

Species distribution models support the need of international cooperation towards successful management of plant invasions

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ABSTRACT

To protect native biodiversity and habitats from the negative impacts of biological invasions, comprehensive studies and measures to anticipate invasions are required, especially across countries in a transfrontier context. Species distribution models (SDMs) can be particularly useful to integrate different types of data and predict the distribution of invasive species across borders, both for current conditions and under scenarios of future environmental changes. We used SDMs to test whether predicting invasions and potential spatial conflicts with protected areas in a transfrontier context, under current and future climatic conditions, would provide additional insights on the patterns and drivers of invasion when compared to models obtained from predictions for individual regions/countries (different modelling strategies). The framework was tested with the invasive alien plant *Acacia dealbata* in North of Portugal/NW Spain Euro-region, where the species is predicted to increase its distribution under future climatic conditions. While SDMs fitted in a transfrontier context and using “the national strategy (with Portugal calibration data) presented similar patterns, the distribution of the invasive species was higher in the former. The transfrontier strategy expectedly allowed to capture a more complete and accurate representation of the species’ niche. Predictions obtained in a transfrontier context are therefore more suitable to support resource prioritisation for anticipation and monitoring impacts of biological invasions, while also providing additional support for international cooperation when tackling issues of global change. Our proposed framework provided useful information on the potential patterns of invasion by *A. dealbata* in a transfrontier context, with an emphasis on protected areas. This information is crucial for decision-makers focusing on the prevention of invasions by alien species inside protected areas in a transfrontier context, opening a new way for collaborative management of invasions.

1. Introduction

The global transportation of plant species has occurred for centuries, but due to the intensification of commercial trade and travelling, plant displacement assisted by humans is accelerating (Hulme et al., 2018; Rejmánek, Richardson, & Pyšek, 2013). Many of these species have been introduced in areas where they did not exist before (e.g. for agriculture, forestry or ornamental use), often causing landscape modifications (Buckley & Csergo, 2017; Vilà & Ibáñez, 2011). Some of the species have become naturalised and even invasive (sensu Richardson et al., 2000) in many areas where they were introduced

(Caplat, Hui, Maxwell, & Peltzer, 2013; Rejmánek et al., 2013) and some are now recognised as major threats to native biodiversity (Richardson & Rejmánek, 2011). Invasive species, and especially woody invasive plant species (WIPS), can cause severe negative impacts on invaded ecosystems, such as potentially decrease the number of native species, affect the functions and services provided by an ecosystem, and reshape ecosystems and their interactions at the landscape level (Le Maitre et al., 2011; Vilà et al., 2010, 2011). These negative impacts can occur mainly because WIPS potentially become dominant in the invaded plant communities (Caplat et al., 2013; Haugo, Halpern, & Bakker, 2011; Pyšek et al., 2013), often originating what has been

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called ‘novel ecosystems’, in which the structure and functions are altered (Hobbs et al., 2006).

Due to the strong impacts of plant invasions, increasing attention has been given to the identification of susceptible geographical regions in order to anticipate future invasions (Gundale et al., 2013). Complete control or eradication of established invasive species is difficult and unlikely due to logistical problems and/or financial limitations (Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012; Genovesi, 2005; Hulme, 2012). Therefore, anticipating the introduction and preventing the expansion of invasive species into a specific region is considered the most cost-effective way of managing biological invasions (Broennimann & Guisan, 2008; Gallien et al., 2012; Hulme, 2006; Petitpierre et al., 2012). Predicting the spatial distribution of invasive species, understanding the ecological requirements of those species and the different environmental drivers that influence their distribution can thus have important impacts in management choices (Donaldson, Richardson, & Wilson, 2013; Gallien et al., 2012; Vicente et al., 2013). Species distribution models (hereafter SDM) are useful tools to address and optimize the management of invasive species (Guisan et al., 2013; Vicente et al., 2016), as they rely on the establishment of statistical relationships between environmental conditions and the occurrence of a given species, thereby providing an effective approach to predict current or future invasive species distributions (Elith & Leathwick, 2009; Guisan et al., 2013; Hulme, 2012).

Predicting and managing invasive species across national borders holds several advantages (Martins et al., 2016), but it can be especially complicated, because, as mentioned by Jaksic, Iriarte, Jiménez, and Martínez, (2002), different challenges may occur: 1) political, when the firstly invaded country is not concerned by the invasion in some neighbouring country, and the problem becomes the concern of the newly invaded country; 2) ecological, when the habitats invaded in different countries differ in their susceptibility or resilience to invasions; and 3) geographical, because landscape structure determines the corridors and barriers for invasions, which can be different between neighboring countries. Additionally, truncated occurrence datasets are often used to predict species distributions, which might lead to prediction errors resulting from an incomplete representation of the species geographical range (Hannemann, Willis, & Macias-Fauria, 2016).

The invasion of protected areas threatens native biodiversity and causes changes in ecosystem structure and function (Pyšek, Jarošík, & Kučera, 2002; Theoharides & Dukes, 2007; Thuiller, Richardson, & Midgley, 2007), representing a serious problem due to the static nature of protected areas (Pressey, Cabeza, Watts, Cowling, & Wilson, 2007). The establishment of national parks and natural reserves all over the world, of which the Natura 2000 network in Europe is a remarkable example (consisting of two types of sites established under the Habitats Directive (92/43/EEC) and the Birds Directive (79/409/EEC)), has provided areas where native biodiversity can have some protection from several threats, but biological invasions are now threatening their integrity (Vicente et al., 2013). The protected areas can occur inside a country or across borders therefore calling for cooperation between different countries (Hanks, 2003). Currently, more than 10% of the world's network of protected areas corresponds to areas shared by different countries (Hanks, 2003).

Therefore, it is important to predict current and future invasive species distribution and their potential conflicts with the protected areas not only in a given country (e.g. Vicente et al., 2013), but considering the neighbouring countries together. In such transfrontier context, cooperation between different countries is essential to improve prevention and management of current and future invasions (Martins et al., 2016). This is evident because since 2014, new European legislation (the Invasive Alien Species EU Regulation No 1143/2014) provides a set of measures that should be taken across European Union countries. A hierarchical approach to combat invasive species was proposed covering prevention, early detection and rapid eradication, management or governance measures that the different countries

should apply while also accounting for relevant transboundary impacts and features.

