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Different environmental drivers of alien tree invasion affect different life-stages and operate at different spatial scales

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Abstract

Identifying the key factors driving invasion processes is crucial for designing and implementing appropriate management strategies. In fact, the importance of (model-based) prevention and early detection was highlighted in the recent European Union regulation on Invasive Alien Species. Models based on abundance estimates for different age/size classes would represent a significant improvement relatively to the more usual models based only on species' occurrence data. Here, we evaluate the relative contribution of different environmental drivers to the spatial patterns of abundance of several height classes (or life-stages) of invasive tree populations at the regional scale, using a data-driven hierarchical modelling approach. Before, a framework for modelling life-stages to obtain spatial projections of their potential occurrence or abundance has not been formalized before.

We used *Acacia dealbata* (Silver-wattle) as a test species in northwest of Portugal, a heavily invaded region, and applied a multimodel inference to test the importance of various environmental drivers in explaining the abundance patterns of five plant height classes in local landscape mosaics. The ensemble of height classes is considered here as a proxy for population dynamics, life-stages and age of adult trees. In this test with *A. dealbata*, we used detailed field data on population height structure and calibrated an independent model for each height class. We found evidence to support our hypothesis that the distribution of height classes is mostly influenced by distinct factors operating at different scales. The spatial projections which resulted from several height class models provide an overview of population structure and invasion dynamics considering various life-stages, that is widely used in biodiversity and invasion research.

The approach proposed here provides a framework to guide forest management to deal more effectively with plant invasions. It allows to test the effects of key invasion factors (depending on the focal species and on data availability) and supports the spatial identification of suitable areas for invasive species' occurrence while also accounting for the structural complexity of invasive species populations, thereby anticipating future invasion dynamics. The approach thus constitutes a step forward for establishing management actions at appropriate spatial scales and for focusing on earlier stages of invasion and their respective driving factors (regeneration niche), thereby enhancing the efficiency of control actions on major forest invaders.

Keywords: *Acacia dealbata*, biological invasions, environmental factors, multimodel inference, scale-dependence

1. Introduction

Biological invasions, i.e. the spread of alien species, can cause severe ecological damages and financial costs (Vilà et al. 2010). Invasive plants, particularly trees, have major implications for forest management (Silva & Marchante, 2012) and can substantially alter ecosystem and landscape processes, such as fire regimes (Brooks et al., 2004) and nutrient cycles (Marchante et al., 2008). Invasions can introduce new internal feedback mechanisms (Gaertner et al., 2014) or disrupt the balance of existing feedbacks in ecosystems (sensu Bennett et al., 2005). These effects will depend on the spatial distribution and residence time of invaders (Castro et al. 2005), and on the interplay between biotic (Martínez et al. 2010) and abiotic drivers (Herrero-Jáuregui et al. 2012;), many of which are strongly scale dependent (McGill, 2010).

Understanding the drivers and patterns of invasion processes is crucial for designing and implementing appropriate management strategies (Brundu & Richardson 2016). There is a growing need to predict invasions at finer spatial scales (Fernandes et al., 2014) so as to effectively support different types of intervention, from early detection to management of well-established invaders (van Wilgen et al. 2011). The importance of prevention and early detection was highlighted in the recent European Union regulation on Invasive Alien Species (IAS; EU No 1143/2014). Besides defining coarse climatic envelopes for invasive species (Brundu & Richardson 2016, Pino et al. 2005), fine-scale species distribution modelling and prediction requires including local environmental and habitat factors (Vicente et al., 2011; Fernandes et al, 2014), as well as linking correlative models to demographic variables or demography-based population models (Kueffer et al. 2013). The management of invasions will then benefit from better knowledge and more informative predictions (Chornesky et al. 2005; Genovesi & Monaco 2013).

In the case of alien trees, zooming below the species level (e.g., to different management-relevant categories such as life-stages/height structures of populations/stands) could be very useful for forest invasion management, since the structural characteristics of populations of invasive species will have strong effects on invasion dynamics and on the properties of invaded ecosystems (e.g. Call and Nielsen 2003; Vilà et al., 2011; Valladares et al. 2014). Specific control treatments might be better targeted if the factors driving the presence of specific age or height classes of invasive trees are weighted. For example, predicting the distribution of young life-stages can facilitate early detection and more effective control of invasive species (Di Stefano et al., 2013, Gurevitch et al. 2011, Elith 2016, Hui & Richardson 2017). Models based on abundance estimates for different life-stages/height structure classes will therefore represent a significant improvement on the most usual models which are based on presence/absence data of species independent of age/size classes. Also, since the importance of factors influencing species distribution differs across scales (Thomas et al., 1998; Rouget & Richardson, 2003; Vicente et al., 2011, 2014), models should be calibrated and tested at different spatial resolutions and extents

(Gurevitch et al. 2011, Elith 2016, Hui & Richardson 2017). This way, forest planning instruments will be an even more effective and important tool in controlling invasive trees at both the stand and the landscape levels (Sitzia et al. 2016), especially in the case of species like *Acacia dealbata*, whose spread seems to be reduced by maintaining or facilitating closed canopy and dense forest cover (Hernández et al. 2014; Silva and Marchante 2012).

The silver wattle (*Acacia dealbata* Link) is one of the most widespread woody plant invaders in southern Europe (Sheppard et al., 2006). The success of *A. dealbata* as an invader has been attributed to multiple biological and ecological characteristics of the species, including phenotypic plasticity, adaptability to disturbance and changeable conditions, positive feedbacks with fire occurrence, production of large long-lived seedbanks, and resprouting ability (Lorenzo et al., 2010; Gibson et al., 2011). As with other invasive trees, the occurrence of this species in invaded regions can range from small and localized areas in initial invasion stages, to large areas where native vegetation and managed forest stands have been entirely replaced by *A. dealbata* scrub or woodland (Lorenzo et al., 2012). Depending on abiotic and biotic conditions, local invasion dynamics, and management history, the species may be represented by individuals in a wide range of size and age classes in a given landscape mosaic. This makes *A. dealbata* a good candidate for testing the novel modelling approach that differentiates factors that influence the invasion process and their scale-dependence in different stages of the plant's life cycle (Buhle et al. 2005; Souza-Alonso et al. 2013).

Species distribution models (SDMs) have a long history of applications in ecology and management (e.g., Petitpierre et al., 2012; Vicente et al., 2011). However, SDM-based studies have focused almost exclusively on the static distributions of the adult niche (i.e. adult individuals' distribution) of the species (sensu Grubb 1977). Considering different age classes becomes particularly important for applying SDMs in a time of rapid environmental changes, including climate and land use changes, as adult trees might have regenerated under a very different climate decades ago, and possibly also under different habitat conditions. Thus, current environmental variables might explain the regeneration niche well, but not necessarily the adult niche, and adult individuals can persist across a wider range of environmental conditions than seedlings or young individuals occurring in the 'regeneration niche' (sensu Grubb 1977). Therefore, considering both the "adult" and the "regeneration" niches in models can more accurately identify the environmental factors underlying the potential distribution of individuals in the several age classes of long-lived organisms.

