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A novel downscaling approach to predict plant invasions and improve local conservation actions

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Abstract To successfully protect native biodiversity from the effects of biological invasions, local conservation priorities must be established. For this purpose, fine-grained species distribution data is required but often unavailable. We present a new approach to obtain fine-grained predictions of invasion through the development of downscaled invasion maps based on coarse-grained distribution data. The framework is illustrated for the alien invader *Acacia dealbata* in the Northwest of Portugal. The analytical design was divided in five steps: (1) three individual coarse-grained models were calibrated and their spatial predictions were downscaled into fine-grained models using three different downscaling techniques; (2) a Downscaling Consensus Map was built by spatially combining the predictions from those three models; (3) using coarse-grained (1 km^2) or fine-grained (0.04 km^2) datasets, two different models were fitted and spatially projected; (4) for each spatial resolution, Conservation Value maps were produced, based on the spatial combination of the protection networks represented in the region; and (5) the spatial conflicts between the predicted distribution of the invader and Conservation Value maps were calculated and compared for the several invasion maps. The downscaled models showed high predictive performance (AUC $>$ 0.9). The spatial projections of the different models revealed a general similarity among projections from all modelling techniques, for both the patterns of invasion and the conflicts with conservation areas. The possibility of obtaining detailed and reliable predictions based on coarse-grained distribution data could avoid costly fieldwork to collect fine-grained distribution data while effectively supporting the management of invasions at the appropriate scales.

Keywords Combined predictive modelling · Conservation value map · Downscaling consensus · Ensemble modelling · Species distribution models

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Introduction

Biological invasions are known to be one of the major drivers of global change (Chytrý et al. 2012; Sala et al. 2000; Vilà and Ibáñez 2011) acting at several spatial scales, and multiple ecological and biological levels (e.g. ecosystems, habitats, species; Ohlemüller et al. 2006; Seipel et al. 2012; Walther et al. 2009; Weaver et al. 2012). The most important negative impacts of biological invasions include changes in ecosystems structure and functioning (Theoharides and Dukes 2007; Thuiller et al. 2007), decrease in native biological diversity, and homogenization of species pools, and several downstream economic losses (Giorgis et al. 2010; Le Maitre et al. 2011; Vilà et al. 2010; Vitousek et al. 1997). After the establishment of invasive alien species on a given area, eradication measures are difficult to implement, and time and cost consuming (Gallien et al. 2012; Genovesi 2005). Anticipating and preventing the introduction of invasive alien species into a specific region is therefore considered the most cost-effective way of managing biological invasions (Broennimann and Guisan 2008; Gallien et al. 2012; Hulme 2006).

Species distribution models (hereafter SDMs) are an effective method to anticipate future invasive species introductions since they establish a statistical relationship between species occurrence and environmental data (Elith and Leathwick 2009; Guisan and Thuiller 2005). In the last decade, SDMs have been applied in several different contexts, e.g. to create tools in conservation planning (Araújo et al. 2011), to identify ecological requirements of invasive alien species and environmental drivers of distributions (Gallien et al. 2012; Vicente et al. 2010), and to forecast the potential distribution of invasive alien species under future environmental scenarios (e.g. climate and land use changes; Roura-Pascual et al. 2004; Vicente et al. 2011).

Recently, increasing attention has been devoted to the study of invasions across multiple scales, to determine which particular processes drive invasions at each relevant scale (Pauchard and Shea 2006; Seipel et al. 2012). Methodological advances in SDMs such as the combined predictive modelling framework (CPM; Vicente et al. 2011), which uses subsets of predictors classified by their scale of influence, have contributed to provide more informative spatial projections of species distributions (Boulangeat et al. 2012; Gallien et al. 2012). Additionally, ensemble modelling promoted high improvements compared to SDMs fitted with a single technique (Araújo and New 2007), reducing their predictive uncertainty (Thuiller et al. 2009), since it combines the projections of several different modelling methods into a final prediction that enhances the agreement of predictions (Elith et al. 2010).

The spatial scale to address a research study should reflect the objectives of the task, for example continental or global scales must be considered when macroecological or global changes are the focus of the study, whereas local and regional scales must be considered when detailed ecological processes or conservation planning and management are the main objective (Elith and Leathwick 2009). Coarse resolution datasets are most frequently available for species distribution data (e.g. distribution atlases, opportunistic records, herbarium collections; McPherson et al. 2006) as well as for environmental information (General Circulation Models, e.g. WorldClim; Hijmans et al. 2005; land cover maps e.g. Corine Land Cover; Caetano et al. 2009). The use of coarse resolution data to address fine-scale ecological problems can however lead to misinterpretations of the results and to dubious conclusions (Guisan and Thuiller 2005). Available data on invasive alien species distribution and/or environmental factors are frequently too coarse for local conservation actions, because they don't permit to detect small vegetation/habitat types patches potentially threatened by invasive plants (Araújo et al. 2005; Barbosa et al. 2010; Rouget 2003). To overcome this problem, environmental and distribution data should be collected at higher spatial resolutions (e.g. to calibrate fine-scale SDMs), but this solution requires a costly comprehensive sampling design (Barbosa et al. 2010).

Downscaling methods have been proposed to overcome the problem of coarse data, allowing the detection of fine-grained environmental patterns using the combination of coarse-grained species occurrences and fine-grained environmental data (Araújo et al. 2005; Keil et al. 2013). In recent years, several downscaling approaches for species distribution models have been proposed: the direct approach (Araújo et al. 2005; Barbosa et al. 2010; McPherson et al. 2006); the iterative approach (McPherson et al. 2006); the point sampling approach (McPherson et al. 2006);

the centroids approach (Bombi and D'Amen 2012; Lloyd and Palmer 1998); the envelope approach (Bombi and D'Amen 2012); the clustering approach (McPherson et al. 2006); the hierarchical approach (Pearson et al. 2004); and the hierarchical Bayesian modelling approach (Keil et al. 2013).