Here, we used species distribution models to predict current and future potential distribution of the woody invasive plant species *Acacia dealbata* in the northwest Iberian Peninsula (Portugal and Spain), as well as its potential conflicting invasion of protected areas under current and future climatic conditions. We assess what is the most appropriate approach to predict invasive species distribution and anticipate potential conflicts with protected areas in a transfrontier context, to improve management and monitoring actions. Specifically, we tested different modelling strategies to 1) determine how different the forecasts of potential conflicts with protected areas are, and 2) provide additional insights into the patterns and drivers of invasion in a transfrontier context. To address these objectives, three different modelling strategies to fit and project the models were used: (i) national models and predictions, in which the distribution of the species was modelled for the two different countries separately and the predicted patterns were merged afterwards; (ii) national models projected for the whole area, i.e. the distribution of the species was modelled for the full study area, but fitting the models using only the occurrence data available for either Portugal or Spain, and (iii) transfrontier model and prediction, where the distribution of the species was predicted for the full study area using occurrence data for the full study area to fit the models.

2. Methods

2.1. Study area

The study area is in the Northwest of the Iberian Peninsula and includes the North of Portugal and the South of Galicia (northwest Spain) (Fig. 1), covering an area of 35,017 km². It includes the transition between the Mediterranean and the Atlantic biogeographic regions (Rivas-Martínez, Penas, & Díaz, 2004), and it is a topographically heterogeneous area, with elevation ranging from sea level (at west) to 2050 m in the eastern mountains, resulting in marked variations of environmental conditions. The annual mean temperature ranges from ca. 5 °C to ca. 16 °C, and the total annual precipitation varies between ca. 500 mm and ca. 3000 mm (Mónica & Santos, 2011). These topographic and climatic ranges reflect on a marked ecological heterogeneity, expressed by a complex vegetation cover and a large diversity of land cover and land use types (Caetano, Nunes, & Nunes, 2009; Calvo-Iglesias, Fra-Paleo, & Diaz-Varela, 2009).

About 27% of the study area is covered by protected areas (conservation of native biodiversity and habitats), with most of it being included in the EU's Natura 2000 network (89%). More than 3000 plant taxa are recorded in this area, some of which (> 100) are endemic/sub-endemic or have a limited distribution in Iberia (project BIODIV_GNP; visit www.biodiversidade.eu for additional information). Despite the presence of high levels of plant biodiversity and protected areas, this region is experiencing a high intensity of environmental disturbances, including an increasing presence and expansion of invasive species (Vicente et al., 2011, 2013) and the occurrence of large wildfires (Alonso-Betanzos et al., 2003; Fuentes-Santos, Marey-Perez, & Gonzalez-Manteiga, 2013).

2.2. Test species and occurrence data

Acacia dealbata Link., also known as silver wattle, is a woody plant species of the *Fabaceae* family, native to Australia and Tasmania (Lorenzo, Gonzalez, & Reigosa, 2010). Several species of genus *Acacia* are currently widespread causing severe negative impacts all over the world (Le Maitre et al., 2011). *Acacia dealbata* has become very common in Mediterranean countries after its introduction in Europe (around the 1820s; Carballeira and Reigosa (1999)). This species presents a high colonising capability and can be found invading disturbed

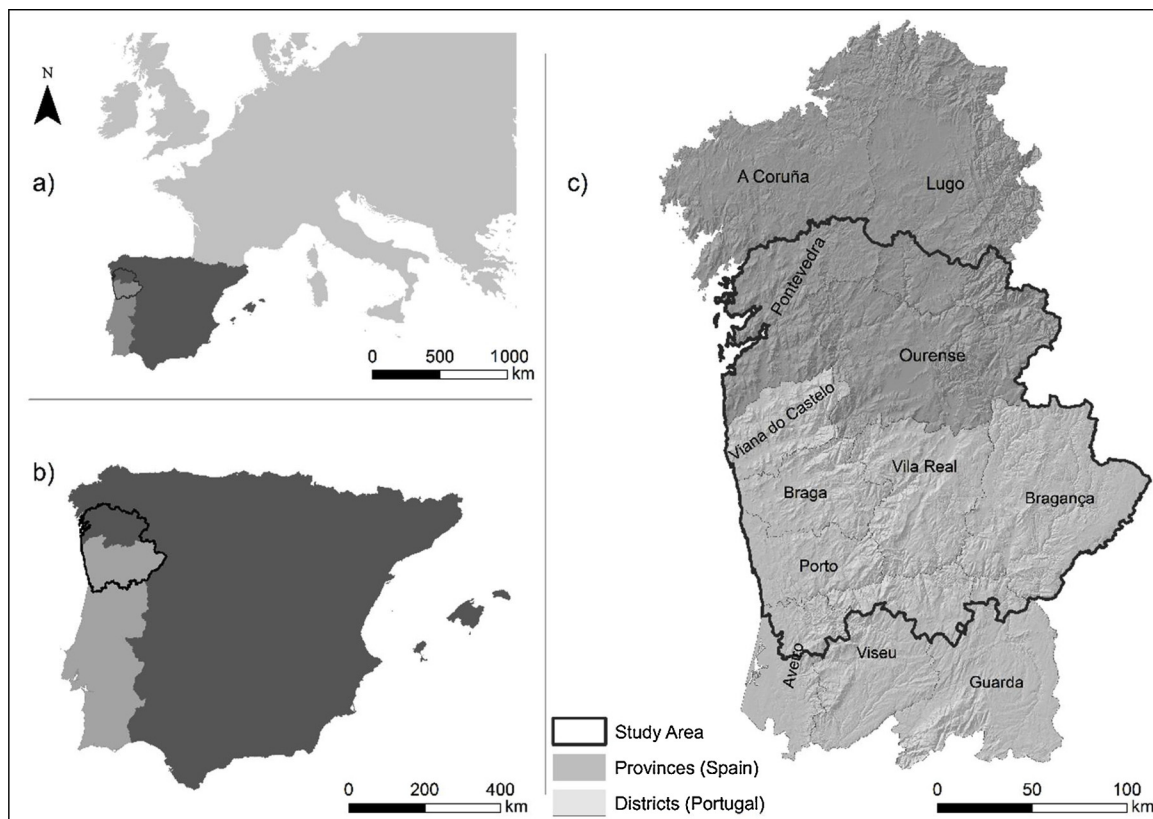


Fig. 1. Study area location in Europe (a) and in the Iberian Peninsula (b). Representation of the protected areas, presence data available in the study area and its provinces (Spain) and districts (Portugal) (c).

forests and scrublands, on the edge of rivers and roads (corridors), or grown as an ornamental plant (Lorenzo et al., 2010). The species can replace native vegetation due to the ability to produce a high number of seeds, the seed germination stimulated by fire, and the re-sprouting after cutting, fire or frost (Lorenzo et al., 2010). As a result, the species is often present as dense populations that prevent native vegetation from regenerating and growing (e.g. through competition for resources; Lorenzo et al. (2010)) and by allelopathic interference; Marchante, Freitas, and Hoffmann, (2011).

