

Where will conflicts between alien and rare species occur after climate and land-use change? A test with a novel combined modelling approach

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Abstract Protecting native biodiversity against alien invasive species requires powerful methods to anticipate these invasions and to protect native species assumed to be at risk. Here, we describe how species distribution models (SDMs) can be used to identify areas predicted as both suitable for rare native species and highly susceptible to invasion by alien species, at present and under future climate and land-use scenarios. To assess the condition and dynamics of such conflicts, we developed a combined predictive modelling (CPM) approach, which predicts species distributions by

combining two SDMs fitted using subsets of predictors classified as acting at either regional or local scales. We illustrate the CPM approach for an alien invader and a rare species associated with similar habitats in north-west Portugal. Combined models predict a wider variety of potential species responses, providing more informative projections of species distributions and future dynamics than traditional, non-combined models. They also provide more informative insight regarding current and future rare-invasive conflict areas. For our studied species, conflict areas of highest conservation relevance are predicted to decrease over the next decade, supporting previous reports that some invasive species may contract their geographic range and impact due to climate change. More generally, our results highlight the more informative character of the combined approach to address practical issues in conservation and management programs, especially those aimed at mitigating the impact of invasive plants, land-use and climate changes in sensitive regions.

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Introduction

To protect global biodiversity from the effects of alien invasions, research efforts should be directed at finding ways to anticipate invasions and protect species

that are considered to be at the highest risk of extinction. Rare species are already particularly threatened by global environmental change and human activities, so there is a pressing need to determine the additional threats of biological invasions on these species (Dale 1997). One way to assess these pressures is by determining the geographic overlap of biological invasions and rare native species. This requires predicting the geographic distribution of invasive species (Thuiller et al. 2005; Theoharides and Dukes 2007), of rare native species (Elith et al. 2006; Guisan et al. 2006), and finally of overlay areas of potential invasive threat to rare species, both under present and future climates and/or land-uses. To our knowledge, such study of rare-invasive conflicts under both climate and land-use change scenarios has not been conducted before.

A multi-scale approach is important because most pathways of alien species introduction result from human activities at several spatial and temporal scales, and ongoing climate and land-use changes are forecasted to boost invasion in a number of habitats (Theoharides and Dukes 2007). Ecosystem invasion by alien species is still increasing and is a major contributor to the loss of biodiversity in individual habitats and whole landscapes (Levine 2000; Millennium Ecosystem Assessment 2005; Theoharides and Dukes 2007), and the efficiency and cost-effectiveness of control and eradication measures remain to be evaluated (Perrings et al. 2002; Culliney 2005).

The ability to make spatial predictions of both native and invasive species distribution requires an understanding of the underlying ecological processes, collecting and analysing relevant biodiversity information, and developing a set of statistical tools capable of describing species and diversity patterns as a function of environmental conditions by quantifying species-environmental relationships (Guisan and Thuiller 2005). Environmental, historical and human factors jointly determine to shape the geographic distribution of plants (Brown et al. 1996), and can be used as explanatory predictors of plant distribution within statistical models (usually designated as Species Distribution Models, hereafter SDM; Guisan and Zimmermann 2000; Guisan and Thuiller 2005). SDMs have been used to address fundamental ecological questions, such as the ecological impacts of climate and land-use changes or of biological

invasions (Guisan and Zimmermann 2000; Parmesan and Yohe 2003; Guisan and Thuiller 2005; Broennimann et al. 2006; Heikkinen et al. 2007). Ensemble forecasting (Araújo and New 2007), obtained by assembling predictions from a series of SDMs fitted with different modelling techniques, represent a valuable improvement over SDMs fitted with a single technique (Thuiller et al. 2009). This is important, because distinct modelling techniques calibrated on the same dataset can provide different results (Thuiller 2004; Broennimann et al. 2007). Combining distinct modelling algorithms accounts for the inherent uncertainty among individual models, and determines an optimal solution from an ensemble of predictions (Thuiller 2004; Araújo and New 2007; Broennimann et al. 2007).

Modelling species distribution is a challenging procedure due to the complex nature of species range dynamics and of the related factors acting at multiple spatial scales (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Elith and Leathwick 2007; Murphy and Lovett-Doust 2007; Randin et al. 2009a). Most SDM studies have considered explanatory predictors derived for a single grain size and a fixed spatial extent. However, factors driving the distribution and abundance of organisms often act at different spatial scales (Wiens 1989, Wiens 2002; Pearson et al. 2004; Guisan and Thuiller 2005; Guisan et al. 2007). For instance, climate can explain plant distribution at the continental scale (Thuiller et al. 2004), while topography, geomorphology, human land-use or biotic interactions are usually required at regional and local scales (Dirnböck et al. 2003; Guisan and Thuiller 2005; Lassueur et al. 2006; Randin et al. 2009b). Multi-scale approaches to SDMs, integrating predictors acting at different scales, may capture dimensions of species distributions that are ignored by approaches conducted at a single scale (Pearson et al. 2004; Gelfand et al. 2005). Hierarchical multi-scale approaches can also contribute to improve conservation planning (Elith and Leathwick 2007). Hierarchic predictive models, as used in this paper, can be defined as models using subsets of predictors classified by their scale of influence and by the ecological context in which they operate. These hierarchical subsets of predictors can be applied to multiple sizes of grain and extent (“multi-scale approach”; Pearson et al. 2004; Lassueur et al. 2006; Bradley 2010).

In this paper, we assess how biological invasions can impact native biota. More specifically, we aim to identify present and future areas of potential conflict between an invasive and a rare species occurring in similar habitats. To do this, we developed a combined predictive modelling (CPM) approach to assess the condition and dynamics of such conflicts. It starts by fitting SDMs using two subsets of predictor maps available at a same extent and grain size (“fixed extent-grain approach”), but classified a priori according to the ecological scales—“regional” or “local”—at which they are expected to operate. The latter classification is based on spatial autocorrelation analyses (Cliff and Ord 1981; Legendre and Legendre 1998) to ensure that each predictor is objectively assigned as either a local or a regional predictor (Vicente et al. 2010). A sequential modelling procedure that spatially combines projections from the two models is then developed to calibrating the regional and the local model.. To support our combined approach, we compare it to a non-combined predictive model (NCPM) in which all (unclassified) predictors are entered together in a single model. To our knowledge, such a combined modelling framework has only been formalized once in species distribution modelling (Bradley 2010) and we developed our study independently of this work.

We illustrate the CPM approach with SDMs for an alien invader (*Acacia dealbata* Link.) and a rare species (*Ruscus aculeatus* L.) with similar observed distribution patterns in northwest Portugal. In particular, when compared to a non-combined model and when applied with predictors at a same extent and grain size, we expect the CPM to provide: (1) more informative predictions for single taxa under current conditions, (2) refined predictions of changes in species distributions under climate and land-use change, and (3) refined predictions of potential areas of present and future conflicts between invading and rare species. By this, we do not imply that our predictions will be more accurate than those from non-combined models, but that by formalizing the local versus regional influences into separate predictions, one could better assess the importance of the two predictor groups. Using this approach it is possible to assess which of these two predictor groups is important and how their related predictions, as well as the combined prediction, could be affected by future climate and/or land-use changes for different

sites and across an entire species’ distribution,. In this sense, CPM is expected to provide more information while achieving a similar accuracy to non-combined model.