Although several studies have applied and compared downscaling approaches (Bombi and D'Amen 2012; McPherson et al. 2006), to our knowledge there is no study based on coarse-resolution species data that combines the outcomes of different downscaling techniques into a robust consensus projection map (Downscaling Consensus Map; i.e. combination of different downscaling outputs into a single map). The reasoning behind the development of a Downscaling Consensus Map is similar to the one behind the development of ensemble modelling. We hypothesis that the combination of outputs of different downscaling approaches into a consensus map might help reduce predictive uncertainties of single downscaling approaches. Therefore, the general objective of this work is thus to develop downscaled invasion probability maps from coarse-grained model projections to obtain spatial projections of invasion probability useful for local management actions. We illustrate our approach with the invasive alien plant species *Acacia dealbata* (silver wattle), one of the most problematic woody species in South-western Europe (Lorenzo et al. 2010), and specifically in the protected areas of the study area. Projections from coarse-grained SDMs, based on 1 km^2 pixel species occurrence data, were downscaled by combining results from several downscaling methods into a consensus projection map. It resulted in four possible combinations of predictions (Type III—Presence predicted by three approaches; Type II—Presence predicted by two approaches; Type I—Presence predicted by one approach; and Type 0—Absence predicted by all approaches). The projections of the consensus map were compared with projections from a fine-grained model calibrated using independent fine resolution occurrence data (0.04 km^2). Finally, we use the Downscaling Consensus Map ability to determine possible conflicts between *A. dealbata* and natural protected areas, comparing those conflicts with those obtained with the independent fine-grained model.

Methods

Study area

The study area is a region heavily invaded by alien plants, located in the extreme Northwest of Portugal (Fig. 1). It covers an area of 3,462 km^2 and is located at the transition between the Euro-Siberian ("Atlantic") and the Mediterranean biogeographic regions (Costa et al. 1998). The region is topographically heterogeneous, with elevation ranging from sea level (in the west) to 1,450 m a.s.l. in the eastern mountains, resulting in marked variations of environmental conditions. The annual mean temperature ranges from about 9 °C to about 15 °C, and the mean total annual precipitation varies between about 1,200 mm in the lowlands to about 3,000 mm in the eastern mountain summits (Vicente et al. 2011). The heterogeneity of the area, in terms of topography and climate, is demonstrated by a wide variety of land uses and vegetation covers (e.g. vineyards, olive groves, pine forests, oak forests, grasslands; Caetano et al. 2009).

Test species

Acacia dealbata Link., known as silver wattle, is a woody plant species from the Leguminosae family and native to Australia and Tasmania (Lorenzo et al. 2010). Australian *Acacia* species are problematic plant invaders in many parts of the world (Le Maitre et al. 2011). *A. dealbata* was introduced in Europe in the 1820s (Carballeira and Reigosa 1999), and it has become very common in Mediterranean countries where it can be found both in the wild (as an invader in disturbed forests and scrublands) and grown as an ornamental plant (Lorenzo et al. 2010). *A. dealbata* has a high colonizing ability leading to low cover of undergrowth species. This is mainly because of its capacity to produce large amounts of seeds (Lorenzo et al. 2010), the germination of which is stimulated by fire, and to occur in dense populations eliminating native vegetation by preventing its regeneration (e.g. through competition for resources; Lorenzo et al. (2010) and by allelopathic interference; Marchante et al. 2011). In our region of interest, the species is widespread and is projected to further expand its current distribution under future climate and land use change scenarios (Vicente et al. 2011).

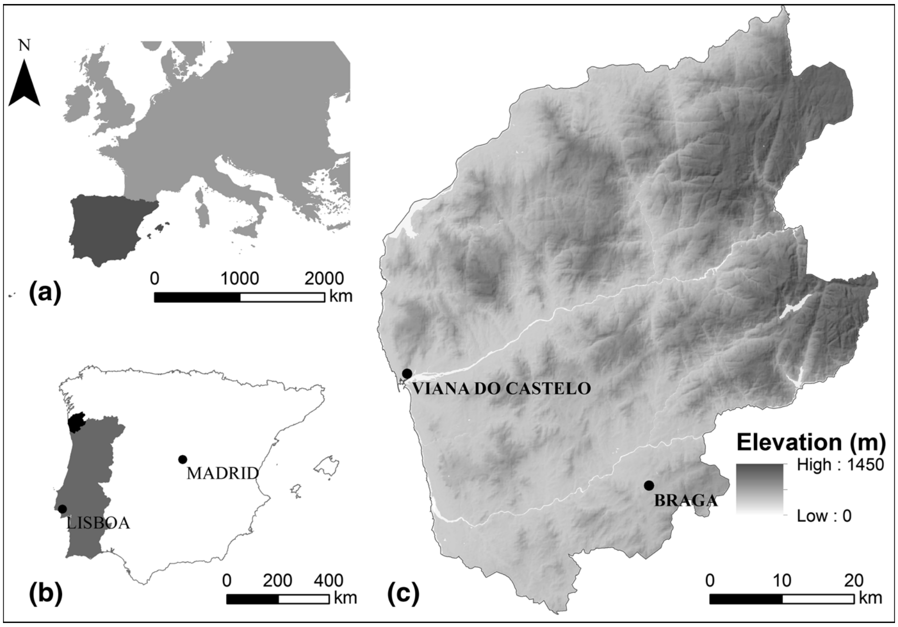

Fig. 1 The study site Minho is located in northwest Portugal in southwestern Europe (**a**) on a western edge of the Iberian Peninsula (**b**). The elevation of Minho varies from sea level on the west coast to 1,450 m above sea level in the eastern portion (**c**)

Sampling strategy

Two independent occurrence datasets for *A. dealbata* were used in this study as response variables for SDMs calibration (see Fig. 2): a coarse-grained set (1 km^2) and a fine-grained set (0.04 km^2).