Here we address this challenge by evaluating the relative contributions of different environmental drivers to the spatial patterns of abundance of several height classes of invasive tree populations at the regional scale, using a data-driven hierarchical modelling approach. We used *A. dealbata* as a test species in northwestern Portugal, a heavily invaded region (Vicente et al., 2010, 2011). We applied an information-theory approach (multimodel inference) to test the importance of environmental drivers in explaining the abundance patterns of several plant height classes in local landscape mosaics. To explore the size- and scale-dependence of invasion factors, we formulated two general research hypotheses to be tested under this multimodel inference framework. The first hypothesis relates the diversity of invasion factors to *Acacia* life-stages. The regional distribution of various life-stages, represented by different *Acacia* height classes, is known to be associated with distinct sets of prevailing environmental factors (Kempes et al., 2011; Lasky et al. 2013). Since invasion patterns in the test area are strongly constrained by climate (Vicente et al., 2010, 2011), we expected that the abundance of younger life-stages would be explained by one or few major drivers (namely climate). Once established, *Acacia* trees can then cope better with climate conditions and their inter-annual variations, but to reach adulthood they will have to endure the effects of other survival filters throughout their establishment and growth. Thus, we expect that more factors (namely those related to habitat conditions and landscape processes) would be needed to adequately predict the abundance of older plants.

Our second hypothesis advocates that the main factors underlying the distribution of each height class are influenced by the extent of the study area and are scale-dependent (Vicente et al. 2014a). The effects of factors acting at different spatial scales have been demonstrated before in the study area at the species level, for the invasion by multiple alien plants (Vicente et al., 2010) and specifically by *A. dealbata* (Vicente et al., 2011). Building on the same rationale as for the first hypothesis and on the selective role of habitat filtering (Lasky et al., 2013, Richardson et al., 2000), we expected that regional factors (namely climate) would be more important for seedlings and saplings, especially across larger spatial extents, since younger plants are more sensitive to frost or drought than older plants. In contrast, local factors would hold the highest explanatory power for trees (e.g. due to habitat filtering; Lasky et al., 2013) as well as for smaller spatial extents (where landscape factors tend to override the effects of climate; Vicente et al., 2010).

2. Methods

2.1 Study area and test species

The study area is located in northwestern Portugal (Fig. 1) and is heavily invaded by alien plants (Vicente et al. 2010). It covers 3,462 km^2 at the westernmost transition between the Temperate-Atlantic and the Mediterranean regions of Europe (Mesquita and Sousa 2009). The area is topographically heterogeneous, with elevation ranging from sea level in the west to 1,450 meters above sea level in the eastern mountains, resulting in marked variations of environmental conditions. Mean annual temperature ranges from about 9ºC to about 15ºC, and the mean total annual precipitation varies between about 1,200 mm in the lowlands to about 3,000 mm in the eastern mountain tops. The topographic and climatic heterogeneity of the area leads to a wide variety of land-uses and vegetation types, ranging from annual crops and pastures to planted pine or eucalypt stands and natural oak forests.

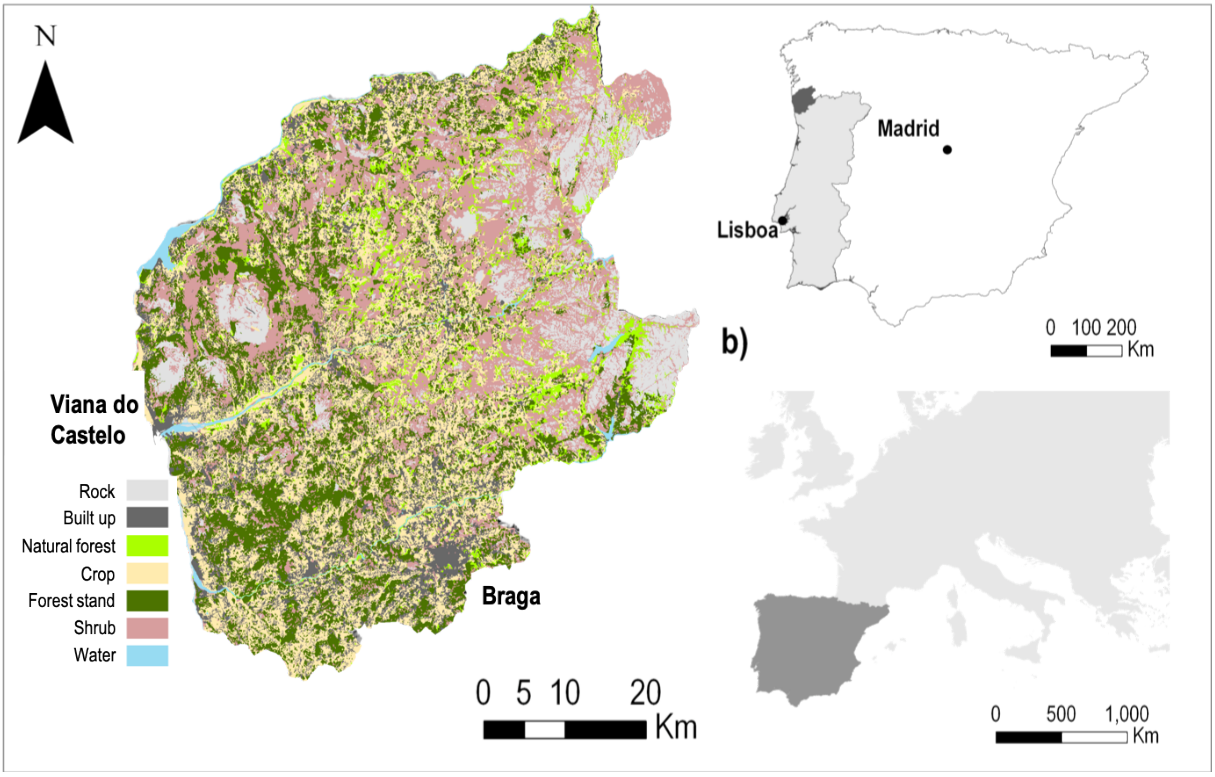


Figure 1 The study area in northwestern Portugal, showing the main land cover categories (http://ftp.igeo.pt/e-IGEO/egeo_downloads.htm) (left), its location in the Iberian Peninsula (top right), and southwestern Europe (bottom right).

Acacia dealbata (silver wattle; *Fabaceae*) is a tree species native to southeastern Australia and Tasmania (Lorenzo et al. 2010). It can grow up to 15 meters (www.invasoras.pt), and the typical time to maturity is usually less than 4 years. It presents a long lifespan for acacia species, exceeding 20 years (Boland et al. 1984). The species was introduced to Europe around 1800 (Ellena et al. 2008) and was planted as an ornamental in the 19th century in many areas of southern Europe (Sans-Elorza and Sánchez 2004), including Portugal (Alves 1858). Since then, it has become very common in Mediterranean countries where it occurs as an invader in disturbed forests, scrublands (Lorenzo et al. 2010) and margins of roads and water courses. *A. dealbata* has a high colonizing ability and the capacity to produce large numbers of long-lived seeds (Gibson et al., 2011), the germination of which is stimulated by fire. Invasive populations usually form dense thickets, and have the capacity to replace native vegetation by inhibiting its regeneration after disturbance (e.g., through competition for resources, by allelopathic interference and also due to vigorous re-sprouting or coppicing after cutting; Lorenzo et al., 2010; Le Maitre et al., 2011). The species is widespread in the study area and is projected to expand its current distribution under future climate and land-use scenarios (Vicente et al. 2011).

2.2 Sampling strategy and *Acacia* population data

The population structure dataset for *A. dealbata* was collected through field surveys between January and March 2013, during the flowering period of the species. Surveys were done in 0.04 km^2 (200 x 200 m) grid cells. To select the cells to be surveyed, we first used a coarse-grained occurrence dataset (Vicente et al. 2013) to calibrate a generalized linear model for *A. dealbata* (with 1 km^2 resolution) which was projected for the study area. In this 1 km^2 resolution model, climatic variables (minimum temperature of the coldest month, and summer precipitation) were used as the only environmental predictors, since these are the primary determinants of woody alien invasions at a regional scale in the study area (Vicente et al. 2010). Grid cells predicted as suitable for the species occurrence by the 1 km^2 model (with binarization threshold maximizing the percentage of presences and absences correctly predicted; Liu et al., 2005) were then stratified based on the percentage of land covered by planted forest stands (3 classes obtained by natural breaks) and on landscape edge density (3 classes obtained by natural breaks) to capture the main compositional and structural landscape gradients of the area (9 final strata; see Fernandes et al. 2014; Appendix 1). We then used an equal-stratified sampling design to randomly select 21 plots of 0.04 km^2 size in each stratum (21*9 = 189 plots). The final dataset used for model fitting included 187 records (two plots were not surveyed due to their inaccessibility).