Using such a combined approach could therefore provide new insights on the scale at which environmental factors are constraining the distribution of a species within a given area (e.g. Pearson et al. 2004) and yield more informative projections of environmental suitability under alternative climate and land-use change scenarios.

Methods

Study area and test species

Study area

The study area is located in the extreme Northwest of Portugal ($8^{\circ}52'–8^{\circ}2'W$; $41^{\circ}24'–42^{\circ}9'N$; Fig. 1), covering an area of 3,462 km² at the transition between the Atlantic and Mediterranean biogeographic regions. Elevation ranges from sea level (west) to 1,540 m in the eastern mountains, with major rivers running from east to west. The annual mean temperature ranges from ca. 9°C to ca. 15°C, and the mean total annual precipitation varies between ca. 1,200 mm in the lowlands to ca. 3,000 mm in the eastern mountain summits. The general summer dry period of 1–2 months highlights the climatic transitional character of this area.

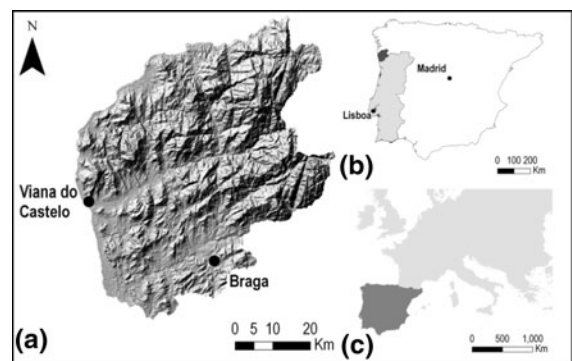


Fig. 1 Study area (a) and its location in Iberian Peninsula (b) and in Europe (c)

Test species

Two plant species were selected on the basis of three criteria: (1) one being an aggressive alien invasive species and another being a rare native species; (2) having similar habitat requirements; (3) both occurring in the region with some overlapping distribution in the study area.

Ruscus aculeatus L. is a native monocotyledonous evergreen shrub-like perennial belonging to the *Liliaceae* family and occurring in thermophilous oak woods as well as in evergreen and deciduous shrublands. Biogeographically, it is considered a Mediterranean species, mostly distributed in Southern Europe, and protected by international law (EU Habitats Directive, Annex V). This species has a scattered distribution in the study area, usually related to forest habitats and is sometimes locally abundant.

Acacia dealbata Link is a small tree from the *Leguminosae* family and native to Australia and Tasmania. Introduced in the European continent in the 1820s (Carballeira and Reigosa 1999), it is very common in Mediterranean countries where it is both found in the wild (as an invader in disturbed forests and shrublands) and farmed for ornamental use. In addition to its great colonizing capacity it leads to a very low covering of undergrowth species caused by its allelopathic ability (Carballeira and Reigosa 1999).

The occurrence dataset was collected during a field survey, planned using an environmental stratification of the study-region based on climate (mean annual temperature) and bedrock type (Hirzel and Guisan 2002). Selected 1 km² grid cells were surveyed to determine the presence (or absence) of the considered species. A fixed sampling effort was established and all habitat types occurring in each grid cell were visited. Distribution records for *Ruscus aculeatus*, available from previous surveys, were added to the dataset. The final occurrence dataset included 90 records (38 presences, 52 absences) for *Acacia dealbata*, and 155 records (71 presences, 84 absences) for *Ruscus aculeatus*.

Environmental predictors and predictor classification

Environmental predictors

First we selected 20 predictors that, by expert knowledge and according to previous reporting in

the scientific literature, act as determinants of the ecology and distribution of the target species. In the second phase of selection we applied data dredge statistics (dredge—*MuMIn* R package; available at <http://r-forge.r-project.org>) to run Generalized Linear Models (GLMs) with all valid combinations of environmental analysis for both species. We performed the GLMs with a binomial variance and a logistic link function. To avoid multicollinearity, the most significant predictors for each species were tested for pair-wise correlations using Spearman's rho correlation coefficient using the results of the best models obtained by data dredge, and only predictors with correlation lower than 0.7 were considered (Elith et al. 2006; Wisz and Guisan 2009). In the case of correlated pairs of predictors, we chose the one with the most direct ecological impact on plant species distributions (Guisan and Zimmermann 2000).

We selected the eight best environmental predictors (four regional plus four local) to calibrate the models for each species. Some of those predictors were common to the two species, while others were only selected for one species (Table 1). Climatic predictors were obtained from the Worldclim database (Hijmans et al. 2005) while the other predictors were obtained from detailed environmental maps (see “Annex 1”).

Predictor classification

We classified environmental predictors a priori as “regional” or “local” based on a theoretical framework supported by ecological theory, namely concepts from landscape ecology (meta)community ecology, phytosociology, and biogeography (see Table 1). The underlying rationale is that the distribution of species is driven by processes linked to several levels of ecological complexity, and is therefore expressed at different spatial scales (Klijn and de Haes 1994; Pauchard and Shea 2006).

We divided the variables into two groups based on their spatial scale of variation using a statistical predictor classification based on spatial autocorrelation. Using point pattern statistics (PPSA—*spdep* R package; available at <http://cran.r-project.org/web/packages/spdep/>), we calculated Geary's *c* autocorrelation measure (Cliff and Ord 1981; Legendre and Legendre 1998) for all predictor variables for increasing neighbourhood distances. Finally, a

Table 1 Environmental predictors used in CPMs and non-CPMs with indication of a priori scale of variation and the models where have been used

Predictors	Description	Scale of variation	Models fitted
TMinim	Minimum temperature of the coldest month	Regional	Ad, Ra
PWettQ	Precipitation of the wettest quarter of the year	Regional	Ra
PColdQ	Precipitation of the coldest quarter of the year	Regional	Ad
disUrb	Distance to the urban areas	Regional	Ra
disHNet	Distance to main rivers	Regional	Ad
SWIslop	Local variation of slope	Regional	Ad, Ra
pRegos	Percentage of regosoils	Local	Ra
pArenos	Percentage of arenosoils	Local	Ad
pArtFor	Percentage cover of forest stands	Local	Ad, Ra
pSemNat	Percentage cover of seminatural habitats	Local	Ra
pAgric	Percentage cover of agriculture	Local	Ad
denHNet	Density of local hydrographic network	Local	Ra
SWIsoil	Local diversity of soil types	Local	Ad

Ad, *Acacia dealbata*; Ra, *Ruscus aculeatus*

hierarchical clustering was performed based on a Euclidean distance matrix of all Geary's c values (complete linkage method). The two first groups in the final classification tree were very well separated (see Fig. 5 in the Results section) corresponding to predictors with local versus regional influence.