The coarse-grained occurrence set (1 km^2) was obtained from data compiled in previous surveys (Vicente et al. 2010, 2011). These surveys were conducted between March and April 2008 (complemented with surveys in 2010 and 2011). The data were collected using a stratified random sampling strategy described in Vicente et al. (2010).

Independently, the fine-grained occurrence dataset (0.04 km^2) was collected through field surveys, between January and March 2012, during the species' blooming period. To gather the 0.04 km^2 dataset, we first used the previously obtained coarse-grained occurrence dataset to calibrate a distribution model for *A. dealbata* (with 1 km^2 resolution).Climate was used as the only source of environmental explanatory variables, since it's the primary determinant of alien invasions in the region (Vicente et al. 2010). Cells predicted as suitable for species presence (in the previously calibrated 1 km^2 model) were stratified based on the percentage of artificial forest cover and on the landscape edge density (9 final strata; for more details see Appendix A1on Online Resource 1). We used an equal-stratified sampling design to randomly select 20 plots of 0.04 km^2 size (200 × 200 m cells) in each stratum. In each of the 0.04 km^2 cells, presence or absence data for *A. dealbata* was collected, with a fixed sampling effort established (about 30 min per cell).

For each of the two independent datasets and to minimize geographic aggregation, we removed from the initial datasets, occurrences geographically less distant to their closest neighbour than a given threshold distance (Clark and Evans (1954) aggregation index *R*). We proceeded iteratively until the aggregation index reached a value $R \approx 1$ (occurrences not clustered). To avoid biases due to edge effects, we computed the Clark and Evans index with the correction proposed by Donnelly (1978). The computation was done in *R* using the *spatstat* package. The final occurrence datasets for *A. dealbata* used for model fitting included 138 records (69 presences, 69 absences) for each of both spatial resolutions (1 and 0.04 km^2).

Environmental variables

First, we selected variables that, according to expert knowledge and to previous reporting in the scientific literature (Lorenzo et al. 2010; Vicente et al. 2010, 2011, 2013a, b), can act as determinants of the ecology and distribution of the test species. To avoid correlation between selected variables, we tested for pairwise correlations using Spearman's *rho* correlation coefficient, and only variables with correlation lower