For each 0.04 km^2 cell, the number of *A. dealbata* individuals across five height classes was calculated as the proportion of individuals per height class (summing 1 for each sampling) multiplied by the total estimated number of individuals in the population. The later was recorded based on standard abundance classes (1, 2-10, 11-50, 51-100, 101-500, 501-1000, >1000) since the exact number of individuals was often impossible to estimate with a reasonable surveillance effort. The sampling was performed using a fixed-time sampling approach (about 30 minutes per cell, sufficient to fit each cell into one *A. dealbata* abundance class and to estimate the proportions of the several height classes). Five height classes (A-

E) were established and associated to the individuals age (e.g. seedlings matches to first year regeneration and saplings to second year), seed production (e.g. only individuals with more than 2 m were able to produce seeds), on the available management options to control or eradicate the individuals, and on the plant response to different management options: A: < 0.5 m (seedlings); B: 0.5 m to 2 m (saplings); C: 2 m to 5 m (small trees); D: 5 m to 10 m (medium trees); and E: > 10 m (large trees)). The numbers of individuals of the five *A. dealbata* height classes per cell were used as response variables for each of the five SDMs calibration.

2.3 Predictor variables

Predictor variables for model calibration were selected based on the factors that have been previously reported in the literature as potential determinants of the phenology and distribution of *A. dealbata*, and also from previous research on alien plant invasions in the test region (Lorenzo et al. 2010; Vicente et al. 2010, 2011, 2013). To avoid multicollinearity, only predictors with a pairwise Spearman correlation lower than 0.6 (e.g., Elith et al. 2006) and generalized Variance Inflation Factor (VIF) lower than 5 (Neter et al. 1983) were considered. In the case of correlated pairs of variables, we chose the variable with the 'a priori' most direct ecological effect on plant species distribution.

These analyses yielded a final set of 25 environmental variables (at 0.04 km^2 resolution) to fit the models: four climatic variables (mean annual temperature, minimum temperature of coldest month, annual precipitation, and precipitation seasonality), four land cover / landscape composition variables (percentage cover of broadleaf forests, artificial forests, built up areas, and scrub and sparse vegetation), four landscape structure variables (mean shape index, mean perimeter-area ratio, number of patches, and patch size standard deviation), four geological and soil variables (percentage of granites, schist, anthrosols, and leptosols), four variables expressing dispersal corridors (river density, road density, distance to main rivers, distance to main roads), four landscape complexity variables (local Shannon diversity of: aspect, geology, altitude, and land-use), and finally one variable expressing the fire regime (number of fires between 1990 and 2013).

Generalized Linear Models (GLMs) were fitted separately for the abundance of the different height classes of *A. dealbata*, using the R software (R Core Team 2016). The number of individuals of each class was used as the response variable in GLMs with Poisson error distribution and log link function (Vincent and Haworth, 1983; Guisan and Zimmermann 2000). Up to second-order polynomials (linear and quadratic terms) were allowed for each predictor in the GLMs, with the linear term being forced in the model each time the quadratic term was retained. The procedure was adapted from Burnham and Anderson (2002) and Wisz and Guisan (2009).

2.4 Analytical framework: hypotheses and competing models

Since *A. dealbata* is known to be sensitive to severe and prolonged frost (Lorenzo et al, 2010), we expected climate to act as a strong primary gradient determining the spatial pattern of tree individuals of each height class, masking the effect of other gradients. For this reason, we used a spatially nested approach (see Vicente et al. 2010) to assess the relative importance of locally acting environmental gradients (such as land cover, soil and geology; see also Carl et al. 2016). First, a model using the total information of *A. dealbata* individuals (sum of the number of individuals sampled in the field, regardless of height class, per cell) was calibrated only with climate predictors (annual mean temperature, minimum temperature of coldest month, annual precipitation, and precipitation seasonality). The spatial projection of that model was then used to sub-sample the study area. Sub-sampling was done by using the quartiles of predictions from the climate-based model, and resulted in areas that are progressively more homogeneous, smaller, and with higher predicted *A. dealbata* densities. In this way we tested the effects of other factors on those areas that are climatically more prone to invasion, allowing more local gradients acting in the *A. dealbata* height classes to be detected, as described in Vicente et al. (2010).

Seven models translating hypothesized effects of specific ecological factors were established for each height class based on combinations of predictor types (Table 1; see Appendix 2 for details about competing models and their ecological rationale). Assuming that all locations and all height classes have the same numbers of individuals, a null model (intercept-only model) was included in all analyses (see Table 1) to test whether the selected competing models were better than a model considering the absence of effects from the environment (i.e., whether the models used as hypotheses are in fact more reliable than an intercept model; Burnham & Anderson 2002). Ranking the importance of competing models should provide insight into the specific responses of different *A. dealbata* height classes to environmental gradients, thereby allowing to test our general hypothesis (1). To address our general hypothesis (2), each group of predictors (and thus the associated model) was classified as coarse-, medium-, or fine-scale (Table 1) based on the resolution of its characteristic spatial structure (a proxy for the scale of influence on invasion patterns; Vicente et al. 2014).

This set of competing models was developed within a multimodel inference framework (MMI; Burnham & Anderson 2002) to assess how well each model was supported by the data. We used a particular implementation of the Akaike Information Criterion (AIC; Akaike 1973) for small sample sizes (AIC_c, Shono 2000); this is recommended when the ratio between n (the number of observations used to fit the model) and K (the number of parameters in the largest model) is lower than 40 (Shono 2000, Burnham and Anderson 2002). Therefore, because of the small sample size, we limited the maximum number of predictors per model to four. To overcome dependence on sample size and allow comparability among models, we calculated the AIC_c difference ($\Delta i = AIC_{c\ initial} - AIC_{c\ minimum}$) for each candidate model to rank the candidate models (Burnham and Anderson 2002). From the Akaike differences (Δi), we derived Akaike weights (w_i), interpreted as the likelihood that a candidate model will be the best approximating and most parsimonious model given the data and set of models. These weights, scale between zero and one, representing the evidence for a particular model as a proportion of the total evidence supporting all models.