Conceptual combined modelling framework

We developed combined and non-combined ensemble forecasting models for current and future distributions of *Acacia dealbata* and *Ruscus aculeatus* using BIOMOD (Thuiller et al. 2009) in the R statistical software (R Development Core Team 2009). By “non-combined” we refer to the traditional approach to model development, where all predictors are included in one single model fitting procedure. In the proposed combined approach, distinct models are fitted using either “regional” or “local” predictors, and a final model is obtained by spatially combining the two partial models (Fig. 2). All models were produced for the same spatial extent and using the same grain size (1 km²).

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

1. first, we the predictor variables were classified as regional or local, based on the Geary's C autocorrelation measure (see “[Predictor classification](#)” section);
2. second, we fitted the two partial models: the regional partial model using the subset of regional predictors, and the local partial models using the subset of local predictors (see Table 1). Both models were fitted using the same response variables (species occurrences) and using the same grain and extent;
3. third, we mapped the partial model outputs (regional and local) in the ArcGIS (ESRI 2008);
4. fourth, we produced the combined model by overlapping the spatial predictions of the regional and the local partial models, obtaining all the four possible combinations of them (see table in Fig. 2d).

Combined models were developed for each species from the spatial combination of two partial models, in which regional and local environmental predictors were used separately (Fig. 2). The predictions resulting from these models were then combined to obtain a final prediction map including both regional and local constraints. This final prediction map included four combinations of predictions. Although these four combinations do not formally represent classes of probability of occurrence we assume that the probability of occurrence is maximum in Type A, and reaches a minimum value in type D.

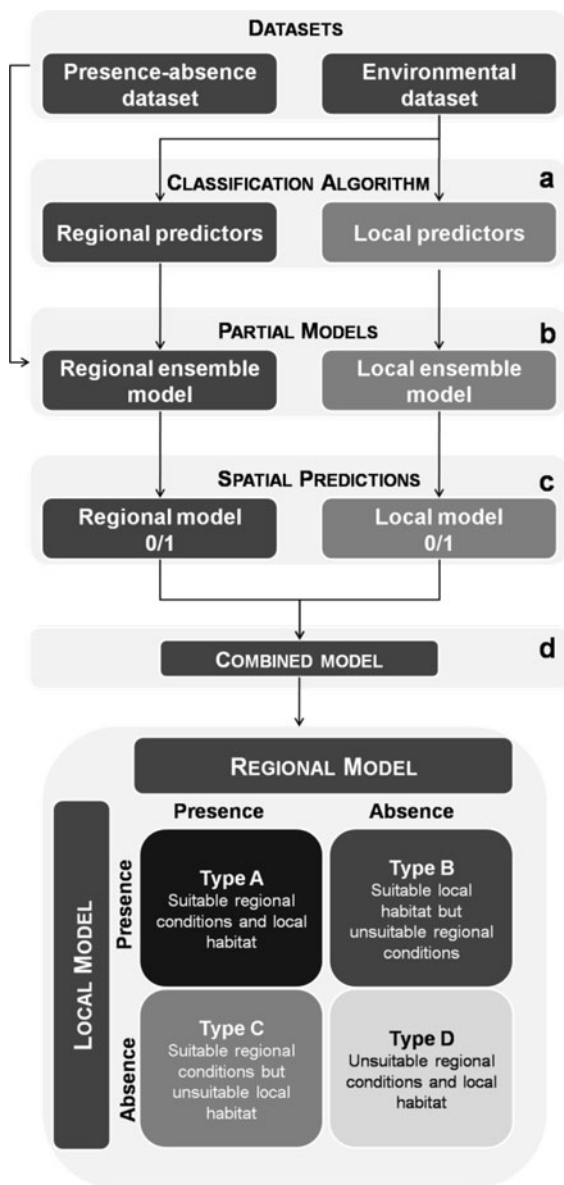


Fig. 2 Analytical design for developing combined predictive models (CPMs), with all the possible combinations (“occurrence types”) obtained in final prediction maps

Model fitting and evaluation

We first used BIOMOD to fit models using seven techniques: (1) Generalised Linear Models (GLM), (2) Generalised Boosting Models (GBM), (3) Generalised Additive Models (GAM), (4) Classification Tree Analysis (CTA), (5) Mixture Discriminant Analysis (MDA), (6) Multivariate Adaptive Regression Splines (MARS) and, (7) Random Forest (RF).

Thuiller et al. (2009) provide details on model parameterisation for the techniques available in BIOMOD. All seven techniques were used to fit models for the non-combined and combined modelling procedures. Interactions among predictors were not explicitly included in model calibration, nor was species invasiveness taken into account in the case of the alien invader. To evaluate the performance of the models predictions, we followed the receiver-operating characteristic-based thresholding (ROC-thresholding) approach used in Elith et al. (2006) and discussed in Liu et al. (2005). The AUC was obtained as an output for each model. BIOMOD uses a repeated split-sample procedure, keeping 20% of the initial data out of the calibration for subsequent validation of the predictions. The number of repetitions was set to 50.

Model predictions were then stacked into a single ensemble model using a weighted approach, available for generating ensemble models in BIOMOD. This approach ranks models by their AUC evaluation score using a decay measure being the evaluation AUC for all the models for both species higher than 0.7 (Fielding and Bell 1997). The decay expresses the relative importance of the model weights, a decay of one being equivalent to a committee averaging (i.e. same weights given to all elements). For our ensemble models we chose the decay of 1.6, as suggested in the BIOMOD operating manual (Thuiller et al. 2009). The probabilistic predictions of the ensemble models were converted into binary following the ROC-thresholding approach used in Elith et al. (2006) and discussed in Liu et al. (2005).

Finally, for indicative comparison purposes, we estimated the number of sampled presences and absences predicted in each class of the models. Predictions from non-combined and combined models for the sampled presences and absences were compared for each species. Here non-combined and combined predictions were reclassified to be comparable. To do so, we classified all the current predictions (non-combined models and combined models) for both species in three classes. For combined model predictions, we considered type A, types B and C pooled together into a single class (as they cannot be ranked), and type D. Non-combined model predictions were classified in three classes (class I, II and III) using ArcGIS (ESRI 2008), by identifying the natural breaks in their distributions.

Spatial projections under current and future climate conditions and land-use change scenarios

Spatially combined scenario projections were mapped over the full geographical extent of the study area, using the ArcGIS (ESRI 2008). For both combined and non-combined models, outcomes from climate and land-use change scenarios for the two species were derived by re-projecting models for 2020.

The foremost use of scenarios in this study was in illustrating the greater informative power of our combined modelling approach. We therefore chose a single, widely used, climate change scenario developed by the Hadley UK Centre for Climate Prediction and Research, for the year 2020. These were derived from a global circulation model (HadCM3; Carson 1999), and are based on the A2 socio-economic scenario of the IPCC (Intergovernmental Panel on Climate Change; Nakicenovic and Swart 2000).

Recent land-use dynamics were estimated based on regional rates of variation between 1990 and 2000 (based on national land cover maps: COS1990 and COS2000). For this period, the average trend shows an increase of artificial forest stands (pArtFor, +6.5%) and agricultural land-use (pAgric, +3.1%), and a decrease of semi-natural areas (pSemNat, -1.2%). The estimated regional rates were applied to 2020 based on the assumption that the obtained trends will keep relatively constant over the 20-year time frame of the study. These variation rates were applied to all environmental variables related to land-use selected in, at least, one model. Although explorations over

longer time scales would require more elaborated explorative land-use change scenarios (Rounsevell et al. 2006; Ficetola et al. 2010), it was beyond the scope of the present study to develop such input data.