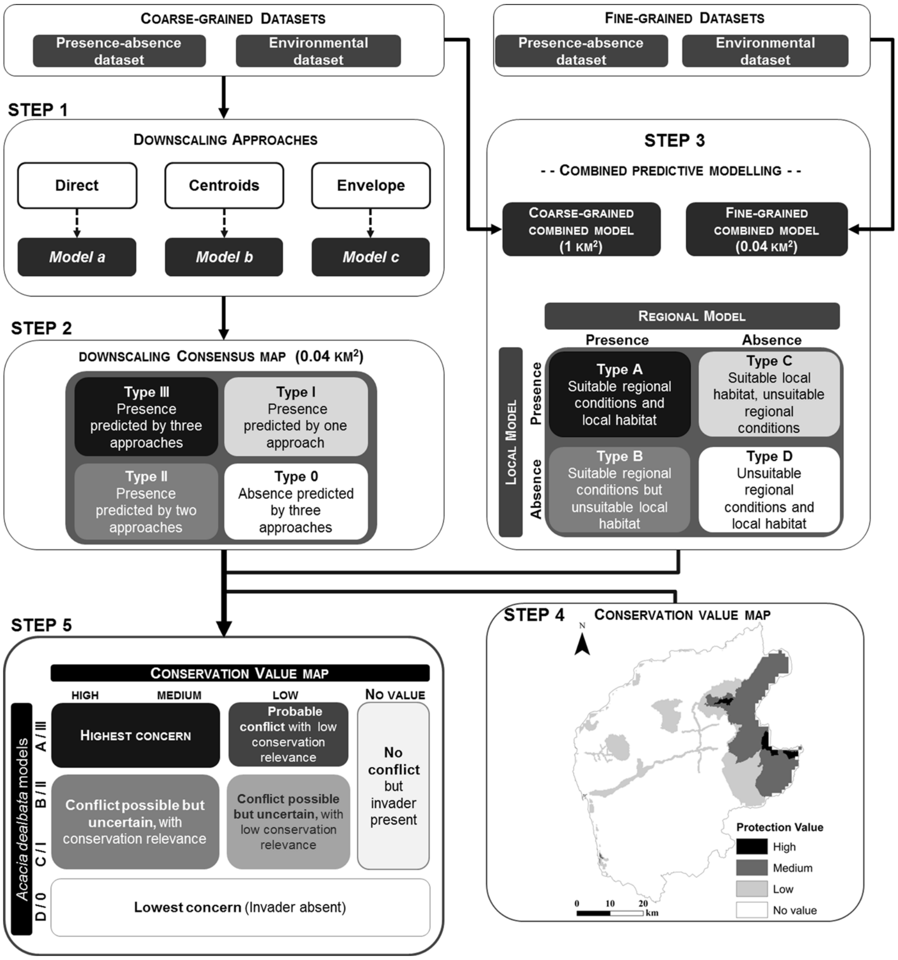

Fig. 2 Analytical framework for modelling and downscaling the distribution of *A. dealbata* and assess the conflicts with CV areas. Using coarse-grained datasets, models *a*, *b* and *c* were downscaled using three different downscaling approaches (*Step 1*). A Downscaling Consensus Map was then built by spatially combining the predictions of the models obtained by the downscaling approaches, resulting in four responses: Type III-presence predicted by the three approaches, Type II-Presence predicted by two approaches, Type I-presence predicted by one approach and Type 0-absence predicted by three approaches (*Step 2*). Using coarse-grained datasets and fine-grained datasets, a Coarse-grained and a Fine-grained model were calibrated and projected for *A. dealbata* using the combined predictive modelling approach (Vicente et al., 2011), resulting in four predicted responses: Type A—Suitable regional conditions and local habitat, Type B—only suitable regional conditions, Type C—only suitable local habitat, and Type D—unsuitable regional conditions and local habitat (*Step 3*). Conservation value (CV) was mapped by combining Natura 2000 sites and Natural Parks each classified into four classes ranging from no protection value to high protection value (*Step 4*). Finally, spatial conflicts between the predicted distribution of the species (A, B, C and D, or III, II, I and 0) and CV were calculated (*Step 5*)

than 0.6 were considered (Elith et al. 2006). In the case of correlated pairs of variables, we chose the variable with the most direct ecological impact (based on expert knowledge of the actual distribution of the species) on plant species distribution (Guisan and Thuiller 2005). This analysis yielded a final set of nine environmental variables to fit the SDMs (Table 1): two climatic variables (Minimum Temperature of Coldest Month, and Annual Precipitation), two land cover/landscape composition variables (percentage cover of broadleaf forests, and percentage cover of artificial forests), one geological variable (percentage of granites), one fire regime related variable (total number of fires between 1990 and 2009), and three landscape structure metrics (density of local hydrographical and road network, mean shape index and edge density; for more detailed information see Appendix A2 on Online Resource 1).

Table 1 Environmental variables used in the different models, grouped into environmental types that reflect their ecological meaning, and their scale of variation in the test region (Vicente et al. 2011; for more details see Appendix A2 on Online Resource 1)

Environmental types	Environmental variables	Scale of variation
Climate	BIO6 (minimum temperature coldest month)	Regional
	BIO12 (annual precipitation)	
Landscape composition	pBlFor (% cover of broadleaf forests)	Local
	pArtFor (% cover of artificial forests)	
Geology	pGra (% of granites)	
Fire regime	NumFir (total number of fire occurrences between 1990 and 2009)	
Landscape structure and function	DHidRoadNe (density of local hydrographic and roads network)	
	MSI (mean shape index)	
	ED (edge density)	

Analytical framework

The analytical design was divided in five major steps, as illustrated in Fig. 2:

Step 1. Using coarse-scale datasets (1 km^2), we built three individual distribution models applying the ensemble forecasting framework of *biomod2* package (Thuiller et al. 2009; available at http://cran.r-project.org/web/packages/biomod2/index.html) in the statistical software *R* (R Development Core Team 2012). These three final ensemble models were based on the combination of nine available algorithms in biomod2 and using the available nine environmental predictors (for more details see *biomod2* help files and vignettes). Each individual model was calibrated using 80 % of available data. The area under the curve (AUC) was then calculated on the 20 % of remaining data. This cross-validation procedure was repeated 30 times. Only models with AUC > 0.7 were kept to build ensemble models. Kept individual model predictions were then used to produce a single ensemble model using the *Mean (all)* consensus method (i.e. decreases the predictive uncertainty of single-models by calculating the mean value of the predictions ensemble; see Marmion et al., 2009). The *Mean (all)* consensus method was used because it 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 maximizing the percentage of presences and absences correctly predicted (i.e. the probability where sensitivity = specificity; Liu et al., 2005). The final output distribution was then downscaled into fine-grained distribution models (0.04 km^2) using three different methods:

- *Model a*, downscaled using the Direct Approach (Araújo et al. 2005; McPherson et al. 2006; Bombi and D'Amen 2012), that projects the distribution of a calibrated coarse-grained distribution model into a fine-grained projection, assuming that species distributions at finer scales (0.04 km^2) are influenced by the same processes as at coarser scales (1 km^2).
- *Model b*, downscaled using the Centroids Approach (Lloyd and Palmer 1998; Bombi and D'Amen 2012), uses the centroids of all sampled presence pixels and the centroids of all unoccupied sampled pixels; the environmental conditions at the finer resolution (0.04 km^2) were sampled for these centroids and used to calibrate and project the models, obtaining fine-grained predictions.
- *Model c*, downscaled using the Envelope Approach (Bombi and D'Amen 2012; Bombi et al. 2012), in which 69 points of presence were randomly generated within the 1 km^2 sampled presence pixels, and 69 points of absences were randomly generated within the 1 km^2 sampled absence pixels. These points were then used to extract fine-grained environmental information that was used to calibrate and project fine-grained models.

Step 2 Spatial projections of the fine-grained models (a, b, and c) were combined to create a Downscaling Consensus Map, resulting in four possible combinations: presence predicted by the three approaches (Type III), presence predicted by two approaches (Type II), presence predicted only by one approach (Type I), and absence predicted by all approaches (Type 0).

Step 3 Using the ensemble forecasting framework applied previously in Step 1, a Coarse-grained (1 km^2) and a Fine-grained (0.04 km^2) combined predictive models (Vicente et al. 2011) were fitted for the current distribution of *A. dealbata*. In this combined modelling procedure, separate models were fitted using either "regional" (partial regional model) or "local" (local partial model) predictors (see Table 1; Scale of variation), and a final model was obtained by spatially overlapping the two partial model projections (Vicente et al. 2011), resulting in four possible combinations: suitable regional conditions and local habitat (A), only suitable regional conditions (B), only suitable local habitat (C), and unsuitable regional conditions and local habitat (D). The Coarse and Fine-grained combined models were created to spatially compare and validate the outputs obtained by the Downscaling Consensus Map (Step 2).

