total plots. Roadsides usually have a high percentage of exposed soil with little or no vegetation. This characteristic seems to increase the suitability of the community to the establishment of

eucalypts, increasing the window of opportunity for eucalypt seeds to reach suitable sites.

The productivity of the region was, after site variables, the most important factor explaining the occurrence of eucalypts and the best plantation predictor. This factor is based on climate and soil suitability for *E. globulus* growth (Soares et al. 2007; Tomé et al. 2001). Thus, as climate factors, productivity can be also considered as a proxy for abiotic suitability for the growth of eucalypts at regional scale. The partition analyses revealed that plantation characteristics (e.g. plantation age and area) had a low explanatory strength and shared its explained deviance with site characteristics. The very short rotations (10–12 years) and intensive management of these plantations could explain these results. Thus, the plantations might not have enough time decrease to produce a significant propagule pool. The importance of plantation characteristics might increase in abandoned plantations (not considered in this study), as the propagule pressure builds with time. Thus, future research in abandoned eucalypt plantations is needed to better understand the role of residence time in *E. globulus* colonization.

The occurrence and density of eucalypts were modulated by different variables. In contrast to occurrence, the best models for density data only included site characteristics. These results indicate that once eucalypts have a high probability of establishment then the main aspect determining eucalypts success is the characteristics of the host community. This is in accordance with Milbau et al. (2009), who suggested that small-scale factors are better predictors at finer scales if conditions at higher levels are satisfied. Within site characteristics, disturbance level was the most important factor explaining eucalypts density. Disturbance, specifically native vegetation removal, is an important driver of invasive species expansion (e.g. Alston and Richardson 2006; Davis and Pelsor 2001; Davis et al. 2000; Elton 1958; Higgins and Richardson 1998; Mitchell et al. 2006). Our study found that an increase in the level of disturbance resulted in an increase in the density of eucalypts. This result agrees with previous findings by Lorentz and Minogue (2015) and Silva et al. (2011), where litter and plant removal improved the survival of eucalypts seedlings. In our study, the density of eucalypts found in all highly disturbed plots close to plantations (mean $\pm$ SD = 293 $\pm$ 673 plants ha^{-1}) is similar to

the mean density (277 plants ha^{-1}) calculated by Catry et al. (2015) in roadside transects adjacent to eucalypt plantations in Portugal. However, the observed average eucalypts density in both studies is very low compared to well-known invasive forestry species such as pines for example (Richardson et al. 1994) and also with native maritime pine planted in Portugal (892 plants ha^{-1}) (Fernandes et al. 2016).

Conclusions

In the present study we show that the establishment of *E. globulus* is limited to the natural habitats adjacent to managed plantations, compared to road-sides (Catry et al. 2015). This was particularity true when the habitat type surrounding the sampled plantations was forest or grassland. The percentage of bare ground had a significant effect on the establishment of eucalypts and our findings suggest that an increase in bare ground increases the suscep-tibility to eucalypts establishment. Therefore, our results suggest that by reducing the disturbance of habitats adjacent to eucalypt plantations during management activities the establishment success of *E. globulus* would be greatly reduced. In summary, our study suggests that eucalypts establishment is highly limited by biotic interactions (i.e. competition with other plants), low light and water availability. Nowadays, the expansion of trees into habitats outside of a plantation is a concern for managers and conservationists. These small-scale factors are essential to precise predictions at more local scales. Other higher scale factors, namely climate and productivity region, had lower explanatory strength on the establishment probability of eucalypts. As a cultivated tree, the current distribution of *E. globulus* in Portugal has resulted from human activity, target-ing environmental conditions highly suitable for the species. Thus, monitoring efforts should focus on the site factors determining the colonization (i.e. ground cover, habitat type and disturbance). Industrial *E. globulus* plantations are grown with very short rotations and with regular basis management, so there are multiple opportunities for detection and control over the life of a plantation. Taking into account our results, we also suggest the establishment of "sentinel sites" using remote sensing tools (e.g. Google Earth) as described by Visser et al. (2014) or

in situ visits during conventional management. This monitoring could provide an early-warning system for prevention management and, over time, it will produce very valuable data contributing to our understanding of eucalypts colonization dynamics.

Appendix

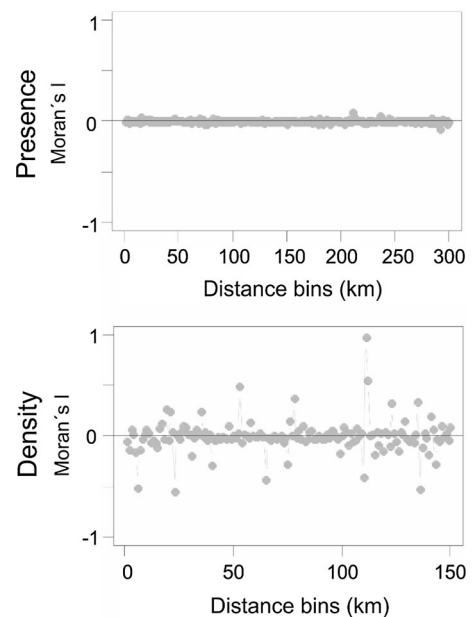See Figs. 4 and 5 and Tables 4, 5, 6, 7 and 8.