Table 1. Competing models, scale of predictors used in each model, and supporting literature references (M_8 null model, an intercept model, assumes that all locations have the same abundance of *A. dealbata* individuals)

Competing models	Resolution of spatial structure (based on Vicente et al. 2014)	Predictors	References
M_1 - Climate	**Coarse**	***AMT*** *(annual mean temperature)* ***TMN*** *(minimum temperature of the coldest month)* ***APR*** *(annual precipitation)* ***PSE*** *(precipitation seasonality)*	Pino et al., 2005 Godoy et al., 2008
M_2 – Geology/Soils	**Medium**	***pGra*** *(percentage of granite)* ***pSchi*** *(percentage of schists)* ***pAnt*** *(percentage of anthrosols)* ***pLep*** *(percentage of leptosols)*	Rose and Hermanutz, 2004 Dufour et al., 2006
M_3 – Dispersal corridors	**Medium**	***dRoad*** *(density of roads)* ***dRiv*** *(density of rivers)* ***distRo*** *(distance to main roads)* ***distRi*** *(distance to main rivers)*	(Procheş et al. 2005, Minor et al. 2009, Säumel and Kowarik 2010)
M_4 - Complexity	**Fine**	***SWIasp*** *(local variation of aspect)* ***SWIlit*** *(local variation of lithology)* ***SWIalt*** *(local variation of altitude)* ***SWIlu*** *(local variation of land-use)*	Holmes et al., 2005 Dufour et al., 2006
M_5 - Landscape structure	**Fine**	***MSI*** *(mean shape index)* ***MPAR*** *(mean perimeter-area ratio)* ***NumP*** *(number of patches)* ***PSSD*** *(patch size standard deviation)*	Le Maitre et al., 2004 Dufour et al., 2006 Foxcroft et al., 2007
M_6 - Landscape composition	**Fine**	***pNFo*** *(% cover of natural forest)* ***pBUp*** *(% cover of built up areas)* ***pAFo*** *(% cover of forest stands)*	Pino et al., 2005 Song et al., 2005

		pSSV *(% cover of shrubs and sparsely vegetation)*	
M_7 - Fire regime	**Fine**	***NFir*** *(number of fire occurrences 1990-2013)*	Keeley et al., 2005
M_8 – Null model			Burnham and Anderson, 2002

We averaged all competing models weighted by their w_i and used the averaged model for spatial prediction (Burnham and Anderson 2002). The average model of each height class was spatially implemented using the raster calculator in the ArcGIS Spatial Analyst extension (ESRI 2016). Finally, to achieve realistic predictions based on height class transitions for *A. dealbata*, the spatial projections from each height class were spatially overlaid with the ones for the immediately smaller class. We assumed that *A. dealbata* individuals of a given height class can only be present in a given area if the area was also predicted as suitable for the immediately smaller class, representing the current niche under environmental conditions where the species could complete its life cycle.

Therefore, for each height class, besides the projection for the whole study area ('predicted area'), a projection is also presented for those areas predicted as suitable simultaneously for both the focal height class and the proximate smaller class ('filtered area').

3. Results

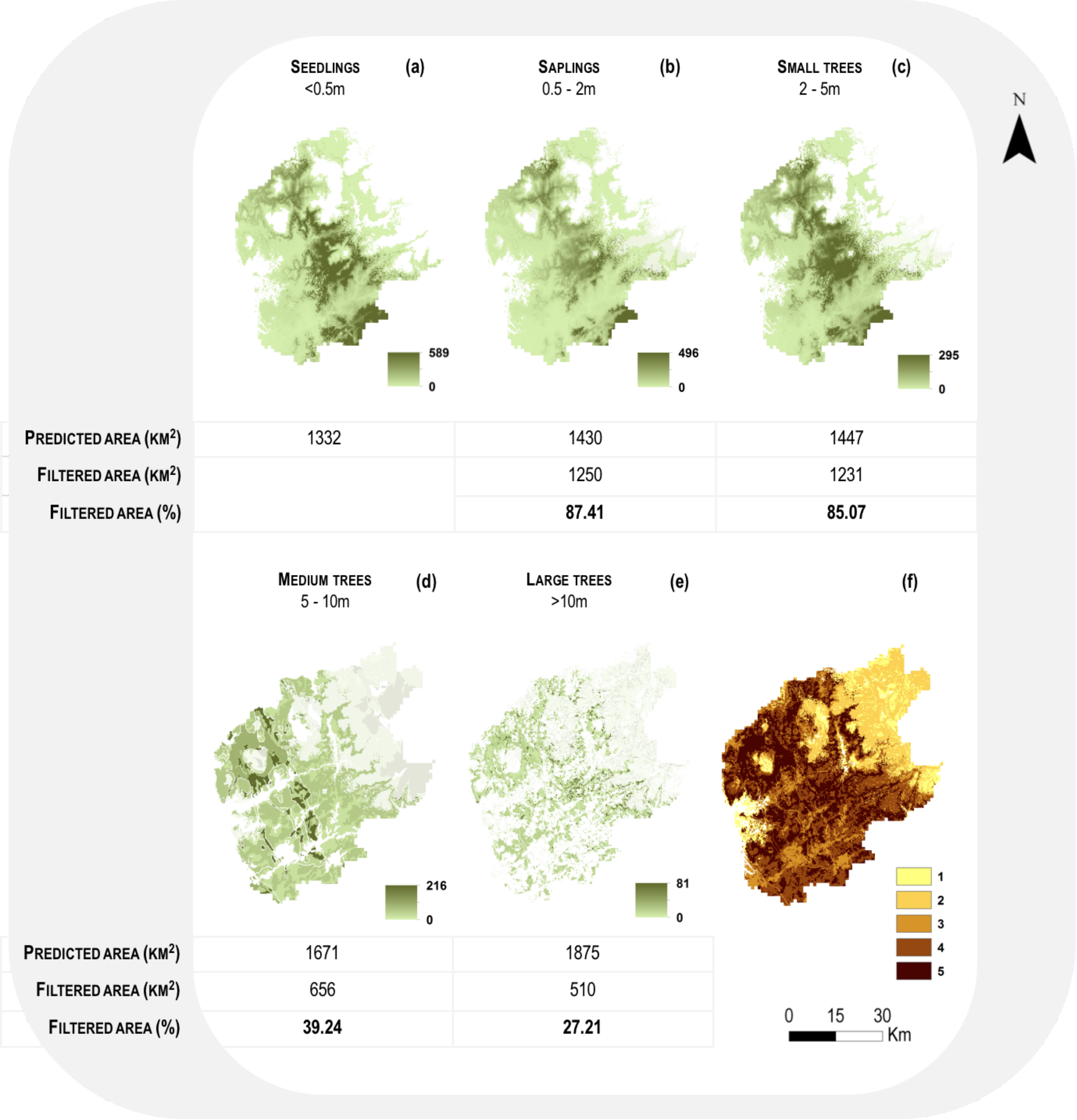
Height classes and *A. dealbata* invasion drivers (hypothesis 1)

The distribution of the various height classes of *A. dealbata* was found to be related to different sets of environmental factors (Table 2), thus confirming our hypothesis 1. Still, the most parsimonious model to explain the abundance of *A. dealbata* for the three classes representing smaller plants (i.e. Seedlings, Saplings, and Small trees) was the one based on climate (M_1). The most important climatic variables for Seedlings and Saplings were *precipitation seasonality* and *annual precipitation*, whereas *annual mean temperature* and *minimum temperature of the coldest month* were the most important for Small trees. Conversely, *geology* attained the best fit for Medium trees (M_2), with *percentage of schists* as the most important predictor. The number of Large trees was best explained by landscape composition (M_6), mainly by the *percentage cover of natural forest* and *percentage cover of shrub sparsely vegetation*. The models based on landscape complexity (M_4), landscape structure (M_5), dispersal corridors (M_6) or fire regime (M_7) were not selected for any of the height classes, nor was the null model (M_8). Climate, geology and land cover thus seem to explain the abundance distribution of the various height classes for the test species across the whole study area (Table 2). An increased model accuracy (adj.D^2 – adjusted variance - Table 2) was found from smaller/younger (Seedlings – 0.651, Saplings – 0.640, and Small trees – 0.643) to taller/older classes (i.e. Medium - 0.727, and Large trees – 0.797).

Table 2 Results of information-theoretic-based model selection and multimodel inference Akaike weights (w_i) and adjusted deviance explained (adj.D^2), for the five *A. dealbata* height classes in the full area (Full; 187 plots used to fit the model); note that the Akaike weights (w_i) always sum up to 1. The best model for each height class is highlighted with grey shading. For further information see *Appendices 3 to 7*.