Step 4. For each spatial resolution (1 km^2 and 0.04 km^2), we produced Conservation Value (CV) maps based on the two nature protection networks present in the region: the European Natura 2000 network, and the National Natural Parks network (see Appendix A3 on Online Resource 1 for more details).

Step 5. We calculated and compared the spatial conflicts between the predicted distribution of *A. dealbata* (obtained in Steps 2 and 3) and the CV maps (at coarse and fine scales). We obtained six possible conflict outputs: (i) combinations of highest concern, where *A. dealbata* has suitable regional conditions and local habitat available (type A or III) and the CV is high or medium; (ii) probable conflict with low conservation relevance, where the species has suitable regional conditions and local habitat available (type A or III) but the CV is low; (iii) conflict possible but uncertain, with conservation relevance, where the species has only suitable regional conditions or local habitat available (type B or II; C or I) but the CV is high or medium; (iv) conflict possible but uncertain, with low conservation relevance, where the species has only suitable regional conditions or local habitat available (type B or II; C or I) and the CV is low; (v) areas without conflict (no CV) but invader species predicted to be potentially present; and (vi) areas of lowest concern, where the invasive species is predicted to be absent (type D or 0).

Results

Downscaling the potential distribution of *A. dealbata*

The performances of all three downscaling approaches were considered very high, with AUC values above 0.9 (Table 2). The number of pixels predicted as presences were clearly higher for the Centroids Approach (53,701 presences) and for the Envelope Approach (52,513 presences) than those predicted in the Direct Approach (29,441 presences), which thus yielded more conservative projections of the potential distribution of the focal invasive plant.

The two combined models (Fine-grained and Coarse-grained) and the Downscaling Consensus Map predicted different proportions of suitable habitat for *A. dealbata* in the test region (Table 3). Areas with suitable regional conditions and local habitat (Type A) were the predominant response type predicted by the Coarse-grained Combined Model (42 % of the total area). Conversely, in the Fine-grained Combined

Table 2 Predictive accuracy of the ensemble models (measured as the area under the curve, AUC) for the three used downscaling approaches, and the number of pixels (1 pixel = 0.04 km^2) predicted as presences and absences in each ensemble model (for more information see Appendix A4 on Online Resource 1)

Downscaling approach	AUC	Presence	Absence
Model a—direct approach	0.952	29,441	52,734
Model b—centroids approach	0.943	53,701	28,474
Model c—envelope approach	0.966	52,513	29,662

Table 3 Percentage of the study area predicted for each of the four response classes in combined models (A = Suitable regional conditions and local habitat, B = Only suitable regional conditions, C = Only suitable local habitat, and D = Unsuitable regional conditions and local habitat), for the two combined models (Fine-grained and Coarse-grained Combined Models) and for the Downscaling Consensus Map (III = Presence predicted by all downscaling approaches, II = Presence predicted by two downscaling approaches, I = Presence predicted by one downscaling approach, and 0 = Absence predicted by all downscaling approaches)

Combined model	Type A (%)	Type B (%)	Type C (%)	Type D (%)
Fine-grained combined model	13	35	10	42
Coarse-grained combined model	42	18	12	28
Consensus model	Type III (%)	Type II (%)	Type I (%)	Type 0 (%)
Downscaling consensus map	31	28	16	25