Future species dynamics can be predicted from the spatial combination of current and future species distributions. Binary predictions from non combined-models can predict species dynamics of “no change”, “colonisation” or “extinction” (Fig. 3, left), while our combined modelling framework (CPM; Fig. 3, right) can provide additional predictions indicating a deterioration or improvement of conditions for the species at local and regional scale. These latter predictions have direct management implications as previously discussed.

Current and future distribution of rare-invasive conflict areas

The possible combinations resulting from the non-combined approach (Fig. 4, left) includes: areas of conflict (where both species are predicted to be present), areas where only one of the two species is predicted present (no conflict), and areas where both species are predicted absent (no conflict). The distribution maps derived from the combined modelling approach (Fig. 4, right) allow a refined detection of present and future conflict areas, as they are able to predict:

1. combinations of highest concern, where both species have suitable regional conditions and local habitat available (rare species type A/invaser A),

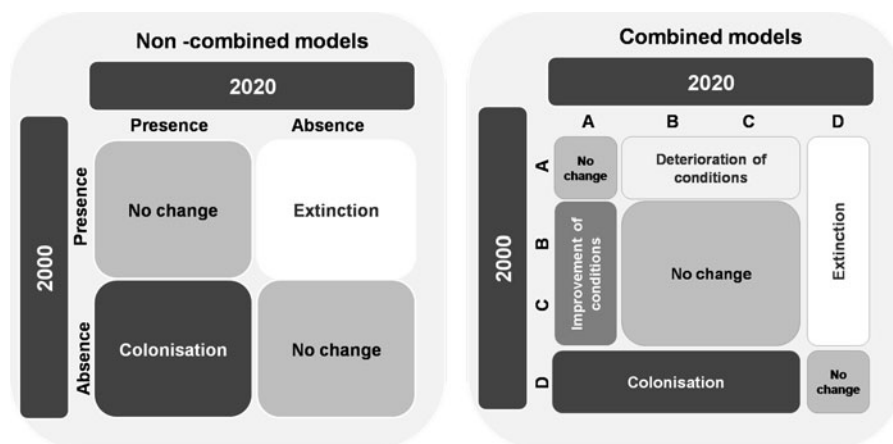
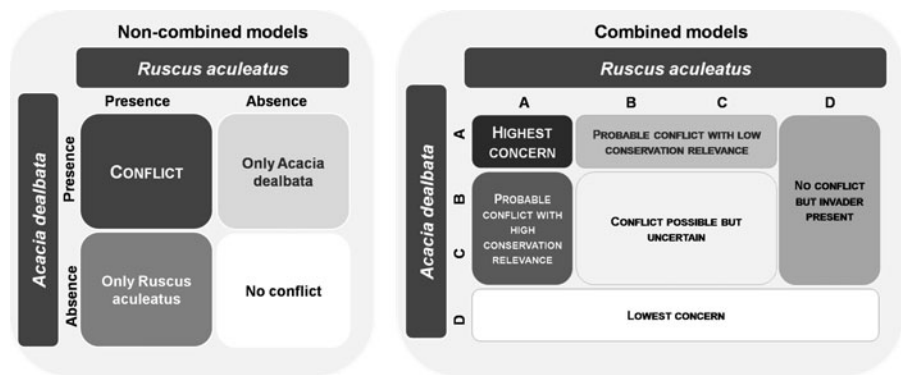


Fig. 3 Possible combinations for species distributions dynamics using non-combined (*left*) and combined (*right*) models

Fig. 4 Results of the possible conflicts combination between *Acacia dealbata* and *Ruscus aculeatus* using predicted distribution maps derived of non-combined (*left*) and combined (*right*) models



- probable conflict with high conservation relevance, where the rare species has suitable regional conditions and local habitat and the invader has only regional or habitat suitability (rare species type A/invader type B or C),
- probable conflict, with low conservation relevance, where the rare species only has regional or local habitat suitability and the invader species has both regional and local habitat suitable (rare species type B or C/invader type A),
- conflict possible but uncertain, where both of the species have only regional or local habitat suitability (rare species type B or C/invader type B or C),
- no conflict but invader present, where only the invader species is predicted to be present (rare species type D/invader type A, B or C), and
- areas of lowest concern, where the invader species is predicted to be absent.

Results

Predictor classification

The classification of the environmental predictors based on the Euclidean matrix of Geary's c autocorrelation measure, reveals a dichotomy (Fig. 5) between two distinct clusters discriminating locally structured predictors (those related to soils, land-use, and topography, left group), versus regionally structured predictors (those concerning climate, terrain morphology, and urbanization; right group). These results confirm the ecological classification based on theoretical and empirical knowledge (cf. Table 1).

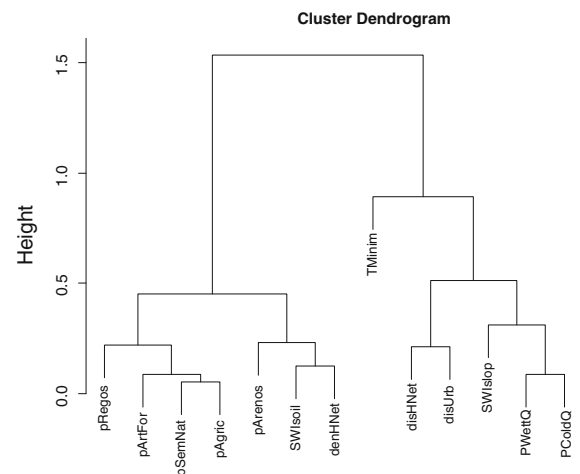
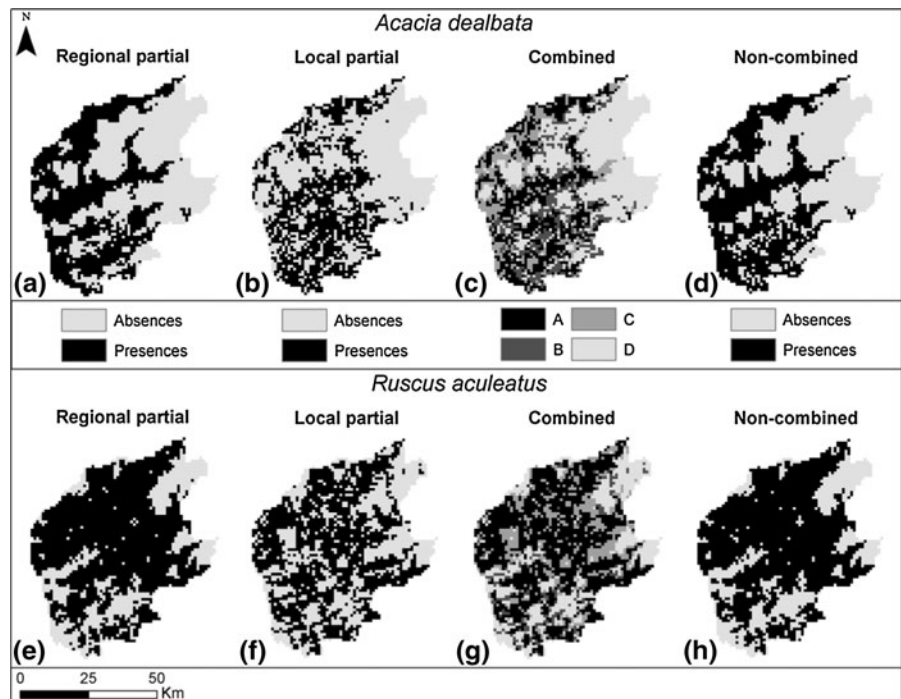


