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MODEL-ASSISTED MONITORING OF BIODIVERSITY

Cost-effective monitoring of biological invasions under global change: a model-based framework

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Summary

- 1. Ecological monitoring programmes are designed to detect and measure changes in biodiversity and ecosystems. In the case of biological invasions, they can contribute to anticipating risks and adaptively managing invaders. However, monitoring is often expensive because large amounts of data might be needed to draw inferences. Thus, careful planning is required to ensure that monitoring goals are realistically achieved.
- 2. Species distribution models (SDMs) can provide estimates of suitable areas to invasion. Predictions from these models can be applied as inputs in optimization strategies seeking to identify the optimal extent of the networks of areas required for monitoring risk of invasion under current and future environmental conditions. A hierarchical framework is proposed herein that combines SDMs, scenario analysis and cost analyses to improve invasion assessments at regional and local scales. We illustrate the framework with *Acacia dealbata* Link. (Silver-wattle) in northern Portugal. The framework is general and applicable to any species.
- 3. We defined two types of monitoring networks focusing either on the regional-scale management of an invasion, or management focus within and around protected areas. For each one of these two schemes, we designed a hierarchical framework of spatial prioritization using different information layers (e.g. SDMs, habitat connectivity, protected areas). We compared the performance of each monitoring scheme against 100 randomly generated models.
- **4.** In our case study, we found that protected areas will be increasingly exposed to invasion by *A. dealbata* due to climate change. Moreover, connectivity between suitable areas for *A. dealbata* is predicted to increase. Monitoring networks that we identify were more effective in detecting new invasions and less costly to management than randomly generated models. The most cost-efficient monitoring schemes require 18% less effort than the average networks across all of the 100 tested options.

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5. Synthesis and applications. The proposed framework achieves cost-effective monitoring networks, enabling the interactive exploration of different solutions and the combination of quantitative information on network performance with orientations that are rarely incorporated in a decision support system. The framework brings invasion monitoring closer to European legislation and management needs while ensuring adaptability under rapid climate and environmental change.

Key-words: Acacia dealbata, climate change, connectivity, monitoring networks, northern Portugal, optimization, risk management, scale dependence, species distribution models, surveillance effort

Introduction

Alien plant invasions can threaten biodiversity (Pyšek et al. 2008; Pejchar & Mooney 2009) and impose severe impacts on social and economic dimensions of human well-being (Simberloff et al. 2013; Shackleton et al. 2014). The globalization of trade has accelerated the establishment and expansion of numerous invasive species (Meyerson & Mooney 2007; Rejmánek & Richardson 2013; Humair et al. 2015), including woody plant species that rank among the most problematic invasive species world-wide (Pyšek et al. 2008; Richardson & Rejmánek 2011). Invasive woody plant species have great potential to transform landscapes, potentially leading to losses in revenue from production ecosystems and losses in the production of ecosystem goods and services (García-Llorente et al. 2011).

It is widely recognized that eradication and containment of Invasive woody plant species is both difficult and costly. Therefore invasive woody plant species prevention, early detection, and containment (Meyerson & Mooney 2007) should be based on time- and cost-effective actions (Chornesky *et al.* 2005; Genovesi & Monaco 2013). This includes cost-effective monitoring of the expansion and impacts of invasive woody plant species (Pejchar & Mooney 2009; Simberloff *et al.* 2013) even though explicit legal regulations or obligations for monitoring or reporting on alien plants are almost non-existent (Chornesky *et al.* 2005).

Ecological monitoring programmes aim to assess changes in biodiversity and ecosystem properties. For example, they can be implemented to anticipate invasions and identify areas with a high risk of invasion, thus enabling the adaptive management of ecosystems (Nichols & Williams 2006). In times of great changes in both land use and climate, monitoring schemes can be useful to anticipate and assess ongoing shifts in environmental and social–ecological systems (Vicente *et al.* 2013a), and evaluating the effectiveness of policy and funding instruments targeting invasive woody plant species (Rannow *et al.* 2014).

Monitoring programmes can be set up at different spatial scales (e.g. Cacho & Hester 2011; Epanchin-Niell *et al.* 2014). In Europe, the Natura 2000 network of protected areas represents an opportunity for testing and implementing adaptive management of invasive woody plant species

at regional scales since many LIFE EU funded projects have been undertaken in those areas (EEA 2012). Moreover, the new European Union (EU) regulation for prevention and management of invasive alien species has entered into force on the 1st of January 2015 representing a milestone in the conservation of European biodiversity (European Parliament and Council of the European Union 2014). The core of the EU invasive alien species regulation is the list of invasive alien species of 'European Union concern'. The list contains 37 species, and monitoring networks will have to be set up for these species by mid-2017. Member states are expected to ensure coordination and cooperation of invasive species management by establishing a European monitoring system that is implemented and harmonized across countries. Cost-effective monitoring programmes should allow the early identification of changes in invasive woody plant species' distributions. Simultaneously, they should allow costs to be minimized while ensuring that the monitoring goals are realistically achieved (Hui et al. 2011; Vicente et al. 2013b).