	FULL AREA									
	SEEDLINGS <0.5M		SAPLINGS 0.5 - 2M		SMALL TREES 2 - 5M		MEDIUM TREES 5 - 10M		LARGE TREES >10M	
Competing models	w_i	adj.D^2	w_i	adj.D^2	w_i	adj.D^2	w_i	adj.D^2	w_i	adj.D^2
M_1 – climate	**1.00**	**0.65**	**1.00**	**0.64**	**1.00**	**0.64**	0.00	0.26	0.00	0.37
M_2 - geology	0.00	0.15	0.00	0.16	0.00	0.23	**1.00**	**0.73**	0.00	0.48
M_3 – dispersal corridors	0.00	0.14	0.00	0.08	0.00	0.16	0.00	0.13	0.00	0.23
M_4 – landscape complexity	0.00	0.11	0.00	0.18	0.00	0.20	0.00	0.15	0.00	0.43
M_5 – landscape structure	0.00	0.08	0.00	0.10	0.00	0.12	0.00	0.11	0.00	0.29
M_6 – landscape composition	0.00	0.20	0.00	0.25	0.00	0.24	0.00	0.21	**1.00**	**0.80**
M_7 – fire regime	0.00	0.04	0.00	0.06	0.00	0.08	0.00	0.09	0.00	0.20
M_8 – null model	0.00	0.00	0.00	0.02	0.00	0.04	0.00	0.02	0.00	0.01

The spatial predictions from average models for the five *A. dealbata* height classes and for the full area (Figure 2) reflect the prevailing influence of distinct invasion drivers. Spatial predictions for Seedlings, Saplings and Small trees reflect the fact that they primarily respond to climatic factors (Figure 2, a-c), whereas predictions for Medium trees and for Large trees express the fact that they are more responsive to the presence of specific bedrock types or land cover classes, respectively (Figure 2, d-e). A complex spatial pattern of potential invasion emerged, with prevalence of Seedlings, Saplings and Small trees in low-mid elevation areas, where climatic conditions are more favorable (Figure 2, a-e). Medium trees prevail in areas where schist prevails, and Large trees are predominant in areas where production forest stands are the main land cover type. The number of height classes represented in each grid cell ranges from one to five, with many local landscapes (0.04 km^2) across the study area hosting four or even all five classes (Figure 2, f). An increase of the predicted area and a decrease of the filtered area were observed from smaller to taller *A. dealbata* height classes (Figure 2).



	(a)	(b)	(c)
PREDICTED AREA (KM^2)	1332	1430	1447
FILTERED AREA (KM^2)		1250	1231
FILTERED AREA (%)		**87.41**	**85.07**

	(d)	(e)
PREDICTED AREA (KM^2)	1671	1875
FILTERED AREA (KM^2)	656	510
FILTERED AREA (%)	**39.24**	**27.21**

Figure 2 Spatial predictions from average models for the five response variables, i.e. abundance (number of individuals) of (a) Seedlings, (b) Saplings, (c) Small trees, (d) Medium trees, and (e) Large trees. Predictions are represented for the predicted area in all cases (color + grey scales). Color scales represent the filtered area (i.e. the area predicted as suitable for the modelled *A. dealbata* height class and for the immediately smaller height class) and grey scales represent areas predicted as suitable only for the modelled class. The map in (f) represents the total number of predicted height classes that coexist in each grid cell. For each height class, numerical results are presented for the predicted area and for the filtered area (number of km²) as well as the percentage (%) of the predicted area corresponding to the filtered area.

Scale dependence of tree invasion factors (hypothesis 2)

The abundance distribution of the various height classes was explained by factors structured at different spatial scales, and those factors were often influenced by the spatial extent of model calibration (Figure 3), providing support to our hypothesis 2. For smaller plants (Seedlings, Saplings and Small trees) the relative importance of invasion factors differed with the spatial extent (and total environmental heterogeneity) of the study area, with the importance of coarse- and medium-scale factors decreasing (and the importance of fine-scale factors increasing) towards smaller (and more homogeneous) study areas (Figure 3). Medium and Large trees showed consistent selection of environmental factors along all four nested areas, but they differed in terms of spatial scale: Geology (medium-scale) for Medium trees, and Landscape composition (fine-scale) for Large trees.

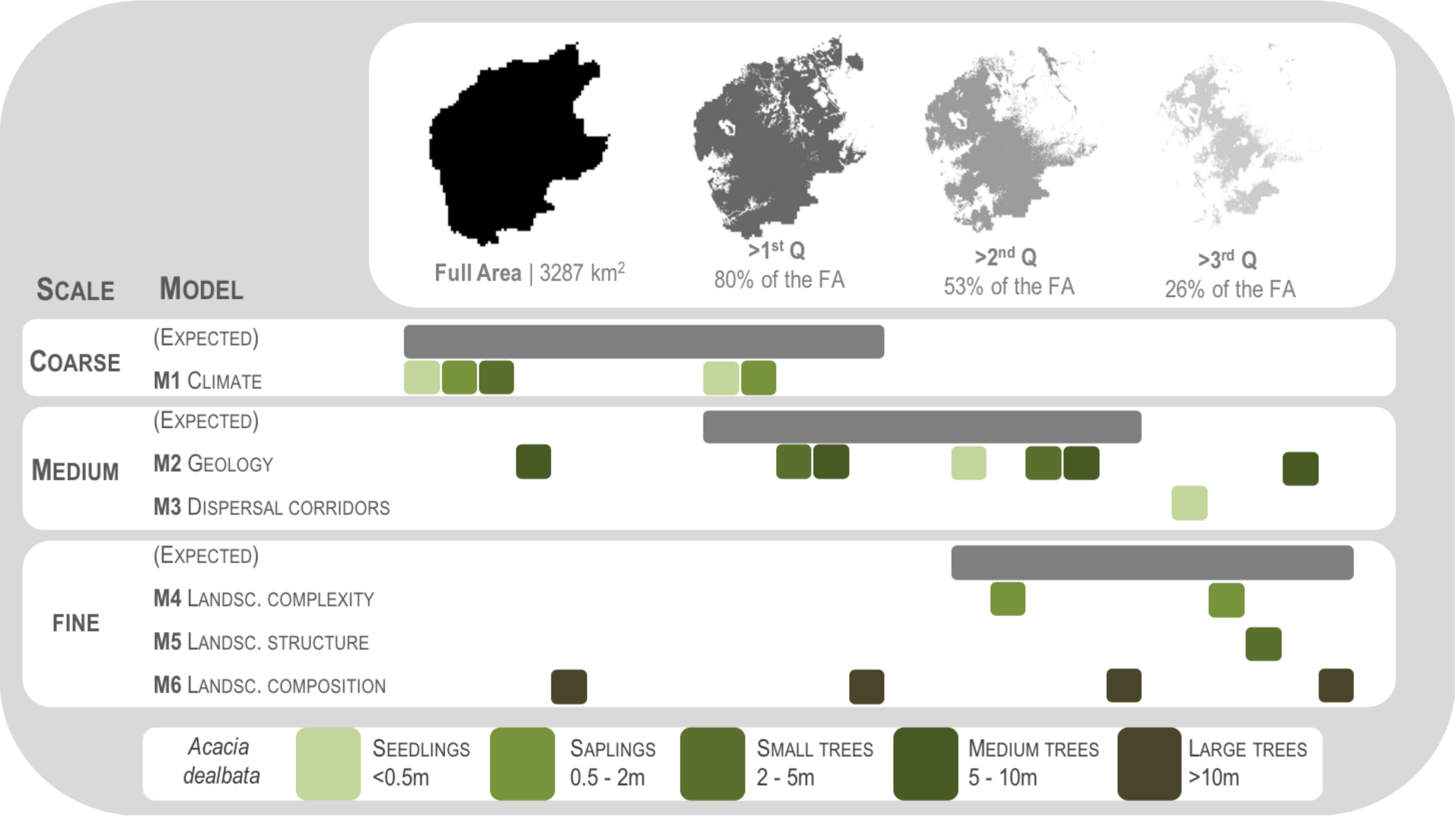


Figure 3 Scales of spatial structure/influence (coarse-, medium-, and fine-scale) and associated models (M_1-M_6; competing models representing environmental factors) selected by multimodel inference for each *A. dealbata* height class (Seedlings, Saplings, Small trees, Medium trees, and Large trees) for each nested area/extent (full area, area above the first quartile, area above the second quartile, and area above the third quartile). Horizontal grey bars represent the expected patterns based on the research hypothesis and on previous research.