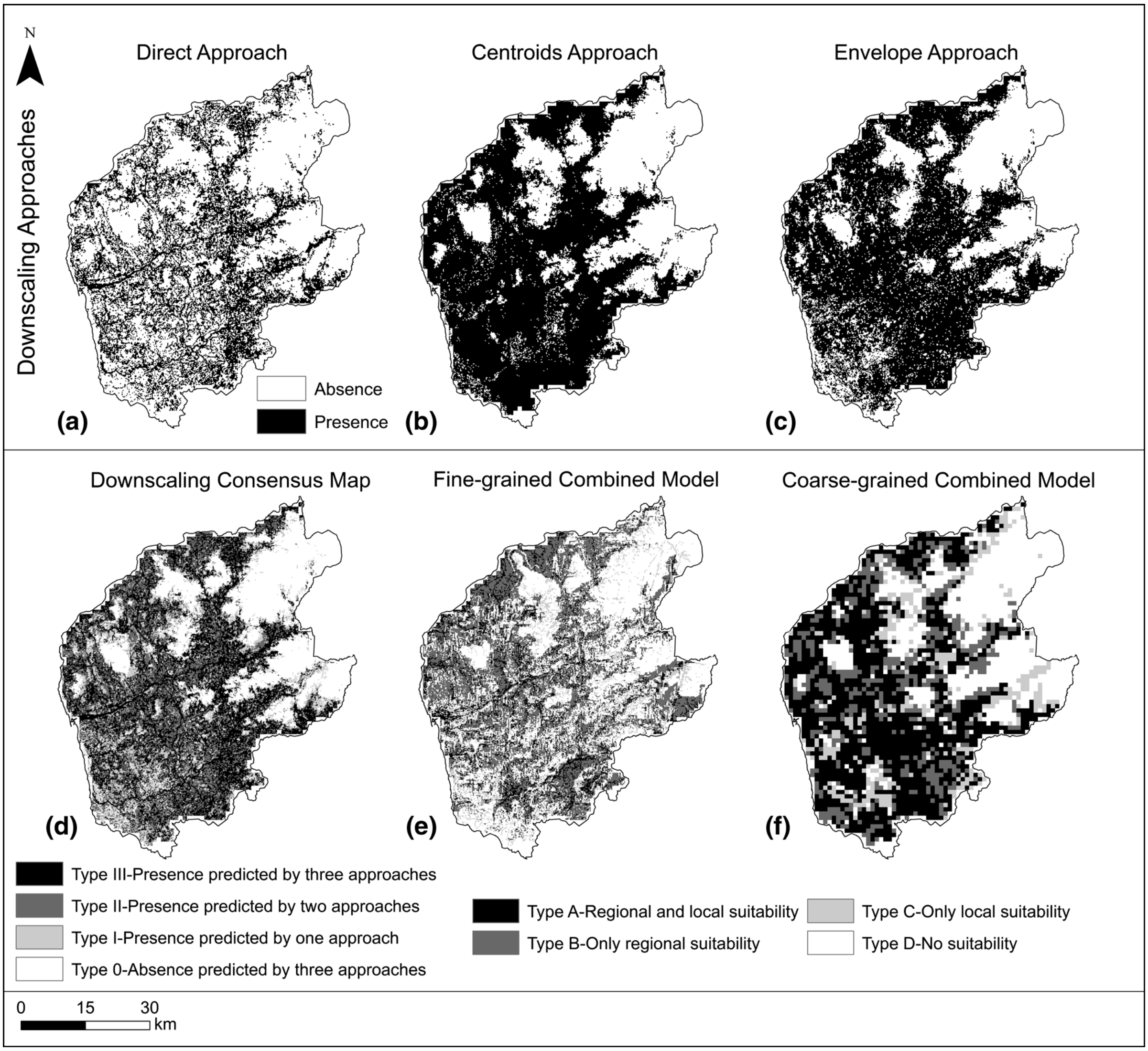

Fig. 3 Downscaled spatial projections for *A. dealbata* using three different downscaling approaches: direct approach (**a**), centroids approach (**b**), and envelope approach (**c**). spatial projections of the different suitability models obtained for *A. dealbata*: downscaling consensus map (**d**), fine-grained combined model (**e**), and coarse-grained combined model (**f**)

Model, areas with unsuitable conditions (Type D) was the predominant projection (42 %), while areas with suitable regional conditions and local habitat (Type A) were predicted to occur in only 13 % of the total area. In the Downscaling Consensus Map, the presence of *A. dealbata* was predicted by the three downscaling approaches (Type III) for almost one-third of the total area (31 %), while the areas where all three approaches predicted absences (Type 0) covered a quarter of the total area (25 %). Overall, the Fine-grained Combined Model thus yielded more conservative projections for the distribution of the focal invader.

The three downscaling procedures yielded generally comparable spatial projections for *A. dealbata* (Fig. 3a–c). Comparing the projections of the different approaches, the Direct Approach (Fig. 3a) provided a more spatially scattered projection of presences and absences than the other two approaches. Conversely, the Centroids Approach (Fig. 3b) produced a more aggregated projection for presences (and absences) than the two other downscaling approaches. In the Envelope

Table 4 Percentage of the area of possible spatial conflict between *A. dealbata* predicted invasion and the areas with conservation value (CV map), for each combination of spatial conflict: *Highest concern* (response Type A or III and high protection value), *Probable conflict with low conservation relevance* (response Type A or III and low protection value), *Conflict possible but uncertain, with conservation relevance* (response Type B or C (II or I) and high or medium protection value), *Conflict possible but uncertain, with low conservation relevance* (response Type B or C (II or I) and low protection value), *No conflict but invader present* (response Type A, B or C (III, II or I) and no protection value), and *Lowest concern*, with invader absent (response Type D or 0)

Invasion and CV conflicts	Highest concern (%)	Probable conflict with low conservation relevance (%)	Conflict possible but uncertain, with conservation relevance (%)	Conflict possible but uncertain, with low conservation relevance (%)	No conflict but invader present (%)	Lowest concern (invader absent) (%)
Downscaling conflicts	1.4	3.9	2.4	4.2	62.9	25.2
Fine-grain conflicts	0.8	1.9	4.1	5.4	46.2	41.7
Coarse-grain conflicts	1.1	3.8	2.2	3.3	61.5	28.1

Approach (Fig. 3c) the spatial projections are comparable (though less dense) to the Centroids Approach map (Fig. 3b). The spatial projections of the different suitability models (Fig. 3) presented an overall similarity between projections of species presence in the Downscaling Consensus Map (Fig. 3d) and projections of suitable conditions in the combined models (Fig. 3e and f), despite the more conservative projections obtained with the Fine-grained Combined Model (cf. Table 3).

Spatial conflict between conservation value and *A. dealbata* invasion

Different levels of potential spatial conflicts were obtained through the spatial combination of the distribution predictions of *A. dealbata* and CV maps (Table 4). Areas of *highest concern* and of *probable conflict with low conservation relevance* were more predicted by the Downscaling Consensus Map (1.4 and 3.9 % of the total area, respectively) and by the Coarse-grained Model (1.1 and 3.8 %, respectively). The lower values predicted by the Fine-grained Model (0.8 and 1.9 % of the total area, respectively), were in agreement with the more conservative distribution projections described above. The Fine-grained Model also predicted smaller areas of *no conflict but invader present* (46.2 %) and larger areas of *lowest concern* (invader absent; 41.7 %).

Considering the spatial patterns of conflict in the test area (Fig. 4a–c), the areas of major concern are located in the eastern lowlands, where high conservation value areas (Peneda-Gerês National Park) spatially coincide with predicted suitable conditions for *A. dealbata*. Areas of *no conflict but invader present* and of *lowest concern* were, for the three different conflict maps/scenarios, the predominant predictions and with generally coincident spatial patterns. When comparing the two fine-grained projections, the areas of *highest concern* predicted by the Downscaling Consensus Map (Fig. 4a) are more aggregated in the main river valleys than those predicted by the fine-grained model (Fig. 4b). The spatial combination of the fine-grained CV map (Fig. 4d) with the areas predicted as of *highest concern* by the Downscaling and the Fine-grained models simultaneously (Fig. 4e) revealed that there are important areas, inside Portugal's single National Park, predicted as of *highest concern* (Fig. 4f).