The species occurrence dataset applied in this study was collected and harmonized as part of the transfrontier cooperation project BIODIV_GNP (0479_BIODIV_GNP_1_E). Data for Portugal resulted from previous research conducted in the region (Vicente, Alves, Randin, Guisan, & Honrado, 2010, 2011; Vicente et al., 2013) and data for Spain was provided by the “Dirección Xeral de Conservación da Natureza da Xunta da Galicia”. Because BIODIV was a transfrontier collaborative project aiming (among other goals) to establish reference datasets and models to support plant conservation in the Galicia-North of Portugal Euro-region, all the data was harmonized in this project to remove duplicated records or misidentifications. The spatial resolution of the species occurrences was set at 1 km². We did not use native range data in this specific study, as we wanted to illustrate the transfrontier management issue in the invaded range.

2.3. Environmental data

We initially selected predictors (at 1 km² resolution) that, according to expert knowledge and based on previous reports in the scientific literature (e.g. Lorenzo et al., 2010; Souza-Alonso, Rodríguez, González, & Lorenzo, 2017; Vicente et al., 2011, 2013), could act as determinants of the distribution of the test species. Then, using Spearman's ρ correlation coefficient, we tested pair-wise correlations to avoid collinearity between those predictors (Dormann et al., 2012).

Only predictors with pairwise correlations lower than 0.5 were considered (Elith et al., 2006), thus much lower than the 0.7 maximum value recommended by Dormann et al. (2012). When correlated pairs of predictors occurred, we kept the predictor with the most direct ecological impact on the species distribution, based on expert judgment or previous findings in the scientific literature (Guisan & Thuiller, 2005). This analysis yielded a final set of 11 environmental predictors to fit SDMs, grouped into four environmental types that reflect distinct ecological drivers of species distributions (climate; landscape composition; soil types; and ecosystem productivity) (see Table A1 in Appendix A).

Predictors expressing current climatic conditions were obtained from the Worldclim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005); available at <http://worldclim.org/download>. Predictors related to future climatic conditions were also used to assess future invasion dynamics under climate change scenarios. As the test different climate change scenarios was not the scope of this study, our predictors were derived from the HadGEM2-ES model, a widely available and standard global circulation model of the Met Office Hadley Centre. These predictors are based on the representative concentration pathways RCP4.5 (mean global warming increase of 1 °C) and RCP8.5 (mean global warming increase of 2 °C between 2046–2065 and 3.7 °C between 2081–2100), for the years 2050 and 2070 (available at <http://worldclim.org/CMIP5v1>). The mentioned pathways were adopted by the IPCC - Intergovernmental Panel on Climate Change - in its Fifth Assessment Report, AR5 (available at <http://www.ipcc.ch/report/ar5/index.shtml>). Remotely-sensed ecosystem productivity data was obtained from the Numerical Terradynamic Simulation Group database (<http://www.ntsg.unt.edu/project/mod17>). Finally, predictors describing current land cover were computed based on data acquired from the European Environment Agency database (EEA; available at <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2000-raster-2>).