Discussion

Height class dependence of tree invasion drivers

Modelling life-stage or size-class transitions is of foremost importance for management. Species distribution models are easy and fast to implement, calibrate and project, and are thus widely regarded as robust tools to assist in prevention and early detection of new invasive plant species (Vicente et al., 2011; Petitpierre et al., 2012; Fernandes et al., 2014). Static models further allow a straightforward prediction of species occurrence areas under discrete current and future environmental conditions (Guisan and Thuiller, 2005; Elith and Leathwick, 2009).

However, most studies that apply species distribution models only consider and predict the occurrence of species based on presence-absence or abundance data. Even if useful for prevention measures (anticipation or early detection of invasions; e.g. Petitpierre et al., 2012), such model outputs are often of limited use in guiding local-scale management actions, as they do not consider the population dynamics of the invader. Our proposed modelling approach provides a way of approach to overcoming this key limitation. To our knowledge, a framework of modelling life-stages or size-classes to obtain spatial projections of their potential occurrence or abundance has not been formalized before.

In this test with *Acacia dealbata*, we used detailed field data on population height structure and calibrated an independent model for each of the several height classes (a proxy for population dynamics, life-stages and age of adult trees). We found evidence to support our hypothesis that the distribution of different height classes is influenced by distinct factors (see Table 1). Also, the spatial projections of the different models for the different height classes (see Figure 2) provide an overview of population structure and dynamics in different stages of invasions, while maintaining a relatively straightforward modelling technique that is widely used in biodiversity and invasion research. By building models for the different height or age classes, our approach avoids the problem of using only presence-absence data for adult individuals, which are affected by the history of the invasion process. Moreover, combining spatial projections of size-class models to predict their potential occurrence, including those of earlier life-stages, can provide useful insights on future dynamics of invasions.

The increased model accuracy (adj.D^2 presented in Table 2) from smaller/younger (i.e. Seedlings, Saplings, and Small trees) to taller/older classes (i.e. Medium and Large trees) may be interpreted as expressing the effect of the 'filter' hypothesis described by Richardson et al. (2000), in which older adult trees have to withstand the effects of a larger number of environmental filters in order to survive, compared to younger life-stages. Thus, using the same set of environmental variables to model different life-stages should result in an increase of model accuracy towards older life-stages, as those models represent better the realized niche for the species in the invaded range. It is important, however, not to neglect the effect of the environmental data grain, since younger classes might require more precise climate data, with higher spatial resolution and from the particular year of establishment (i.e. considering year-to-year climate variability). The effects of other drivers and processes of invasion dynamics (e.g. propagule pressure, introduction history, residence time) should also be considered depending on the focal species and on data availability.

Scale dependence of tree invasion factors

We also found evidence to support our hypothesis that the effects of invasion factors on *Acacia* height classes are scale-dependent. This connection of invasion factors to spatial scales had been observed in the study area for the test *Acacia* species and for invasibility by multiple species (Vicente et al., 2010, 2011), but had never been tested for age/height classes of a focal species.

The scale-dependence was confirmed based on two sets of results. First, when analyzing the whole study area, the scale of the most important factors (Vicente et al., 2010, 2014a) differed among height classes (cf. Figure 3), with coarse-scale factors being more important for younger life-stages (i.e. seedlings/saplings) and medium to fine-scale factors more important for adult trees (habitat filtering; Gonzalez et al., 2010). The fact that the distribution of young *A. dealbata* plants (i.e., Seedlings, Saplings and Small trees) was essentially explained by climate (coarse-scale factor) can be explained by the fact that climate is a primary environmental gradient and a fundamental driver of biodiversity patterns (García-Valdés et al. 2015). It is also a major factor shaping the geographic distribution of alien invaders at a regional scale (Vicente et al. 2010, 2014b; Petitpierre et al., 2012). Minimum temperatures are known to control habitat invasibility by frost-sensitive alien invaders, which is the case with *A. dealbata* (Pino et al. 2005). Summer drought stress is also recognized as a strong mediator alien invasions in Mediterranean ecosystems (Godoy et al. 2008). Successful establishment and growth into mid-large trees then involves an additional set of environmental filters acting in climatically suitable landscapes, with geology/soil conditions (medium-scale) and landscape composition (fine-scale) holding the highest importance for *A. dealbata* at least in the study area. The fact that the distribution of Large trees is mostly determined by landscape composition could be related to the availability of suitable habitats and with landscape barriers to dispersal of *Acacia* (Torimaru et al., 2013; García-Valdés et al. 2015) of adult individuals in forest ecosystems. Overall, our results seem to suggest that models were able to assess both the “adult” and the “regeneration” niches of *A. dealbata*, highlighting the environmental factors underlying the potential distribution of the several age classes (Grubb 1977).

Second, the relative importance of the several factors was influenced by the spatial extent of the study area (cf. Figure 3; Vicente et al., 2014a). This pattern was observed for Seedlings, Samplings, and Small trees, which were mainly constrained by a coarse-scale factor (climate) across larger study areas, and by fine-scale attributes (geology, dispersal corridors, and landscape complexity) in when smaller (and climatically more homogeneous) areas were tested, consistently with previous research on invasion factors in the region (e.g. Vicente et al. 2010). As expected, having endured the filtering effect of a wider range of environmental factors (Richardson et al., 2000), and being influenced by factors structured at finer scales, Medium and Large trees showed no significant scale-dependence of invasion factors.

Outlook: towards improved management of tree invasions

Managing alien plant invasions in forest ecosystems is a challenging endeavor due to the multiscale processes acting upon life-stages, across space and along time (Souza-Alonso et al., 2013; Caplat et al., 2014; Reyer et al., 2015; Brundu and Richardson, 2016). Prevention and early-detection at younger life-stages are the most cost-effective options, compared to species control at later life-stages and/or large invaded areas, since managers can more easily manage species with small population sizes and invasion levels. However, these life-stages are the most difficult to detect in the landscape, which means that modelling outputs become a very important tool to support early-detection by focusing search efforts. When the species is already present and has spread, populations must be managed differently according to their life-stage(s); individuals with distinct sizes and phenological characteristics require different approaches to maximize management success (Buhle et al., 2005; Wilson et al., 2011).

Results from the application of a novel modelling approach to address life-stage population structure of the widespread alien invasive tree *A. dealbata* show that management must be tailored to consider distinct life-stages, spatial scales and extents. Scale dependence of invasion factors is especially important for earlier life-stages (Seedlings, Saplings, and Small trees). Effective management at those early stages of invasion must consider the effect of regional conditions (i.e., climatic, geological) on habitat suitability, but must also give attention to major dispersal corridors (i.e. rivers and roads) which are well-known drivers of invasion (Vicente et al., 2014b). Moreover, silvicultural treatments have been suggested for the control of other invasive trees through forest management and within the EU 1143/2014 regulation framework. In the specific case of the *Acacia dealbata*, the spread of this invasive tree can be buffered by maintaining or facilitating closed canopy and dense forest cover (Hernández et al. 2014, Silva and Marchante 2012).