Discussion and conclusions

Improving predictions of invader distribution through downscaling

The prediction of the spatial (and temporal) patterns of invasion by alien species is particularly useful when made at relevant scales to support conservation and management actions (i.e. at "local" scales; Barbosa et al. 2010). However, in most cases, the quality of available distribution data is incompatible with such needs. Downscaling techniques are a promising approach to overcome this problem and translate coarse-grained data into fine-grained predictions (Araújo et al. 2005; Bombi et al. 2012).

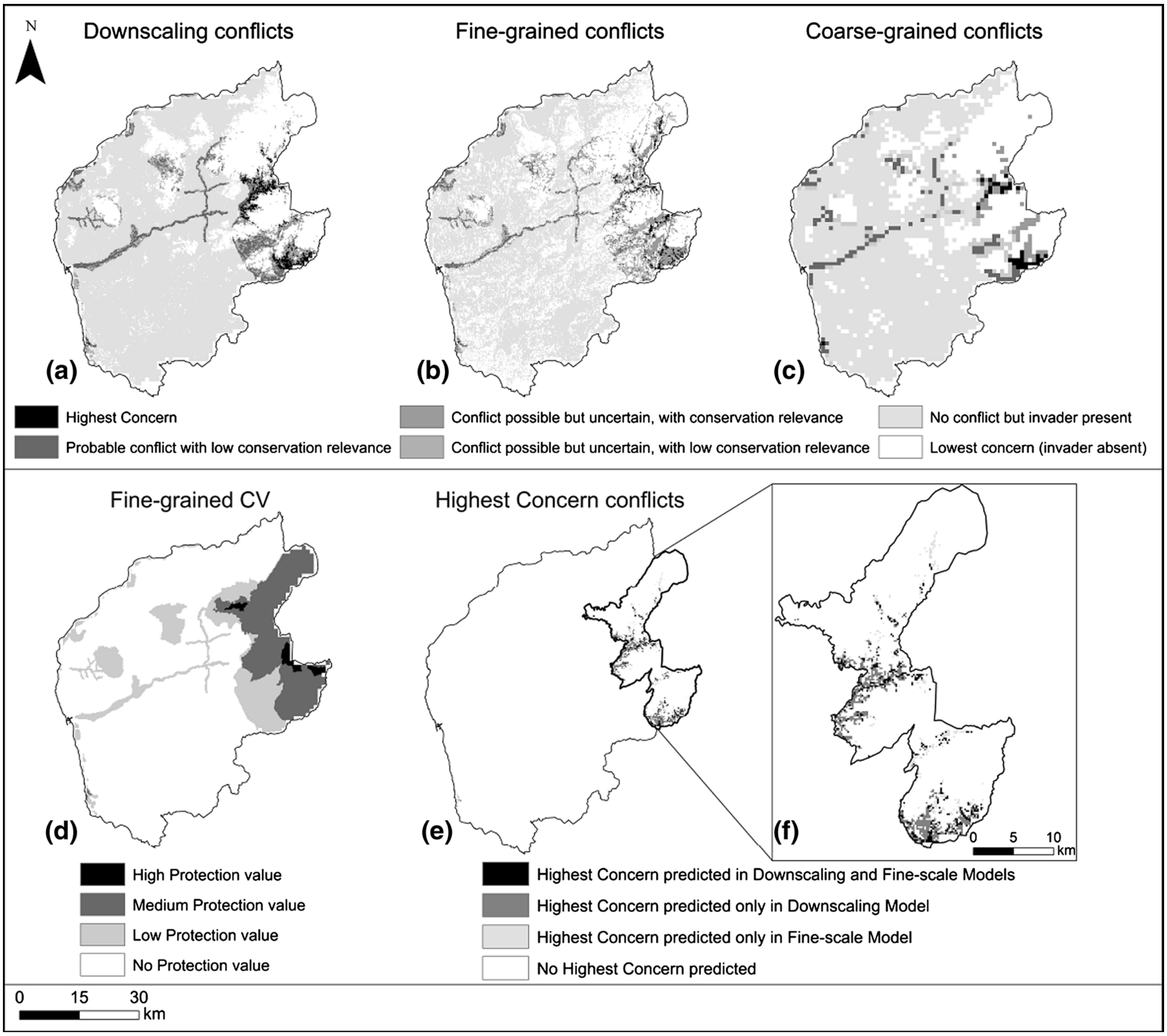

Fig. 4 Spatial conflict between the three *A. dealbata* invasion projections/scenarios and the corresponding CV map: downscaling consensus map and fine-grained CV map (**a**); fine-grained combined model and fine-grained CV map (**b**); Coarse-grained Combined model and coarse-grained CV map (**c**). Detail of the highest concern spatial conflicts: fine-grained CV map (**d**), spatial conflicts of highest concern predicted simultaneously by the downscaling consensus map and the fine-grained combined model (**e**), and areas of spatial conflict of highest concern, viewed in detail for the Peneda-Gerês National Park (**f**)

Over the last decade, several species distribution downscaling approaches have been proposed: the direct approach (Araújo et al. 2005; McPherson et al. 2006); the centroids approach (Bombi and D’Amen 2012; Lloyd and Palmer 1998); or the envelope approach (Bombi and D’Amen 2012). However, even if the results from the different techniques can sometimes be quite different (e.g. Bombi and D’Amen 2012; McPherson et al. 2006), to our knowledge so far no study has tried to combine those results into a final consensus projection.