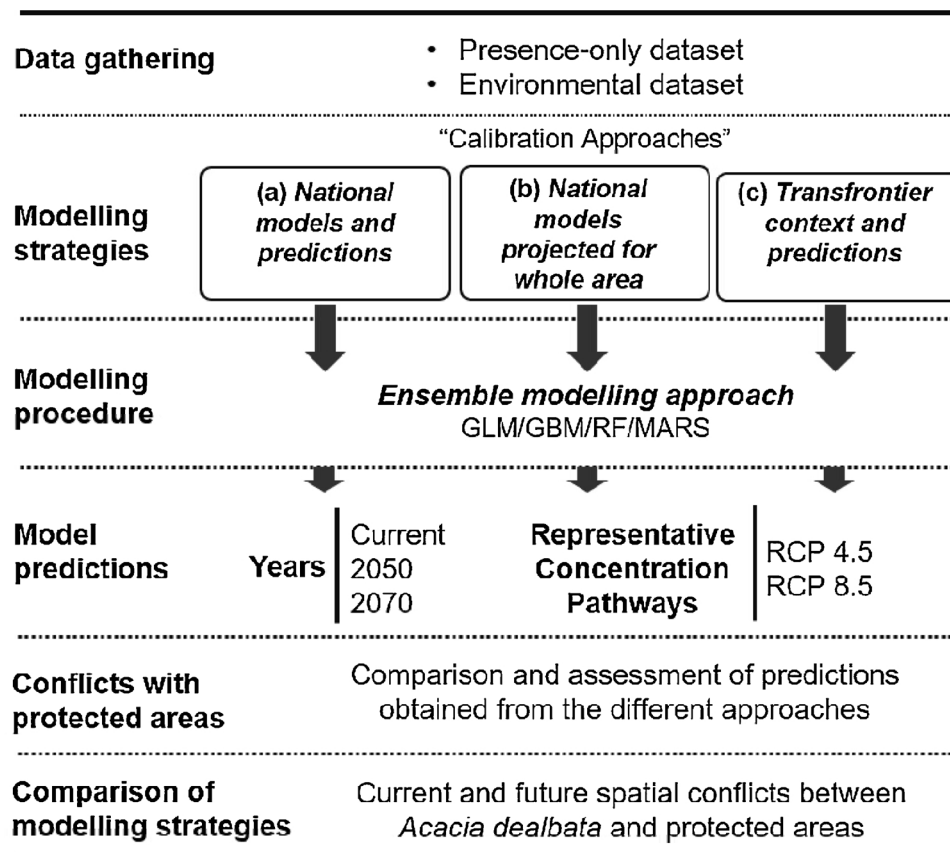


Fig. 2. Analytical framework for modelling the distribution of the species *Acacia dealbata* and assess the spatial conflicts with the protected areas present in the study area. First, we collected environmental variables and presence-only occurrence data for the test species – Data gathering. Then we applied different “calibration approaches” to calibrate several models for the test species – Modelling strategies: (a) national models and predictions (calibration and projection individually for each one of the two different countries and spatially combined to obtain the final output); (b) national models projected for the whole area (projection of the model for the full study area, but using either the occurrence data only for Portugal or for Spain for calibration purposes), and (c) transfrontier context and predictions (calibration and projection for the full study area with occurrence data from the full area). The models were calibrated using an ensemble modelling approach available in biomod2, by fitting generalised linear models (GLM), generalised boosted models (GBM), random forests (RF) and multiple adaptive regression splines (MARS) – Modelling procedure. For each “calibration approach”, models were then projected for the entire study area for current and future (2050 and 2070, under the representative concentration pathways RCP4.5 and RCP8.5) climatic conditions – Model predictions. Finally, we compared and assessed the predictions obtained from the different “calibration approaches” – Conflicts with protected areas.

tested areas - and analysed the potential conflicts between the predicted distribution of *A. dealbata* and the protected areas located in the study area – Comparison of modelling strategies.

2.4. Analytical framework

To analyse the conflicts between the potential distribution of *A. dealbata* and the protected areas present in the study area (under current and future climatic conditions, at 1 km² resolution), in a transfrontier context, we developed an analytical framework divided into six major sections, as illustrated in Fig. 2:

2.4.1. Data gathering

First, we gathered environmental and species occurrence (presence-only) datasets (see *Environmental data* section for a description of how important predictors were selected). The final occurrence dataset for *A. dealbata* used for model fitting included 967 presence records for the full study area (all data available on WGS84 coordinate system).

2.4.2. Modelling strategies

To assess the differences and potential improvements of predicting invasions in a transfrontier context, we used three different strategies to fit the models: (i) National models and predictions (Fig. 2a), where the distribution of the species was modelled and projected for the two different countries separately, and projections were spatially merged afterwards; (ii) National models projected for the whole area (Fig. 2b), where the distribution of the species was projected for the full study area, but models were calibrated using the occurrence data available only for Portugal or for Spain; and (iii) Transfrontier model and prediction (Fig. 2c), where the distribution of the species was modelled and projected for the whole study area using occurrence data also for the whole area. To fit the models in each approach, we used only data available for the specific areas, so that data limitation due to lack of cooperation between entities of the different countries could be simulated (in the first two approaches) and compared with a scenario where cooperation between countries exists, in order to follow the EU

regulation for the prevention, early detection, rapid eradication and management (transfrontier context; third approach). Thus, the occurrence dataset used for the calibration of the individual models consisted of 746 presences (only Portugal) and 221 presences (only Spain). The occurrence data set used to fit the models for the full area consisted of 967 presences.

2.4.3. Modelling procedure

We implemented a modelling procedure using the *biomod2* package (Thuiller, Lafourcade, Engler, & Araujo, 2009); available at <http://cran.r-project.org/web/packages/biomod2/index.html> in the R statistical software. SDMs for the current distribution of *A. dealbata* were fitted and then projected under current and future environmental conditions to predict the species' potential distribution, at 1 km² resolution. The models were fitted using an ensemble modelling approach available in *biomod2*, by fitting generalised linear models (GLM), generalised boosted models (GBM), random forests (RF) and multiple adaptive regression splines (MARS) (for more details see *biomod2* help files and vignettes). As the occurrence dataset consisted only of confirmed presences for the study area (and the actual number of presence records was dependent on the “calibration approach” used; see Step 2), 10 pseudo-absences datasets consisting of 1000 pseudo-absences each were randomly generated (i.e. using the user-defined option in *biomod2* to create pseudo-absences) to fit the models (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). Also, we ensured a prevalence of 0.5, which means that the presences and the pseudo-absences have the same importance in the model calibration process. Although other modelling strategies exist for modelling presence-only data (e.g. Bioclim, GARP, Maxent), the ones used here proved superior in multi-model comparisons (Elith et al., 2006), except Maxent which proved equally performant but was shown recently to be a special type of GLM (Renner & Warton, 2013). Note also that GARP and Maxent also make use of

background data. Each individual model was fitted using 70% of the available data and evaluated on the remaining 30%. This cross-validation procedure was repeated 10 times, and a total of 400 models were run (4 algorithms x 10 repetitions x 10 pseudo-absences datasets). For each model, a single ensemble model was obtained by applying the weighted mean of probabilities consensus method (i.e. estimates the weighted sum of probabilities; see (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). This consensus method provides more robust predictions than single models or other consensus methods (Marmion et al., 2009). Finally, model projections were reclassified into presence-absence using a threshold that corresponds to the point on the Receiver Operating Characteristic (ROC) plot (sensitivity against 1-specificity) with the shortest distance to the top-left corner (0,1) of the plot (Fielding & Bell, 1997; Swets, 1988). The final ensemble models were evaluated primarily using the area under the curve (AUC) of the ROC plot while also calculating the True Skill Statistics (TSS; Allouche, Tsoar, & Kadmon, 2006), Cohen's Kappa (Cohen, 1968) and a “presence-only” evaluation metric, the Boyce index (Hirzel, Le Lay, Helfer, Randin, & Guisan, 2006).

2.4.4. Model predictions

For each modelling strategy, spatial predictions of the species' distribution were made over the full geographical extent of the study area (i.e. individual regions – North of Portugal, NW Spain - or the full area). The outcomes from climate change scenarios were obtained projecting the models for 2050 and 2070, using either RCP4.5 or RCP8.5. In the merged strategy, the spatial predictions of the two individual regions/countries were spatially merged (using ArcGIS 10; ESRI, 2011). By comparing the predictions obtained using different calibration strategies, we were able to assess the best method to predict invasions and conflicts with protected areas (i.e. Natura 2000 network; national and natural parks; Step 5) in a transfrontier context.