Fig. 5 Predictor classification tree based on the Euclidean matrix of Geary's c autocorrelation measure. The main dichotomy shows the two clusters representing locally structured predictors (*left-cluster* pRegos, pArtFor, pSemNat, pAgric, pArenos, SWIsol, denHNet) and regionally structured predictors (*right-cluster* disHNet, disUrb, SWIslop, PWettQ, PColdQ)

Combined models for *Acacia dealbata* and *Ruscus aculeatus*

The spatial pattern predicted by ensemble models for *Acacia dealbata* and *Ruscus aculeatus* by the non-combined models (potential presences and absences; Fig. 6 d and h) is very similar to the predicted areas resulting from the combined models (Fig. 6 c and g). However, combined models are more informative since they provide four response types (see Fig. 2; Types A, B, C, and D) instead of the traditional binary presence-absence predictions (for more details see "Annex 2"). For both species, predictions from the non-combined full models (Fig. 6 d and h) are more similar to those from the partial regional models

Fig. 6 Maps of spatial projections under current conditions from ensemble forecasting modelling for *Acacia dealbata*: (a) regional partial model, (b) local partial model, (c) combined model, (d) non-combined model, and for *Ruscus aculeatus*: (e) regional partial model, (f) local partial model, (g) combined model, (h) non-combined model (for more details see “Annex 2”)



(Fig. 6a, e), than to those from the local models (Fig. 6b, f; for more details see “Annex 2”).

For both species the predicted occurrences of the non-combined models (Fig. 6d, h) mostly match Type A in Fig. 2, where both regional conditions and local habitat are suitable (Table 2). However, there is a considerable overlap of the predicted occurrences (from the non-combined models) with the predicted Type C (combined models, Fig. 2), which corresponds with areas where regional conditions are suitable, but adequate local habitats are unavailable (Table 2). Also, most areas predicted as unsuitable by the non-combined models correspond

to Type D areas of the combined predictions, with a smaller area classified as Type B (i.e. where adequate local habitats are available, but regional conditions are unsuitable; Fig. 2).

Combined models (Types A, B + C and D) and non-combined models (classes I, II and III; see “Model fitting and evaluation” section) provided similar numbers of wrong predictions (Table 3). Both modelling frameworks performed worse with *Ruscus aculeatus* than with *Acacia dealbata* (Table 3), but overall the performance of combined models did not differ much from that of non-combined models.

Table 2 Percentage of areas predicted as presences and absences by the non-combined models and that correspond to each response type of the combined models

Predictions from non-combined models	Presence		Absence	
	Ad (n = 1,577) (%)	Ra (n = 2,302) (%)	Ad (n = 1,710) (%)	Ra (n = 985) (%)
Type A—regional and local suitability	59.1	71.7	0.3	1.4
Type B—only local suitability	10.1	1.3	14.6	16.6
Type C—only regional suitability	30.1	26.8	6.4	5
Type D—no suitability	0.7	0.2	78.8	77

Ad, *Acacia dealbata*; Ra, *Ruscus aculeatus* species; n, total presences or absences for both species predicted by the non-combined models

Table 3 Comparison of the sampled Presences (P) and Absences (A) with predictions from combined and non-combined models

Species	Models	Class I Type A		Class II Type B + C		Class III Type D	
		P	A	P	A	P	A
<i>Acacia dealbata</i> (38 P 52 A)	Non-combined	29	3	7	14	2	35
	Combined	26	3	9	11	3	38
<i>Ruscus aculeatus</i> (70 P 82 A)	Non-combined	61	4	3	5	6	73
	Combined	53	4	11	11	6	67

This comparison was performed by classifying all predictions into the three occurrence types (A, B + C and D) of combined models and the three probability classes (I, II, III) of non-combined models (see the “[Model fitting and evaluation](#)” section). False presences and absences predicted by models are presented in the table as bold style number

Range dynamics from climate and land-use changes

Predicted changes in potential habitat and range dynamics for *Acacia dealbata* and *Ruscus aculeatus* between 2000 and 2020, under climate and land-use change scenarios and with non-combined and combined predictions, are shown in Fig. 7 and summarized in Table 4. Areas without change are the predominant patterns predicted by both non-combined and combined models for both species (Fig. 7 and Table 4). However, the combined models also predict that, in some of these areas, the conditions for both studied species may deteriorate with climate and land-use change. Most areas predicted by the non-combined models to be newly colonised are forecasted as experiencing no change by the combined models, with a smaller predicted distribution proportion coincident with the colonisation predictions (Table 4). Only less than half of the areas where the species are predicted to suffer local extinction by the non-combined models are also predicted as areas suffering “extinction” or “deterioration of conditions” by the combined models (Table 4; for more details see “[Annex 3](#)”).

Conflicts

In the assessment of spatial conflicts between *Acacia dealbata* and *Ruscus aculeatus* for years 2000 and 2010, using non-combined (Fig. 8a and c) and combined (Fig. 8b and d) models, the most important contrasts are found when analysing areas predicted as of “conflict” by non-combined models (Fig. 8 and Table 5). For these areas, combined models in 2000 mostly predicted either “highest concern” or “probable conflict with high conservation relevance”; however, in 2020 they were predominantly predicted as of “conflict probable but

uncertain” even if the predicted areas of “highest concern” and “probable conflict” categories remain important (for more details see “[Annex 4](#)”).

Discussion

Model predictions and projections

Both ecological and biogeographical theories predict that species distributions are determined by processes acting at multiple spatial and temporal scales (Klijn and de Haes 1994, Pauchard and Shea 2006). Climate is known to determine species distributions at broader spatial scales (i.e. regional to continental; Thuiller et al. 2004), while land-use and soil properties are usually more determinant at local scales (Dirnböck et al. 2003). The multi-scale nature of species-environment relations has been explored using hierarchic frameworks (e.g. Pearson et al. 2004), which have provided consistent predictions based on robust modelling procedures. Our results are in agreement with the hierarchical study of Bradley (2010), showing that climate and land use change impacts on invasive species operate at different scales and are both likely to increase in importance in the future.