The approach proposed here provides a framework to guide forest management to deal more effectively with plant invasions. It provides the spatial identification of suitable areas for invasive species occurrence while also accounting for the structural complexity of invasive populations, thereby anticipating future invasion dynamics. The approach thus constitutes a step forward for focusing management actions at appropriate spatial scales (Fernandes et al., 2014) and prioritizing attention on earlier stages of invasion and their respective driving factors, thereby enhancing the efficiency of control actions targeted at major forest invaders (Pyšek and Richardson, 2010).

Conclusions

The pilot application of a novel modelling framework to *Acacia dealbata* in northwest Portugal revealed that the regional distribution different height classes can be influenced by distinct sets of environmental factors (Kempes et al., 2011; Lasky et al. 2013). From the projection of our results in the geographical space it was also possible to perceive a different spatial mosaic pattern for each height class. Areas where suitable climatic conditions, geological and soil characteristics, and dispersal corridors (both rivers and roads) were present (corresponding to the central vertical belt of the study area) correspond to areas of highest concern in the study-site, because all height classes of *A. dealbata* were predicted to occur (cf. Figure 2). Our results also confirmed the hypothesis of scale-dependence of tree invasion factors, considering the scale of influence of those factors, density of stands and also the extent of the study area. The main factors underlying the distribution of the several *A. dealbata* height classes show a scale-dependent behavior reflecting the importance of different management strategies for different height classes as well as dense vs. low density Acacia stands.

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Appendices

Appendix 1 Sampling design stratification

Variables and classes used in the equal-stratified sampling design.

Variable type	Variable	Breaks	Classes
Landscape structure	Edge density between land cover patches	Natural breaks	0.004 – 0.008 >0.008 – 0.016 >0.016 – 0.0215
Landscape composition	Percentage of artificial stands	Natural breaks	0 – 20 >20 – 60 >60 - 100

Appendix 2 Ecological rational of the competing models

Competing models with their ecological rationale to test the role of environmental drivers explaining different height classes of *Acacia dealbata* populations.

Competing models	Name	Rationale
M_1	Climate	Minimum temperatures control habitat invasibility by frost-sensitive alien invaders (Pino et al. 2005), and summer drought stress controls alien invasion in Mediterranean ecosystems (Godoy et al. 2008).
M_2	Geology	Susceptibility to invasion is pre-determined by bedrock geology (Rose and Hermanutz 2004), and different bedrock types support distinct landscape units in the region, thus providing different sets of habitats for alien invaders. Also, more alien invaders can find suitable conditions in landscapes with greater soil diversity (Dufour et al. 2006).
M_3	Dispersal corridors	The spread of invaders is often facilitated by natural corridors as rivers (Procheş et al. 2005, Minor et al. 2009, Säumel and Kowarik 2010)
M_4	Landscape complexity	The local diversity of terrain morphology controls species richness, since more complex terrain usually provides a wider diversity of habitat types (Dufour et al. 2006). Topographic diversity is also related to local hydrographic networks, thus controlling alien invasion in riparian habitats (Holmes et al. 2005).

M_5	Landscape structure	Landscape invasibility is controlled by patch shape and size, since these determine ecotone density and diversity (Le Maitre et al. 2004, Dufour et al. 2006). The density of the local hydrographic network is related to landscape fragmentation, which provides more opportunities for local survival and dispersal (Foxcroft et al. 2007).
M_6	Landscape composition	Land cover/-use controls alien invasion since it determines suitable habitat availability, and man-made habitats have been shown to provide suitable conditions for more invasive species (Song et al. 2005). Also, more alien invaders can find suitable conditions in landscapes with greater compositional diversity (Pino et al. 2005).
M_7	Fire regime	Fire is a common source of disturbance in Mediterranean areas and influences population dynamics of invasive plants (Keeley et al. 2005).
M_8	Null model	A null model was included in all procedures in order to test how the competing models are better than a model that considers the absence of effect (Burnham and Anderson 2002).

Appendix 3 Multimodel inference results for *Acacia dealbata* seedlings

Results of information-theoretic-based model selection based on the Akaike information criterion for seedlings number (number of *Acacia dealbata* individuals with height < 0.5 meters), detailing number of model parameters (k; linear and polynomial terms of variables and intersect), the small-sample bias-corrected form of Akaike's information criterion differences (Δi), Akaike weights (wi), and adjusted deviance explained (adj.D^2), for each of the four areas: full area (Full; 187 plots used to fit the model), area above the first quartile (>1st Q; 168 plots used to fit the model), area above the second quartile (>2nd Q; 84 plots used to fit the model), and area above the third quartile (>3rd Q; 69 plots used to fir the model). Note that the Akaike weights (wi) always sum up to 1.

		Seedlings											
		Full area			**> 1st Q**			**> 2nd Q**			**> 3rd Q**		
	k	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi
M_1 – climate	10	0.651	0.000	1.000	0.618	0.000	1.000	0.115	1736.547	0.000	0.636	19.968	4.613E-05
M_2 - geology	10	0.150	3138.644	0.000	0.176	1611.416	0.000	0.643	0.000	1.000	0.378	93.605	4.719E-21
M_3 – dispersal corridors	10	0.135	6529.572	0.000	0.137	5472.602	0.000	0.077	3059.103	0.000	0.834	0.000	1.000
M_4 – landscape complexity	10	0.107	4828.024	0.000	0.097	3964.408	0.000	0.188	1551.773	0.000	0.308	116.226	5.778E-26
M_5 – landscape structure	10	0.082	5149.510	0.000	0.087	4104.417	0.000	0.182	1050.205	8.932E-229	0.113	137.018	1.766E-30
M_6 – landscape composition	10	0.198	3501.129	0.000	0.197	2663.454	0.000	0.125	405.028	1.120E-88	0.170	137.352	1.494E-30
M_7 – fire regime	4	0.041	7004.853	0.000	0.169	5909.888	0.000	0.040	3072.732	0.000	0.114	151.788	1.095E-33
M_8 – null model	4	0.002	7195.339	0.000	0.048	4788.511	0.000	0.022	2723.809	0.000	0.008	147.086	1.150E-32

Appendix 4 Multimodel inference results for *Acacia dealbata* saplings

Results of information-theoretic-based model selection based on the Akaike information criterion for saplings number (number of *Acacia dealbata* individuals with height between 0.5 and 2 meters), detailing number of model parameters (k; linear and polynomial terms of variables and intersect), the small-sample bias-corrected form of Akaike's information criterion differences (Δi), Akaike weights (wi), and adjusted deviance explained (adj.D^2), for each of the four areas: full area (Full; 187 plots used to fit the model), area above the first quartile (>1st Q; 168 plots used to fit the model), area above the second quartile (>2nd Q; 84 plots used to fit the model), and area above the third quartile (>3rd Q; 69 plots used to fir the model). Note that the Akaike weights (wi) always sum up to 1.