2.4.5. Conflicts with protected areas

To analyse the potential conflicts between the predicted distribution of *A. dealbata* and the protected areas located in the full study area, we spatially overlapped the distribution maps (obtained in the previous step) with a spatial mask containing only protected areas (using ArcGIS 10).

2.4.6. Comparison of modelling strategies

Finally, we used model outputs to compare the three modelling strategies according to the following criteria: (i) model accuracy (AUC, TSS, Boyce); (ii) ranking of predictor importance; (iii) current and future area predicted as suitable for *A. dealbata*; and (iv) current and future predicted conflicts inside protected areas.

3. Results

3.1. Model accuracy

All final ensemble models, independently of the modelling strategy, presented AUC values higher than 0.8 (Table 1). This means that all models can be considered useful for predictions, according to the

Table 1

Evaluation metrics (i.e., accuracy measures; AUC, TSS, Kappa and Boyce index) for the ensemble models of the different “calibration approaches”. In bold, the highest values in each metric.

Approach	AUC	TSS	Kappa	Boyce index
Separate Countries (Portugal)	0.829	0.510	0.304	0.996
Separate Countries (Spain)	0.953	0.791	0.435	0.978
Full projection (Portugal)	0.832	0.516	0.302	0.996
Full projection (Spain)	0.953	0.786	0.426	0.962
Transfrontier context	0.840	0.530	0.194	0.999

Table 2
Variable importance for the invasive species *Acacia dealbata*, assessed using the ensemble modelling approach for the different “calibration approaches”. In bold, the two most important variables in each model.

Variables/ Approach	Separate Countries (Portugal)	Separate Countries (Spain)	Full projection (Portugal)	Full projection (Spain)	Transfrontier context
Minimum Temperature of Coldest Month (Bio6)	0.57 ± 0.32	0.68 ± 0.22	0.53 ± 0.31	0.69 ± 0.23	0.61 ± 0.27
Temperature Annual Range (Bio7)	0.22 ± 0.32	0.24 ± 0.18	0.19 ± 0.17	0.26 ± 0.19	0.22 ± 0.17
Annual Precipitation (Bio12)	0.27 ± 0.19	0.28 ± 0.16	0.22 ± 0.28	0.27 ± 0.16	0.1 ± 0.07
Precipitation Seasonality (Bio15)	0.09 ± 0.07	0.23 ± 0.16	0.07 ± 0.07	0.22 ± 0.16	0.15 ± 0.08
Percentage cover of cambisols (%CamSoils)	0.01 ± 0.02	0.02 ± 0.02	0.02 ± 0.02	0.02 ± 0.02	0.01 ± 0.02
Mean gross annual primary productivity (GPP)	0.05 ± 0.05	0.02 ± 0.03	0.05 ± 0.05	0.03 ± 0.03	0.04 ± 0.04
Percentage cover of broadleaf forests (%BlFor)	0.01 ± 0.01	0 ± 0.01	0.02 ± 0.02	0 ± 0.01	0.01 ± 0.01
Percentage cover of conifer forests (%ConFor)	0.07 ± 0.05	0.01 ± 0.01	0.06 ± 0.04	0.01 ± 0.01	0.04 ± 0.02
Percentage cover of mixed forests (%MixFor)	0.02 ± 0.02	0.04 ± 0.05	0.02 ± 0.03	0.04 ± 0.05	0.04 ± 0.03
Percentage cover of artificial areas (%Art)	0.2 ± 0.07	0 ± 0.01	0.2 ± 0.07	0.01 ± 0.01	0.06 ± 0.03
Percentage cover of arable land (%Arab)	0.07 ± 0.04	0 ± 0	0.05 ± 0.04	0 ± 0	0.06 ± 0.03

interpretation scales described in [Araujo, Pearson, Thuiller, and Erhard, 2005](#); fail: $AUC < 0.7$, fair: > 0.7 , good > 0.8 , excellent > 0.9). The highest AUC values were observed in the national models of NW Spain (both for individual predictions or when projected to the whole area). Additionally, the Boyce index results were also higher than 0.96 for all the strategies, with the transfrontier model presenting the highest value (0.999). Model evaluations based on TSS and Kappa varied among approaches ([Table 1](#)). For both metrics, the highest values were observed for the national model and prediction for NW Spain (TSS = 0.791; Kappa = 0.435). The transfrontier model presented the lowest value of Kappa (0.194).

3.2. Ranking of predictor importance

For all the different modelling strategies, the most important variable was the minimum temperature of the coldest month ([Table 2](#)). This predictor was followed by annual precipitation and temperature annual range, except in the transfrontier model, where temperature annual range and precipitation seasonality were the second and third most important variables, respectively.

3.3. Current and future potential distribution of *Acacia dealbata*

The distribution of *A. dealbata* is predicted to increase under both future climatic scenarios, with this tendency expectedly more pronounced under the climatic scenario RCP8.5 ([Table A2](#)). When

considering the distribution in the whole study area ([Fig. 3](#)), suitable areas are predicted to increase in the future regardless of the modelling strategy and for both climatic scenarios.

Depending on the modelling strategy, the predicted presence areas can differ, with ca. of 30% in the national models and predictions strategy and 34% in the transfrontier model, under current conditions. This difference further increases under the projections for 2070, with a presence area of 63% (RCP4.5) and 78% (RCP8.5) for the national models and predictions, and 75% (RCP4.5) and 83% (RCP8.5) in the transfrontier model.

Even though all the models presented AUC values higher than 0.8 (as well as Boyce index above 0.9; [Table 1](#)), important differences in the distribution and invasion patterns were observed when considering the spatial projections of the different modelling approaches ([Fig. 3](#)). The predictions obtained through the combination of individual models (national models and predictions) presented the most contrasting patterns between North of Portugal and NW of Spain ([Fig. 3](#), first row). Considering the prediction obtained by the national models projected into the whole area, using either North of Portugal or NW of Spain calibration datasets, it is possible to denote very different patterns of invasion ([Fig. 3](#)). Predictions obtained by the transfrontier strategy and the national model of Portugal projected for the full area exhibit similar patterns of distribution of *A. dealbata* (especially under climate change scenarios), with a higher predicted distribution in the transfrontier model ([Fig. 3](#)).