Here we developed a classification scheme for environmental predictors that discriminates regional vs. local variables according to the scales at which they are expected to influence species distributions. This classification was based on a conceptual framework supported by concepts from landscape ecology, community ecology, phytosociology, and biogeography, and was confirmed by the statistical procedure based on spatial autocorrelation (Cliff and Ord 1981; Borcard et al. 2004), which discriminates predictors according to their spatial scale of variation. By doing

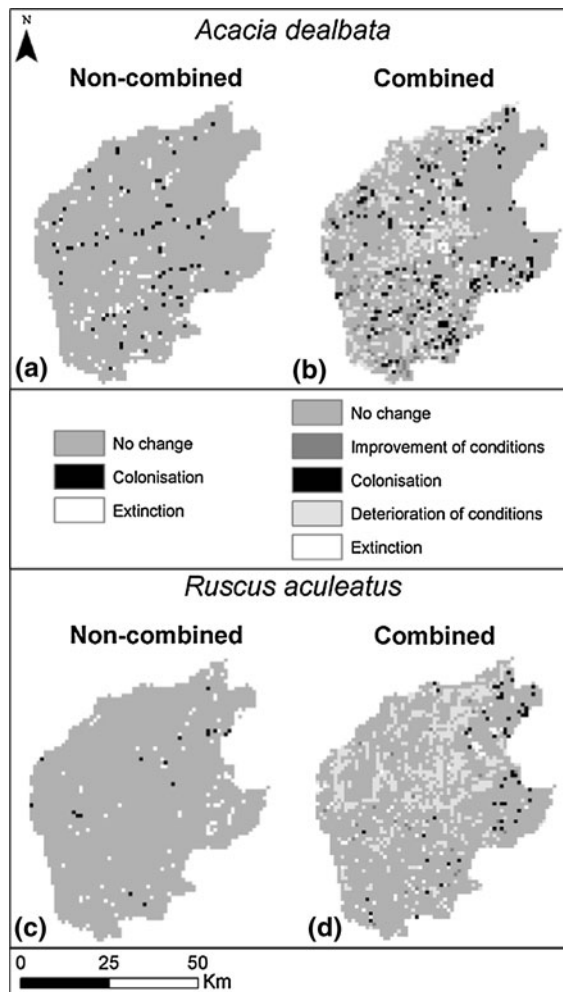


Fig. 7 Change in the potential distribution of *Acacia dealbata* and *Ruscus aculeatus* for non-combined (a, c) and combined (b, d) models between 2000 and 2020 (for more details see “Annex 3”)

Table 4 Percentage of no change, colonisation, and extinction areas predicted by the non-combined models for the 2000–2020 dynamics for each species that correspond to each

	No change		Colonisation		Extinction	
	Ad (n = 3,081)	Ra (n = 3,188)	Ad (n = 130)	Ra (n = 82)	Ad (n = 76)	Ra (n = 17)
No change	74.4	78.0	61.5	57.3	59.2	52.9
Colonisation	4.7	0.8	26.2	34.1	1.3	5.9
Extinction	3.5	1.6	2.3	0.0	21.1	35.3
Improvement of conditions	3.4	0.7	9.2	3.7	0.0	0.0
Deterioration of conditions	14.1	18.8	0.8	4.9	18.4	5.9

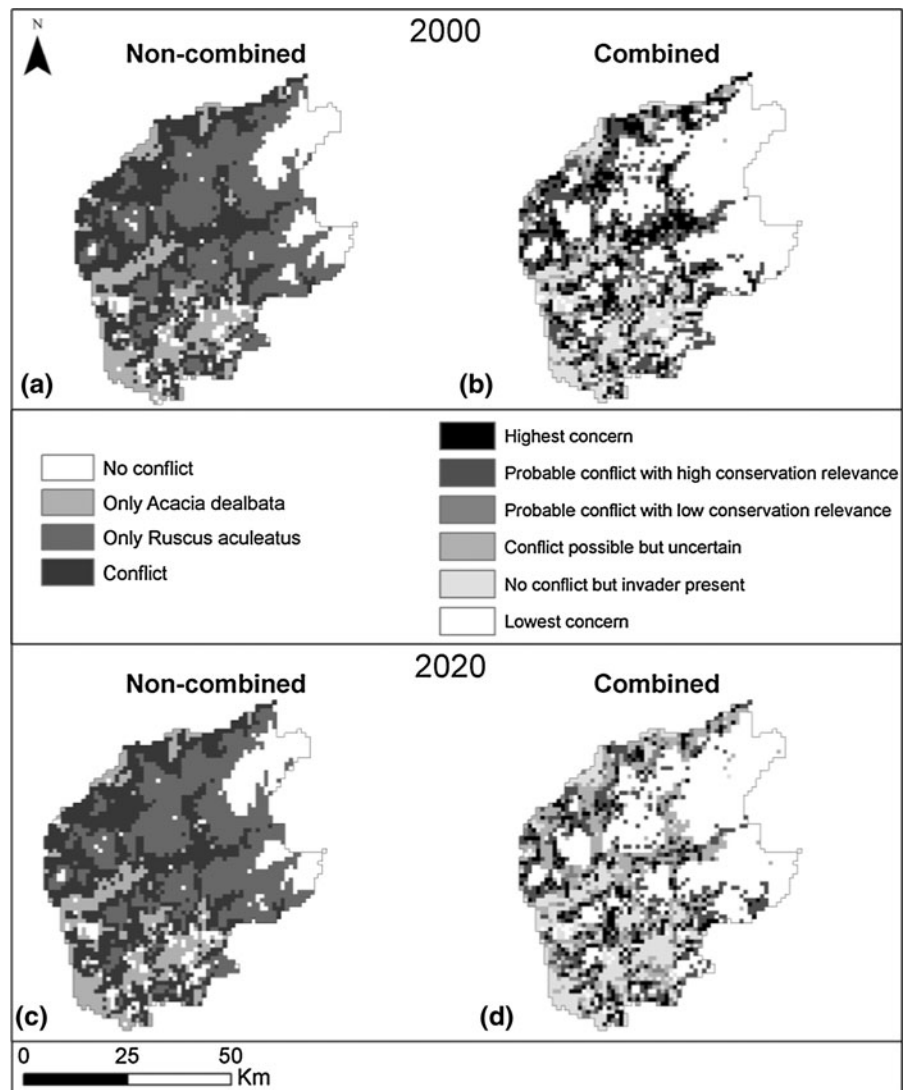
Ad corresponds to *Acacia dealbata* and Ra to *Ruscus aculeatus* species; n represents the total area of each dynamic type of the non-combined models for both species)

so, we gain more detailed insights on species-environment relations, identifying the most important processes operating at each scale and potentially yielding more informative predictions of species distributions and predicting variables.