Here we developed a framework that integrates the predictions of three different downscaling approaches into a single consensus map. We used the same three downscaling approaches that Bombi and D’Amen (2012) compared in their work, also achieving excellent predictive accuracy for our downscaled models. In their study, Bombi and D’Amen (2012) highlighted that different errors and assumptions characterize and influence the different downscaling approaches. These errors and assumptions can explain the observed differences in the spatial projections of our downscaled models (e.g. the more scattered projections of the Direct Approach when compared to the other approaches; see Fig. 3). Considering those different assumptions and sources of error, some choices can be made to produce more accurate downscaled predictions, such as the quality, accuracy and number of occurrence data, the species niche range, the choice of the modelling technique and the selection of environmental variables (Bombi and D'Amen 2012).

Several studies attributed great importance to the use of accurate occurrence data to explain the success (Bombi and D'Amen 2012; Bombi et al. 2012; Lloyd and Palmer 1998) or the failure (Collingham et al. 2000; McPherson et al. 2006) of the downscaling processes. In our work we used accurate (though coarse-grained) occurrences, with low spatial correlation and representative of the environmental variations in our study area. This may have improved the performance of our downscaled models since factors that could lead to poor model calibration (e.g. areas unevenly sampled or data consisting of biased or sparse presence/absence records; Collingham et al. 2000; McPherson et al. 2006) were taken into account. The choice of modelling techniques is also an important factor to explain the good performances of downscaled models, so we used an ensemble forecasting approach to calibrate our models to take into account the uncertainties of the different modelling techniques, resulting in more accurate final projections (Araújo and New 2007; Bombi et al. 2012; Thuiller et al. 2009). The use of this ensemble forecasting approach was important in our work because, as Bombi and D'Amen (2012) noted, different modelling techniques can influence in different ways the accuracy of the downscaling approaches. Finally, the selection of environmental variables also influences the results of the downscaling process (Barbosa et al. 2003; Bombi and D'Amen 2012; Lloyd and Palmer 1998). Therefore, it is important to determine which factors can determine the species distribution at coarse and fine scales. The use of variables important at finer scales (e.g. land-use) can also improve fine-grain predictions (Araújo et al. 2005; Bombi and D'Amen 2012; Pearson et al. 2004). Our downscaling framework performed well also due to the use of ecologically significant environmental variables to explain the distribution of *A. dealbata* at the several relevant scales (see Vicente et al. 2011).

Despite of the choices that can be made to improve the performance and accuracy of the downscaling procedures (and the different model projections produced in the process), there are no "rules of thumb" to choose the downscaling approach based on their different errors and/or assumptions (Bombi and D'Amen 2012). The similarities observed between our Downscaling Consensus Map and the Fine- and Coarse-grained projections suggest that the new framework accurately predicted the fine-grain distribution of *A. dealbata* in our study area, using coarse-grain distribution data, while ensuring that the strengths and weaknesses of each downscaling technique were taken into account.

Improving prediction and management of conflicts with protected areas

Protected areas globally are important refuges of native biodiversity, particularly for species with high conservation value, and also for providing many valuable ecosystem services (Beaumont et al. 2009). Over the last few years, Species Distribution Models have been widely used to predict the expansion of invasive alien species into protected areas and their potential impacts on biodiversity and ecosystem services (e.g. Kleinbauer et al. 2010; O'Donnell et al. 2012; Vicente et al. 2013a, b), however in most cases using a spatial resolution incompatible with local conservation and management needs.

Downscaling procedures have been used in previous studies to: predict the distribution of invasive species at finer scales (Collingham et al. 2000); assess the importance and applicability of downscaling approaches to predict the distribution of threatened species (Barbosa et al. 2003, 2010); assess the limitations and potentialities of different downscaling approaches (Bombi and D'Amen 2012; Keil et al. 2013; McPherson et al. 2006); or discuss the importance and implications of using downscaling approaches for conservation planning (Araújo et al. 2005). To our knowledge, our study is the first to use downscaling approaches to predict the distribution of an invasive species at finer scales with the aim of predicting its potential conflicts with protected areas (or other areas of conservation relevance) and thereby contributing to manage those conflicts. Bombi et al. (2012) focused on identifying priority areas for conservation of indigenous species, and concluded that with accurate downscaling processes the identification of local priority areas with high spatial resolution was possible, even when using coarse-grained distribution data. In our study we have reached a similar conclusion, since conflict predictions from our Downscaling Consensus Map (based on coarse distribution data) presented a spatial pattern generally comparable to the one predicted by the Fine-grained Model (see Fig. 4). In fact, our downscaling framework could predict spatial patterns of conflicts similar to those predicted using fine-grain distribution data, making this a suitable approach to obtain models for conservation actions in those areas that are more prone to invasion.

The Convention on Biological Diversity proposed three steps for the management of alien invasive species: prevention, eradication, and, if the first two steps fail, control (Secretariat to the Convention on Biological Diversity 2005). It has been recognized that prevention is the most cost-effective way to manage an invasion by an alien species (Broennimann and Guisan 2008; Gallien et al. 2012; Hulme 2006). It is also known that for local conservation and management actions to become successful at protecting native biodiversity, their application must be designed with high spatial detail (Barbosa et al. 2003; Bombi et al. 2012). In our study, we created a fine-grained map of the spatial conflict between the potential distribution of the invasive *A. dealbata* and areas with conservation value. Our results can be useful to help implement management and monitoring actions to prevent (through early detection) the establishment of invasive alien species in areas where species and habitats of high conservation value could become threatened by changes in landscape and habitat quality, and to identify areas of high concern that should be considered as the primary target areas against invasions. Focusing the application of scarce resources in those areas of highest concern can contribute to the success of invasion control measures as well as to the overall cost-efficiency of both management and monitoring.

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