The transfrontier strategy and the Portugal national model projected

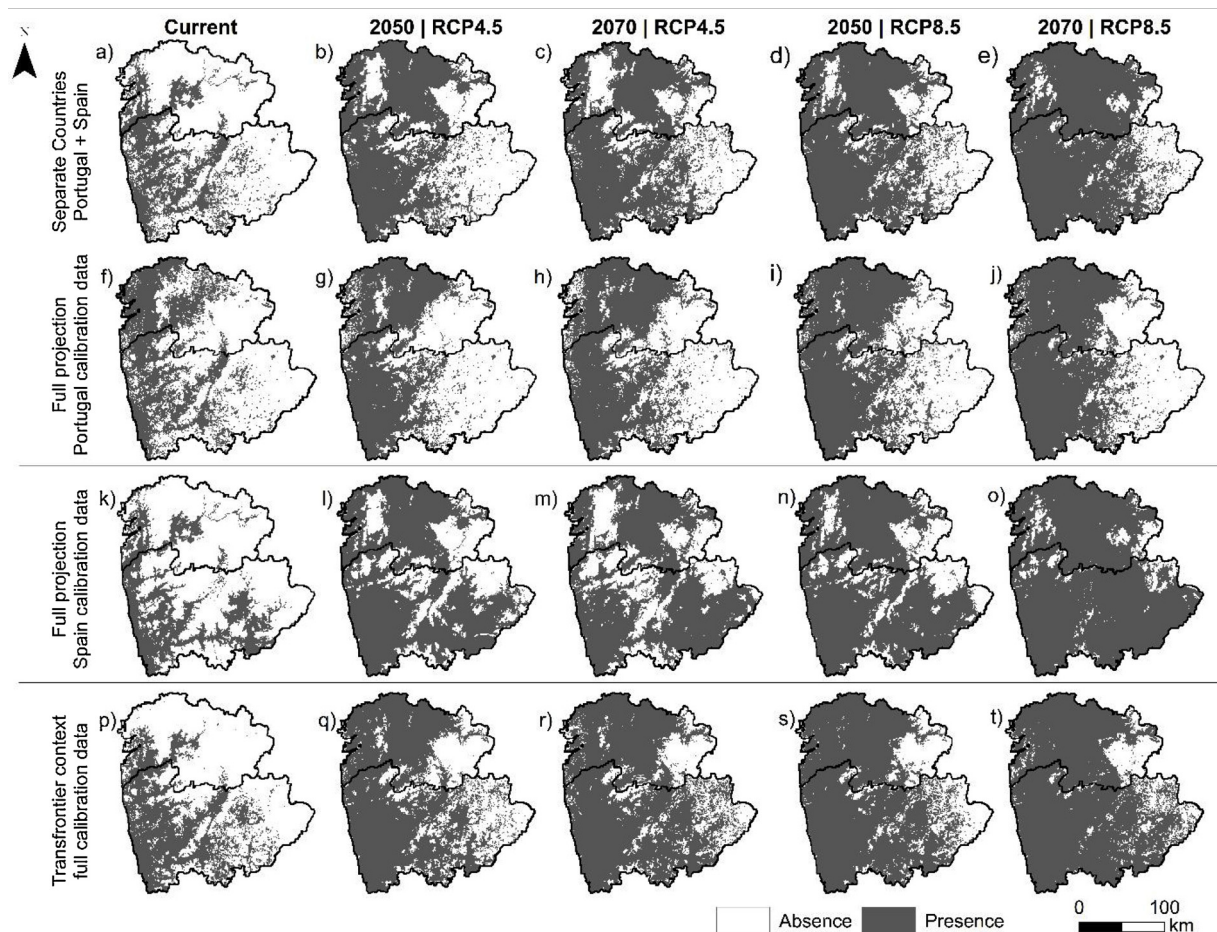


Fig. 3. Spatial potential distribution of *A. dealbata* obtained from the different “calibration approaches”: using separate countries calibration data (first row, a, b, c, d, e)), full projections using data available for Northern Portugal only (second row, f, g, h, i, j), full projections using data available for Spain only (third row) and the transfrontier context, where the distribution of the species was modelled and projected for the full study area using occurrence data also for the full area (bottom row). The models were calibrated for current climatic conditions (first column), for 2050 (second and fourth columns) and 2070 (third and fifth columns) for the two selected representative concentration pathways (RCP4.5 and RCP8.5).