By providing four possible combinations for environmental suitability (cf. Fig. 2) combined predictive models provides more informative projections of species distributions than traditional binomial outputs of SDMs. For instance, types B (local habitats available but regional conditions unsuitable) and C (regional conditions suitable but local habitats not available) provide extra information on the nature of the factors constraining species occurrence in areas where the species may (or may not) be present. For our test species *Acacia dealbata* and *Ruscus aculeatus* we found that they are both mostly determined by regional variables, as most presences from the non-combined models are predicted in Types A and C (regional conditions suitable), and absences from the non-combined models are mostly predicted in Types B and D (regional conditions unsuitable). This is consistent with previous empirical data that both species are able to colonize several types of woodland and scrubland habitats and that their distribution in the study area is strongly determined by climate at the regional scale. However, this will not be the case for all species, since many are constrained by the local availability of specific habitats within a wide range of climatic conditions (e.g. Pearson et al. 2004; Gelfand et al. 2005; Pauchard and Shea 2006). Even for our two regionally constrained test species, the presence of suitable local habitats (i.e. forest patches) may allow their expansion to climatically unsuitable

response type of the combined models (no change, colonisation, extinction, improvement of conditions and deterioration of conditions)

Fig. 8 Possible conflict areas between *Acacia dealbata* and *Ruscus aculeatus* and combined models. Panels *a* and *c* corresponds to potential areas under current and future conditions (2020) respectively using non-combined models and panels *b* and *d* corresponds to potential conflicts obtained using the combined models (for more details see “Annex 4”)



areas, since forest species benefit from microclimatic conditions.

Although finer predictions of distribution and conflict areas could also be obtained with traditional SDM outputs, for instance by considering more than two classes (i.e. presence-absence) of predictions and combining these, this would not allow additional consideration of scale influences, as allowed by our combined framework. This is relevant since local versus regional effects on species distribution can prove a determinant factor in many conservation and management issues (Pauchard and Shea 2006).

Combined models can also provide more informative forecasts of future dynamics of species distributions,

since they provide more detailed species responses to climate and land-use changes. Besides the three types of predictions provided by traditional models (colonization, extinction, no change; Guisan and Thuiller 2005; Thuiller et al. 2008) combined models provide forecasts of intermediate dynamics between colonisation and extinction, through the recognition of areas where environmental changes may occur, but the occurrence status of the species may not be affected (cf. Fig. 3). For our studied species, areas without change were the predominant patterns predicted by non-combined models (cf. Fig. 7 and Table 4). Combined models predict that in some of these areas the conditions may deteriorate for both species with climate and land-use

Table 5 Comparison of predictions by the combined and non-combined models

	No conflict		Only Ad		Only Ra		Conflict	
	2000 (n = 497)	2020 (n = 451)	2000 (n = 488)	2020 (n = 469)	2000 (n = 1,213)	2020 (n = 1,205)	2000 (n = 1,089)	2020 (n = 1,162)
Highest concern	0.0	0.0	2.3	0.9	0.1	0.0	45.3	26.8
Probable conflict with high conservation relevance	0.0	0.0	0.4	0.4	19.5	12.9	31.1	26.9
Probable conflict with low conservation relevance	0.0	0.2	16.4	10.0	0.0	0.1	13.1	9.6
Conflict possible but uncertain	3.8	4.2	10.2	11.3	4.0	9.8	9.7	35.6
No conflict but invader present	11.5	15.7	70.1	76.1	0.0	0.0	0.1	0.4
Lowest concern	84.7	79.8	0.6	1.3	76.3	77.3	0.6	0.6

Ad, *Acacia dealbata*; Ra, *Ruscus aculeatus*; n, total area of each conflict combination of the non-combined models for both the 2000 and 2020 years

changes. This means that some aspects of range dynamics may be expected to occur in the future in areas where non-combined models predict that no changes would occur. When compared to traditional models, combined models thus provide refined insights on species dynamics as a response to changes in climate and land-use, particularly outside areas where extinction or colonisation are most likely to occur. On the other hand, most areas predicted by the non-combined models to be newly colonised or to suffer extinction are forecasted as suffering no change (or only changes in conditions) by the combined models, which thus seem to provide more conservative predictions of range dynamics than those from traditional, non-combined approaches.

By allowing more informative predictions of species distributions and range dynamics, we illustrate that combined models can provide refined results for the study of conflicts between rare and invasive species, a major goal in conservation biology and in the study of invasions (Settle and Shogren 2002). Since conflict maps result from the spatial overlap of the combined models for the two potentially conflicting species, the results are more detailed than the ones obtained from non-combined models (cf. Fig. 4). This was the case when analysing conflicts between *Acacia dealbata* and *Ruscus aculeatus*, particularly for those areas predicted as of “conflict” by non-combined models (cf. Fig. 8 and Table 5).

Predictions by these combined models are not only more informative in terms of conflict types but also in terms of the spatiotemporal dynamics of the modelled species’ ranges and of their spatial conflicts. In fact, a striking result is that areas with conflict of highest concern or with high conservation relevance are predicted to decrease over the next decade (cf. Fig. 8 and Table 5). This result is a nice illustration of how our approach can provide better conservation strategies for mitigating the impact of invasive plants, land-use and climate changes in sensitive regions. Previous studies have already shown that invasive species may contract their geographic range due to climate change (Broennimann and Guisan 2008; Mika et al. 2008; Bradley 2009; Bradley et al. 2009). In this context, the change in geographic distribution of our two model species could generate opportunities for conservation and ecosystem restoration. As a cautionary note however, the results presented here—based on a single climate change scenario, on a single simplistic land-use change scenario and for only one rare and one invasive species—, were only designed to present the novel approach. As such, they should not be used for assessing and mitigating directly future dynamics of potential rare-invasive conflict areas. For actually supporting conservation and management actions, the outcomes of a wider range of climate change scenarios (Hijmans et al. 2005) and of a wider set of land-use change scenarios (cf Rounsevell et al. 2006)

should be considered and compared over a much larger number of rare and invasive species.

Implications of the novel combined approach for nature conservation

Predictive models have been used in a wide array of applications directed at evaluating and planning the conservation of valuable elements of biodiversity and ecosystems (Pearce and Ferrier 2001; Muñoz et al. 2005; Gray et al. 2008), as well as for forecasting their responses to environmental changes (Guisan and Theurillat 2000; Araújo et al. 2005; Broennimann et al. 2006). The more informative character of the combined models compared to the non-combined, traditional models, can make them particularly valuable for multiple applications in fields related to conservation, management and monitoring.

Combined models should prove particularly valuable for conservation planning targeted at rare species. For such conservation projects it is essential to know if the current distribution of the species is more determined by drivers operating at local or regional scales. Furthermore, it is important to know the specific local factors that are most constraining for a given species, since it is possible to act upon their condition and influence their future trends. For example, land-use and landscape structure can be planned according to conservation needs, particularly in nature reserves, where human activities are expected to accommodate biodiversity and the conservation of threatened species (Araújo et al. 2002, 2004). By contrast, if regional factors such as annual mean temperature determine the distribution, local conservation effort will have limited effect. Identifying local versus regional factors can of course also be done in a non-combined framework, based on reasoning or further analyses (e.g. post-modelling spatial autocorrelation assessment), but at the cost of losing the formalism and automation associated with the combined procedure, two important criteria for managers.

The more detailed predictions provided by combined models may also prove to be important for the study of meta-population dynamics e.g. in the identification of source and sink populations (Muñoz 2005; Titeux et al. 2007), with sink populations corresponding to those inhabiting areas where regional or local

conditions are unsuitable (or may become so in the near future). Also, the more detailed predictions may support reliable forecasts of whether species of conservation priority may be driven out of nature reserves by environmental changes (Araújo et al. 2004).