Fig. 4 Moran´s Index calculated in 1 km bins for the models explaining the presence and density of *Eucalyptus globulus* natural regeneration
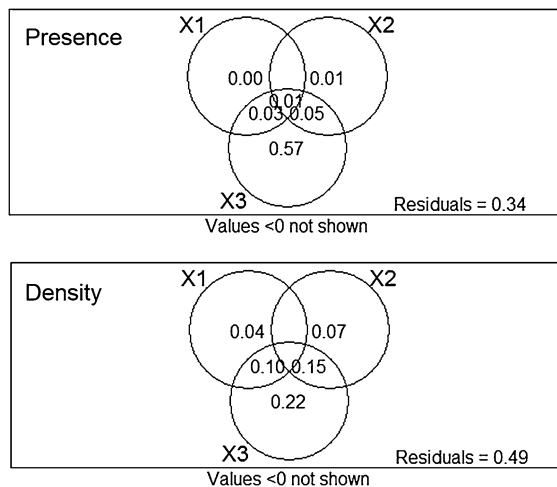
Fig. 5 Deviance partitioning of *E. globulus* presence and density using generalized linear mixed models among climate (X1), propagule pressure (X2) and site characteristics (X3) predictors. Each group of predictor included only the two of the most important non-collinear variables explaining each dependent variables. Each circle corresponds to a group of variables. Numbers within circles are the proportion of deviance explained by each set of predictors alone (non-overlapped part of circles) or shared. Residuals indicate the deviance non-explained by the models

Table 4 Multimodal inference results: weight of evidence, averaged coefficient estimates, adjusted standard error and confidence intervals (95% CI) of climate, plantation and site predictors for *E. globulus* density in shrubland habitat (n = 115)

Variable	Type	W	β Averaged	Adjusted SE	Lower CI	Upper CI
Intercept			1.163***	0.256	0.646	1.662
Disturbance	S	1.00				
Non-bare ground (%)	S	1.00	− 0.184*	0.061	− 0.328	− 0.041
Favourable aspect	S	0.59	0.228	0.257	− 0.060	0.835

Predictors of each model are sorted by importance according to the weight of evidence. Regression coefficients for the categorical variable disturbance are not shown. Significance of averaged coefficients: *** $p < 0.001$; * $p < 0.05$

Table 5 Pearson´s correlation coefficients among the predictors (only continuous variables) used to model the occurrence of *E. globulus* in habitats surrounding plantations (n = 1579)

	Area (ha)	Age (years)	Time of introduction	Temperature seasonality	Annual precipitation	Non-bare ground cover
Age	− 0.270***					
Time of introduction	− 0.334***	0.433***				
Temperature seasonality	− 0.367***	0.334***	0.211***			
Annual Precipitation	− 0.526***	0.285***	0.460***	0.276***		
Non-bare ground cover	0.094***	− 0.018	− 0.051**	− 0.005	− 0.144***	
Canopy cover	− 0.005	0.065***	− 0.037*	0.029	− 0.084***	− 0.095 ***

Significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Table 6 Pearson´s correlation coefficients among the predictors (only continuous variables) used to model the density of *E. globulus* in habitats surrounding plantations (n = 120)

	Area (ha)	Age (years)	Time of introduction	Temperature seasonality	Annual Precipitation	Non-bareground cover
Age	− 0.330***					
Time of introduction	− 0.136	− 0.366***				
Temperature seasonality	− 0.501***	0.468***	− 0.009			
Annual Precipitation	− 0.525***	0.331***	− 0.348***	0.483***		
Non-bare ground cover	0.149	0.034	0.072	0.045	− 0.004	
Canopy cover	− 0.009	0.102	− 0.083	0.021	− 0.041	0.012

Significance: *** $p < 0.001$

Table 7 Selection of best models considering AICc criteria (Delta < 4: all models within 4 AICc units from the best model) for eucalyptus occurrence considering climate, plantation and site variables

Model	df	logLik	AICc	Delta	Weight
3 + 4+5	7	− 120.79	255.66	0.00	0.26
1 + 3+4 + 5	**8**	**− 119.89**	**255.86**	**0.21**	**0.24**
2 + 3+4 + 5	8	− 119.96	256.00	0.35	0.22
1 + 2+3 + 4+5	9	− 119.62	257.36	1.70	0.11
1 + 3+5	6	− 123.18	258.42	2.76	0.07
3 + 5	5	− 124.39	258.81	3.15	0.05
1 + 2+3 + 5	7	− 122.63	259.34	3.68	0.04

In bold the best model considering climate

1: Annual precipitation; 2: Temperature seasonality; 3: Habitat type; 4: Productivity; 5: Understory cover

Table 8 Selection of best models considereing AICc criteria (Delta < 4: all models within 4 AICc units from the best model) for eucalyptus density considering climate, plantation and site variables

Model	df	logLik	AICc	Delta	Weight
1 + 2+3	**7**	**− 250.37**	**515.75**	**0.00**	**0.54**
2 + 3	6	− 252.03	516.81	1.06	0.32
1 + 2	6	− 252.84	518.43	2.68	0.14

1: Aspect; 2: Disturbance; 3: Understory cover

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