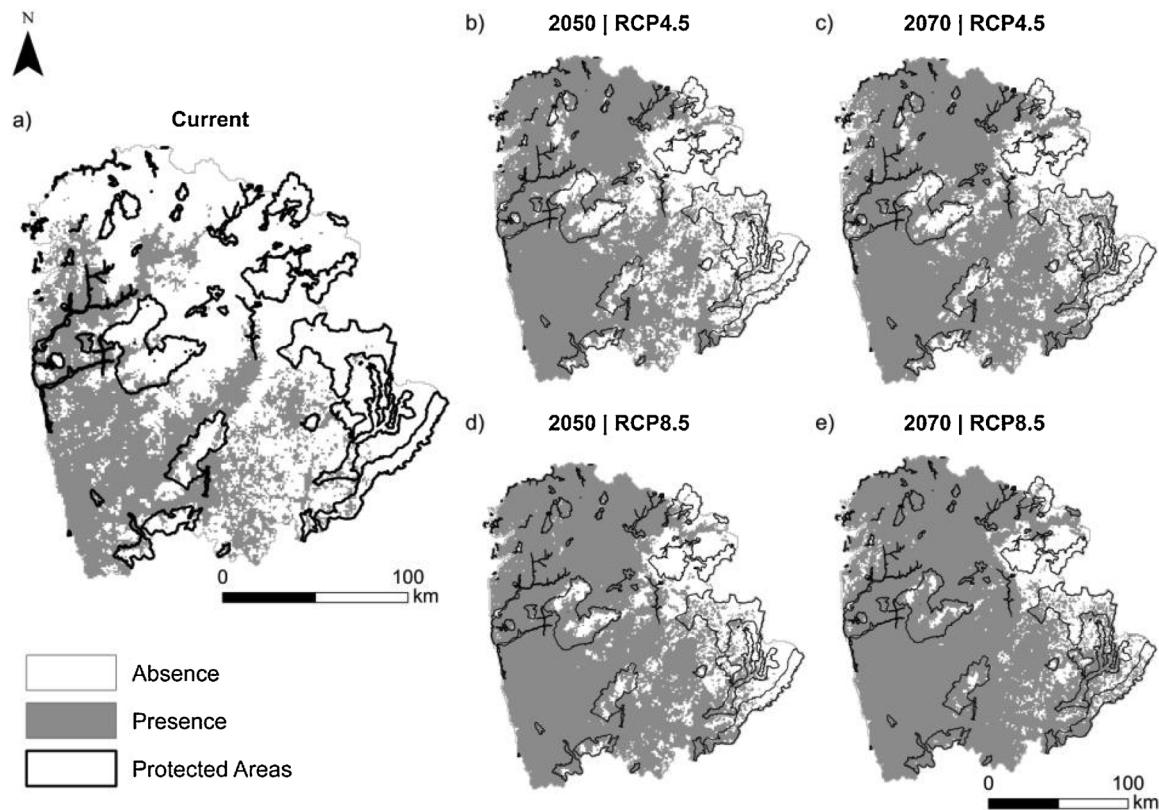


Fig. 4. Potential distribution of *A. dealbata* across the full area and inside protected areas, applying the “transfrontier context” approach, under current climatic conditions (a) model projections for 2050 (b; d) and for 2070 (c; e), for the two selected representative concentration pathways RCP 4.5 (less extreme; b) and c)) and RCP 8.5 (more extreme; d) and e)).

into the full area predict an increase of the species’ distribution towards more interior areas (Fig. 3), while the opposite occurs in the Spain national model projected to the whole area, with a big spatial gap in the distribution of the species between coastal areas and the interior of NW Spain. This gap is particularly evident for year 2070 in RCP4.5, and similar patterns can be observed for year 2050 under both RCPs.

3.4. Current and future predict conflicts inside protected areas

When considering the distribution of the species only inside protected areas (Table A2), the same previous patterns are observed, with additional presence areas predicted by the transfrontier model compared to the other approaches under both climate change scenarios. While only around 15% of protected areas are predicted as suitable for the invasive species under current conditions, under future conditions and especially in the transfrontier model, the suitable area can reach 49% (RCP4.5) or 65% (RCP8.5) in 2070. Considering the spatial distribution of the species inside protected areas, specifically for the transfrontier model (Fig. 4), it was possible to predict an increase in the distribution of *A. dealbata* regardless of the climatic scenario. The predicted future suitable areas are mainly located in the east and centre of Portugal but also at the north of Spain, this pattern being consistent both for 2050 and 2070.

4. Discussion

4.1. Current and future distribution of *Acacia dealbata*, and conflicts with protected areas in a transfrontier context

Under current conditions, our projections show that the area where *Acacia dealbata* is predicted as present reflects most of the study area. This is particularly alarming considering the amount of protected areas

suitable for the species invasion (especially under extreme climate change scenarios). These results are in line with the patterns of invasion previously reported by Vicente et al. (2013) for *A. dealbata* in the North of Portugal, who considered this species to be one of the most problematic invasive species in the region, taking into account its distribution pattern and dynamics of invasion. The projections of the current distribution of the species might also suggest that the main areas of introduction of *A. dealbata* are in the west, with highways and rivers apparently acting as the main dispersal corridors (see Fig. 4). Although this was not something directly studied here, it is consistent with previous literature showing that rivers and roads can enhance the spread of invasive species (Säumel & Kowarik, 2010).

Our predictions also stress that the spatial conflicts between the species and protected areas will mainly occur in the western part of the study area, in agreement with previous studies developed by Vicente et al. (2010) and by Vicente et al. (2013). We can also observe that some protected areas in the inland part of the Spain region are predicted to be occupied by the invasive species. This may relate to the fact that additional areas of introduction may be located outside the study area (e.g. in the coastal region of Coruña, North of Spain) and also to the high concentration of dispersal corridors in that region (see e.g. Proches et al., 2005; Simberloff, 1988; Saunders & Hobbs, 1991). Predictions of future conflicts support the recommendation that prevention measures should be applied in protected areas located in the eastern part of the study area, to avoid further establishment or expansion of *A. dealbata*, as we have predicted an even larger future area of conflict with protected areas under both climate change scenarios. These measures, fulfilling the previously mentioned EU regulation on Invasive Alien Species, would certainly be more effective if useful models (in a transfrontier context) could be used to aid in the decision-making process. Prevention and control measures should also be conducted in protected areas located in the western part of the region, to avoid

additional and more severe invasions by *A. dealbata* and other alien invasive species. These invasions will be enhanced by future climatic and fire conditions, with an expected increase in the frequency of wildfires due to climate change (IPCC, 2013), which in turn will boost seed germination of *A. dealbata* (Lorenzo et al., 2010; Souza-Alonso et al., 2017), increasing their distribution areas.

4.2. The added value of predicting invasions and conflicts with protected areas in a transfrontier context

It is widely accepted that the most efficient way to manage biological invasions is through effective prevention and anticipation of invasions (Broennimann & Guisan, 2008; Gallien et al., 2012; Guisan et al., 2013; Hulme, 2006). To do so, the best available tools and frameworks should be applied to understand the influence that different environmental drivers can have on the distribution of invasive species and thus to improve or support management decisions (Donaldson et al., 2013; Gallien et al., 2012; Guisan et al., 2013). International cooperation is of the utmost importance in invasive species management, as exemplified by callings for a coordinated strategy on invasive species at the European level (Commission of the European Communities, 2008; Hulme, Pysek, Nentwig, & Vila, 2009). Here we addressed the added value of analysing invasions in a transfrontier context, providing evidence that such an approach allows for additional insights on the patterns and drivers of invasion, resulting in different forecasts of conflicts when compared to the analyses of the two countries separately (or using calibration data of a single region and projecting for the full area), and thereby having the potential to improve management and monitoring decisions.