The more informative character of the combined approach is also potentially valuable to predict where biological invasions will tend to occur along a given time frame (Vicente et al. 2010). Predictions for current distribution allow the identification of areas where the invader may be more problematic i.e. areas where the more suitable conditions make landscapes more prone to invasion (i.e. increased invasibility; Thuiller et al. 2005). Our combined models also identify non-invaded areas where the invasive species has suitable regional conditions, which may become invaded if landscape management creates suitable local conditions for the species and there are no significant dispersal constraints. Overall, this added information provided by combined models has obvious implications for land management aimed at preventing and controlling biological invasions, a widespread phenomenon included among the most threatening for native biodiversity and ecosystems (Broennimann and Guisan 2008).

Conflict maps obtained with the combined models are valuable for multiple applications, since they allow the discrimination of an “invasion concern gradient” related to the potential conflict between alien invaders and valuable elements of native biodiversity. This way, a prioritization of the areas in need of action can be based on the highest concern classes related to potential spatial conflicts (cf. Fig. 8). This is most important when facing financial resource limitations for land management and invasion control (Perrings et al. 2002; Culliney 2005). Also, conflict maps (both current and future) can support the development of optimized monitoring networks targeted at the impacts of specific drivers (e.g. alien invasion) on the condition and trends of valuable elements of native biodiversity (e.g. rare species). By targeting monitoring efforts for areas where highest concern conflicts are expected to be occurring (or to occur in the near future), early signals of impacts may be detected and the cost-effectiveness of the monitoring programs will thus be improved (Nehrbass et al. 2006; Ficetola et al. 2007).

Limitations and further prospects

Interactions among variables have been a major topic of discussion in ecological modelling (e.g. Austin 2007; Dormann et al. 2007), but they are difficult to implement in the current combined modelling framework. Even if adding interactions in models can make their transferability more difficult due to the local character of many interactions (Randin et al. 2009a), this is an issue demanding further work in order to allow the explicit consideration of their possible synergistic or antagonist effects on species distributions and dynamics.

Another issue for future development of the combined modelling framework is performance evaluation and comparison with other modelling techniques, since the final projections result from the spatial combination of two partial models and because occurrence types B and C cannot be ranked. The direct use of probabilistic projections from partial models may provide future developments in this issue and increase the comparability between combined models and those fitted through standard, non-combined approaches.

Conclusion

Using a combined modelling approach for identifying areas of potential conflicts between invasive and rare species provides:

1. More informative projections from species distributions models based on the combinations of regional and local predictors;

2. Better information about the relative importance of local (e.g. land-use) and regional (e.g. climate) drivers of species distributions and dynamics;
3. More informative insights regarding rare-invasive conflict areas, under current conditions and under future climate and land-use change scenarios; and
4. From a more applied perspective, more informative outcomes to support practical issues in conservation, restoration and monitoring.

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Annexes

Annex 1

Environmental predictors used in the combined and non-combined models with indication of the original dataset, information format, data source characteristics and corresponding species models fitted.

Predictors	Models	Dataset	Information format	Characteristics and data source
TMinim	Ad, Ra	Climate	Raster (pixel 1 km ²)	Bioclimatic indices related to temperature and precipitation regimes (http://www.worldclim.com)
PWettQ	Ra	Networks	Vectorial (polygons)	Road network
PColdQ	Ad			Hydrographical network (http://www.projectosign.org/ , by courtesy of J. Alonso)
disUrb	Ra			
disHNet	Ad			

Predictors	Models	Dataset	Information format	Characteristics and data source
denHNet	Ra	SRTM	Raster (pixel 100 m ²)	Shuttle Radar Topography Mission Digital Elevation Model (http://srtm.usgs.gov/index)
SWIslop	Ad, Ra			
pRegos	Ra	Soil map	Vectorial (polygons)	Multi-criteria classification of soils and lithology (bedrock) (http://www.projectosign.org/ , by courtesy of J. Alonso)
pArenos	Ad	Land cover map	Vectorial (polygons)	Soil occupation categories by aerial photography interpretation (2000) (http://www.projectosign.org/ , by courtesy of J. Alonso)
SWIsoil	Ad			
PArtFor	Ad, Ra			
pSemNat	Ra			
pAgric	Ad			

Annex 2

Numerical results of the non-combined, partial and combined models. For non-combined and partial models are represented in the table the potential presences and absences predicted (km²). For the combined models are represented the four response types results: Type A corresponds to areas where both regional and local

partial models predicts presences; B type show areas where only local partial models predict presences and where regional partial models predicts absences; C type correspond to areas where partial regional model predicts presences and local partial model predicts absences; and finally D type corresponds to areas where both regional and local partial models predicts absences, every results are expressed in km².

Species	Models	Presences	Absences	Type A	Type B	Type C	Type D
<i>Acacia dealbata</i>	Non-combined	1,577	1,710	937	408	584	1,358
	Regional partial	1,521	1,766				
	Local partial	1,345	1,942				
	Combined						
<i>Ruscus aculeatus</i>	Non-combined	2,302	985	1,664	194	667	762
	Regional partial	2,331	956				
	Local partial	1,858	1,429				
	Non-combined						

Annex 3

Numerical results of the range dynamics for *Acacia dealbata* and *Ruscus aculeatus*, for the period 2000–2020 years. The range dynamics resulting from the non-combined models only have three possible combinations, no-change, colonisation and extinction. The range dynamics of the combined ensemble models, resulting of the spatial combination of the combined models with four occurrence types (A,B,C,D) can predict 2 more dynamic types than non-combined predicted range: better conditions and worse conditions (beyond: no change, colonisation, and extinction). All the results represented in km².

Species	Models	No change	Extinction	Colonisation	Deterioration of conditions	Improvement of conditions
<i>Acacia dealbata</i>	Non-combined	3,081	76	130		
	Combined	2,416	126	180	448	117
<i>Ruscus aculeatus</i>	Non-combined	3,188	17	82		
	Combined	2,544	57	56	605	25

Annex 4

Tables showing the numerical results of the conflict areas between *Acacia dealbata* and *Ruscus aculeatus*, for years 2000 and 2020. Using non-combined models to estimate potential conflict areas it's possible to predict areas of: no conflict (where none species are present), only *Acacia dealbata* potentially present (only the invader present), only *Ruscus aculeatus* present (only the rare species present), and finally, conflict areas (where both invader and rare species are potentially present). Using combined models to obtain the conflict maps it's possible to obtain a prioritization of the areas concerning the concern that they represent. All the results are presented in km².

	No conflict	Only <i>Acacia dealbata</i>	Only <i>Ruscus aculeatus</i>	Conflict
Non-combined models				
2000	497	488	1,213	1,089
2020	451	469	1,205	1,162
Combined models				
	Probable conflict with high conservation relevance	Probable conflict with low conservation relevance	Conflict possible but uncertain	No conflict but invader present
2000	578	223	224	400
2020	470	161	604	433
	Highest concern			Lowest concern
2000	504			1,358
2020	315			1,304

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