		Saplings											
		Full area			**> 1st Q**			**> 2nd Q**			**> 3rd Q**		
	k	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi
M_1 – climate	10	0.640	0.000	1.000	0.600	0.000	1.000	0.041	1555.496	0.000	0.093	960.161	3.190E-209
M_2 - geology	10	0.155	2650.665	0.000	0.168	1640.129	0.000	0.241	906.995	1.118E-197	0.177	1380.605	1.605E-300
M_3 – dispersal corridors	10	0.085	5312.080	0.000	0.095	4465.241	0.000	0.170	2195.886	0.000	0.280	688.733	2.777E-150
M_4 – landscape complexity	10	0.183	2236.357	0.000	0.168	1589.984	0.000	0.688	0.000	1.000	0.746	0.000	1.000
M_5 – landscape structure	10	0.102	3597.920	0.000	0.123	2691.615	0.000	0.327	506.167	1.223E-110	0.308	654.260	8.496E-143
M_6 – landscape composition	10	0.247	3372.919	0.000	0.239	2720.475	0.000	0.365	1461.517	4.322E-318	0.391	1351.240	3.819E-294
M_7 – fire regime	4	0.058	4936.105	0.000	0.139	4140.491	0.000	0.126	2337.228	0.000	0.121	2032.230	0.000
M_8 – null model	4	0.025	5879.540	0.000	0.042	4850.803	0.000	0.011	2732.256	0.000	0.014	2679.880	0.000

Appendix 5 Multimodel inference results for *Acacia dealbata* small trees.

Results of information-theoretic-based model selection based on the Akaike information criterion for small trees number (number of *Acacia dealbata* individuals with height between 2 and 5 meters), detailing number of model parameters (k; linear and polynomial terms of variables and intersect), the small-sample bias-corrected form of Akaike's information criterion differences (Δi), Akaike weights (wi), and adjusted deviance explained (adj.D^2), for each of the four areas: full area (Full; 187 plots used to fit the model), area above the first quartile (>1st Q; 168 plots used to fit the model), area above the second quartile (>2nd Q; 84 plots used to fit the model), and area above the third quartile (>3rd Q; 69 plots used to fir the model). Note that the Akaike weights (wi) always sum up to 1.

		Small trees											
		Full area			**> 1st Q**			**> 2nd Q**			**> 3rd Q**		
	k	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi
M_1 – climate	10	0.643	0.000	1.000	0.219	98.677	3.737E-22	0.157	1384.646	2.128E-301	0.059	791.120	1.623E-172
M_2 - geology	10	0.227	497.442	9.590E-109	0.699	0.000	1.000	0.751	0.000	1.000	0.297	149.206	3.983E-33
M_3 – dispersal corridors	10	0.160	2676.412	0.000	0.170	2282.191	0.000	0.105	1567.971	0.000	0.185	828.632	1.161E-180
M_4 – landscape complexity	10	0.203	1388.220	3.560E-302	0.182	1136.211	1.883E-247	0.322	683.705	3.430E-149	0.255	485.376	3.998E-106
M_5 – landscape structure	10	0.115	1355.956	3.610E-295	0.126	911.085	1.447E-198	0.297	212.036	9.056E-47	0.784	0.000	1.000
M_6 – landscape composition	10	0.242	1453.317	2.607E-316	0.226	1180.966	3.601E-257	0.382	731.826	1.219E-159	0.328	494.972	3.298E-108
M_7 – fire regime	4	0.083	2828.173	0.000	0.065	2391.751	0.000	0.114	1638.909	0.000	0.112	1179.555	7.293E-257
M_8 – null model	4	0.036	3588.450	0.000	0.021	2715.260	0.000	0.030	1273.455	2.970E-277	0.002	1438.950	3.435E-313

Appendix 6 Multimodel inference results for *Acacia dealbata* medium trees.

Results of information-theoretic-based model selection based on the Akaike information criterion for medium trees number (number of *Acacia dealbata* individuals with height between 5 and 10 meters), detailing number of model parameters (k; linear and polynomial terms of variables and intersect), the small-sample bias-corrected form of Akaike's information criterion differences (Δi), Akaike weights (wi), and adjusted deviance explained (adj.D^2), for each of the four areas: full area (Full; 187 plots used to fit the model), area above the first quartile (>1st Q; 168 plots used to fit the model), area above the second quartile (>2nd Q; 84 plots used to fit the model), and area above the third quartile (>3rd Q; 69 plots used to fir the model). Note that the Akaike weights (wi) always sum up to 1.

		Medium trees											
		Full area			**> 1st Q**			**> 2nd Q**			**> 3rd Q**		
	k	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi
M$_1$ – climate	10	0.256	176.227	5.406E-39	0.320	512.860	4.304E-112	0.120	1138.963	4.756E-248	0.126	758.359	2.111E-165
M$_2$ - geology	10	0.727	0.000	1.000	0.712	0.000	1.000	0.737	0.000	1.000	0.692	0.000	1.000
M$_3$ – dispersal corridors	10	0.126	1703.277	0.000	0.129	1789.194	0.000	0.101	1205.030	2.143E-262	0.102	816.240	5.699E-178
M$_4$ – landscape complexity	10	0.149	1154.109	2.446E-251	0.128	1310.574	2.585E-285	0.202	860.714	1.254E-187	0.227	580.993	6.903E-127
M$_5$ – landscape structure	10	0.113	1376.919	1.014E-299	0.140	1403.186	2.004E-305	0.299	656.690	2.521E-143	0.273	432.591	1.159E-94
M$_6$ – landscape composition	10	0.212	1059.074	1.059E-230	0.195	1218.101	3.110E-265	0.311	597.991	1.406E-130	0.334	345.288	1.051E-75
M$_7$ – fire regime	4	0.093	2057.328	0.000	0.077	2105.907	0.000	0.205	1397.444	3.540E-304	0.197	1005.696	4.129E-219
M$_8$ – null model	4	0.025	2198.718	0.000	0.004	2174.471	0.000	0.073	1439.988	2.045E-313	0.026	1173.810	1.29E-255

Appendix 7 Multimodel inference results for *Acacia dealbata* large trees.

Results of information-theoretic-based model selection based on the Akaike information criterion for large trees number (number of *Acacia dealbata* individuals with height >10 meters), detailing number of model parameters (k; linear and polynomial terms of variables and intersect), the small-sample bias-corrected form of Akaike's information criterion differences (Δi), Akaike weights (wi), and adjusted deviance explained (adj.D^2), for each of the four areas: full area (Full; 187 plots used to fit the model), area above the first quartile (>1st Q; 168 plots used to fit the model), area above the second quartile (>2nd Q; 84 plots used to fit the model), and area above the third quartile (>3rd Q; 69 plots used to fir the model). Note that the Akaike weights (wi) always sum up to 1.

		Large trees											
		Full area			**> 1st Q**			**> 2nd Q**			**> 3rd Q**		
	k	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi	adj.D^2	Δi	wi
M$_1$ – climate	10	0.374	400.886	8.886E-88	0.299	437.113	1.207E-95	0.106	777.686	1.342E-169	0.096	731.225	1.646E-159
M$_2$ - geology	10	0.485	29.280	4.384E-07	0.488	13.900	0.001	0.415	248.663	1.008E-54	0.356	281.940	5.992E-62
M$_3$ – dispersal corridors	10	0.229	623.605	3.854E-136	0.227	599.719	5.918E-131	0.294	436.665	1.512E-95	0.275	404.591	1.394E-88
M$_4$ – landscape complexity	10	0.432	152.870	6.378E-34	0.451	98.139	4.886E-22	0.503	84.465	4.556E-19	0.502	58.411	2.072E-13
M$_5$ – landscape structure	10	0.289	485.478	3.799E-106	0.287	464.358	1.464E-101	0.380	291.366	5.378E-64	0.361	273.648	3.786E-60
M$_6$ – landscape composition	10	0.797	0.000	1.000	0.794	0.000	0.999	0.853	0.000	1.000	0.841	0.000	1.000
M$_7$ – fire regime	4	0.204	732.148	1.038E-159	0.194	728.507	6.401E-159	0.210	690.551	1.119E-150	0.187	651.061	4.207E-142
M$_8$ – null model	4	0.012	1525.913	0.000	0.007	1164.592	1.293E-253	0.049	672.712	8.366E-147	0.017	878.397	1.813E-191