When trying to predict and prevent invasions, it is important to produce accurate forecasts, able to support and improve management actions. The ability to obtain accurate predictions from SDMs can be improved by increasing the sample size used to fit the models (Wisz et al., 2008). Here, we have shown that analysing invasion in a transfrontier context has important advantages when compared to predicting and analysing invasions of countries that share a common border (and consequently can share a common invasion) individually. This may be because, by including the full records available for the area of interest into a single model calibration, instead of multiple calibrations with data from each individual country, the sample size of the calibration dataset considerably increased. At the same time, the larger extent may allow the model to capture a more accurate representation of the species' niche (Barbet-Massin, Thuiller, & Jiguet, 2010; Suárez-Seoane, Virgós, Terroba, Pardavila, & Barea-Azcón, 2014), as areas with a particular set of suitable conditions may be present in only one of the areas (Broennimann & Guisan, 2008). While the effects of sample size and larger extents are widely known, our results suggest that the prediction, prevention, and management of possible conflicts in protected areas should nevertheless be improved with such transfrontier analysis. However, even with all this knowledge, this is not commonly done, and our work can therefore encourage international cooperation in data sharing as well as policy and management initiatives.

Also, due to its increased exactitude when compared to predictions obtained from models for individual regions, predictions made in a transfrontier context could allow additional insights into the factors that are driving each invasion process at such regional scale. This will also permit more accurate forecasting of potential distributions under future conditions, and therefore for improved predictions of future dynamics and conflicts. Combining improved model predictions with robust analytical frameworks, it is possible to obtain better information regarding the threat of invasive species for protected areas (Vicente et al., 2013).

4.3. Important modelling challenges and limitations

Our work also raises some important challenges for SDM research

and applications, and some limitations of our approach. In our transfrontier context, we used data from different countries, resulting from previous separate research and management activities, and thus collected in different ways. As a result, we had available presence-absence data for one region and presence-only data for another, which needed to be combined in a same model fitting procedure. We employed one possible solution to use these data, namely to use sets of pseudo-absences for the full area and removing the recorded absences from the analyses, but there may be other approaches that need to be tested like a hierarchical modelling approach (e.g. Pearson, Dawson, & Liu, 2004; Petitpierre et al., 2016) or models that use presence data from both native and invaded ranges (e.g. Bradley, Blumenthal, Wilcove, & Ziska, 2010; Broennimann & Guisan, 2008; Jiménez-Valverde et al., 2011). In this regard, as no data from the species' native range were used here, one cannot rule out that some suitable climatic conditions in the native range, but not yet invaded in the invaded range and thus not captured in the models, might be missing or biasing our predictions (e.g. western part being more predicted). Other aspects deserving further research are how different modelling techniques (e.g. Elith & Graham, 2009; Fernandes, Scherrer, & Guisan, 2018), how the choice of environmental variable (e.g. Mod, Scherrer, Luoto, & Guisan, 2016; Scherrer & Guisan, 2019) and variable selection (Petitpierre, Broennimann, Kueffer, Daehler, & Guisan, 2017) can affect model performance and predictions. In any case, even if using native range data, it is important to note that neighbouring countries in an invaded range would benefit from joining efforts and establishing common monitoring/prevention measures regarding invasive species control. This was also recognized under the EU regulation on Invasive Alien Species, which provides guidance and financial support for trans-border cooperation to prevent the spread, eradication and control of invasive species.

Another limitation of our study was that some non-climatic variables in the models, such as mean gross annual primary productivity or the different forest types, depend potentially on climate but were not allowed to change in the future, therefore implicitly assuming that these would remain constant in the future. Although this assumption is not fully unlikely given the important human influence on land cover in this area (Caetano et al., 2009; Calvo-Iglesias et al., 2009), and even though climate variables anyway proved more important in our models, future studies could also include scenarios of how these variables might change according to the climate change scenarios used (e.g. using land-use change scenarios; Vicente et al., 2010).

4.4. Current and future challenges for the conservation of protected areas in a transfrontier context

Designating and managing protected areas is one of the most important approaches to preserve global biodiversity, but as mentioned in Pyšek et al. (2002), invasive species are present in many protected reserves worldwide. In some cases, protected areas are a last refuge for endemic, rare or endangered species, capturing important biodiversity and mitigating possible negative effects of external pressures (i.e. climate change, habitat fragmentation, invasive species; Gaston, Jackson, Cantú-Salazar, & Cruz-Piñón, 2008). Assessing these pressures, especially the conflicts and impacts of invasive species, so they can be effectively anticipated and addressed, has become an important effort for the scientific community (Davis, Thompson, & Philip Grime, 2005). A review of 199 articles describing the impacts of 135 alien plant taxa assessed that the diversity and abundance of native species decreased in invaded sites, providing evidence that invasive plants can cause important ecological impacts (see Vila et al., 2011). Vicente et al. (2013) also showed that protected areas are predicted to suffer impacts caused by invasive species under future climatic conditions.

Here, our framework provided useful information on the potential patterns of invasion by *A. dealbata* in a transfrontier context, with an emphasis on protected areas. This information can be crucial for decision makers focusing on the prevention of invasions by alien species

inside protected areas in a transfrontier context, opening a new way for collaborative management of invasions. Fairly recent policy initiatives also highlight the need for international cooperation to tackle this global change driver (e.g. G8, 2009). Despite this, additional efforts are needed to improve monitoring and management actions on threatened protected areas, mainly because of the lack of cooperation/communication between the scientific community, stakeholders and decision makers (Guisan et al., 2013).

5. Conclusions

In this work, we expect to contribute to the improvement of management and monitoring actions in a transfrontier context using SDMs, thereby helping to implement recent EU regulation for the prevention, eradication and management of woody invasive plant species. With our proposed framework, we assessed the most appropriate approach to predict the distribution of *Acacia dealbata*, and its potential conflicts with protected areas in a transfrontier context. Therefore, considering our framework and results, we highlight that:

- 1) all the “calibration approaches” presented high evaluation values, with the models being considered as having excellent predictive accuracy;
- 2) the minimum temperature of the coldest month and annual precipitation were the most important variables to explain the distribution of the species;
- 3) differences in spatial patterns were observed under the different “calibration approaches”;
- 4) the species distribution areas are higher under the transfrontier context, both for the full and protected areas;
- 5) the distribution of *A. dealbata* was predicted to increase under both climatic change scenarios, regardless of the “calibration approach”;
- 6) spatial conflicts between the species and protected areas were predicted to mainly occur in the western part of the study area;
- 7) the transfrontier approach allows for additional insights on the current and future patterns of invasion, having important advantages when compared to predicting and analysing invasions of individual countries that share a common border.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jnc.2019.04.001>.

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