We propose integrating species distribution models (SDMs), scenario analysis and estimates of surveillance effort hierarchically, to improve assessment of woody plant species invasions at regional and local scales. Specifically, the framework seeks to identify the network of areas that should be focus of monitoring efforts such that the geographical coverage of the areas and their surveillance costs are minimized, while maximizing inference ability of species' invasions. We illustrate the framework using Acacia dealbata Link. (Silver-wattle; Fabaceae) in the North of Portugal. The species is considered one of the top 100 most invasive species in Europe (http:// www.europe-aliens.org/speciesTheWorst.do) and especially problematic in south-western Europe (Lorenzo, González & Reigosa 2010). Over the last decades, the species has expanded throughout Portugal and the projections under future climate and land-use change scenarios indicate further expansions (Vicente et al. 2011, 2013b). The implementation of the proposed framework aims at identifying the current and future areas where the species is predicted to occur and to prioritize the areas where monitoring networks will be most effective in capturing the state and trends of the species. The framework is developed using a

multifactorial hierarchical decision scheme, based on inputs from SDMs and prioritization of conservation areas, thereby allowing a better integration of the needs of invasion monitoring, policy and management, as well as ensuring cost-effectiveness and adaptability in the face of rapid environmental change.

Materials and methods

ENVIRONMENTAL PREDICTORS AND PREDICTOR CLASSIFICATION

Based on a literature review and expert knowledge, we selected 45 environmental predictors potentially determining the ecology and distribution of the target species (Table S1, Supporting Information). To handle multicollinearity, Spearman's rho correlation tests between variables and generalized variance inflation factors (VIF) were used. For cases in which pairwise correlation coefficients were < 0.7 (Broenniman & Guisan 2008) and VIF < 5 (Gallien et al. 2012), we considered the predictors expected to more directly determine the ecological distribution of the species (Hulme 2006). This approach yielded a final set of 24 environmental predictors. These predictors were classified into eight categories: (i) climate, (ii) dispersal corridors, (iii) geology, (iv) landscape composition, (v) landscape structure, (vi) fire regimes, (vii) phenology metrics and (viii) productivity metrics (Table 1). The climatic predictors were obtained from WORLDCLIM (Hijmans et al. 2005; http://worldclim.org/download). The baseline climate data was based on interpolations of observed data from 1950-2000. Future climates were based on projections from one global climate model (GCM) and two socio-economic scenarios: HadCM3 A1B (temperature rise between 1.4 and 6.4 °C) and B2 (temperature rise between 1.4 and 3.8 °C). The A1B scenario assumes economic growth in a homogenous world (globalization), while the B2 scenario assumes a more sustainable view in a heterogeneous world (regionalization; Nakicenovic & Swart, 2000).

The predictors related to ecosystem phenology and primary productivity were computed from Normalized Difference Vegetation Index (NDVI; O'Donnell et al. 2012) time series, derived from the MODIS satellite sensor. The phenological indices were extracted from time-series envelope fitted using double-logistic functions in TIMESAT software (as described in Pauchard & Shea 2006; Appendix S2). All other predictors were obtained from thematic environmental maps (Table S1).

Based on the spatial autocorrelation structure of each predictor, we classified them into two groups: those varying locally and those varying regionally. Two indices of spatial autocorrelation (Moran's I and Geary C; Seipel et al. 2012) were used with increasing neighbourhood distances (Vicente et al. 2014), and the SPDEP R package (https://cran.r-project.org/web/packages/spdep/). Then, to express the likelihood of each predictor belongs to each class (local vs. regional), a classification based on fuzzy clustering (with function fanny from R software CLUSTER package; https:// cran.r-project.org/web/packages/cluster) was performed. With this process, each one of the 24 predictors was consistently classified (Table S2) as having local or regional patterns of variation (Vicente et al. 2011, 2014; Table 1).

ANALYTICAL FRAMEWORK

Step 1 – Conservation value in protected areas map

In a first step, areas of high conservation value were mapped based on the two conservation areas networks in the region: the

Table 1. Predictors used for model calibration with description, corresponding type of environmental factor and spatial scale of variation/influence

Predictors	Description	Environmental factor	Classification (scale)	
MTCM	Minimum temperature coldest month	Climate	Regional	
TAR	Temperature annual range			
PWM	Precipitation wettest month			
PS	Precipitation seasonality			
DensRiN	Density local hydrographic network	Dispersal corridors	Local	
DensRoN	Density local road network	Î		
pCambi	Percentage cambisols	Geology		
pGran	Percentage granites			
pAnnC	Percentage cover annual crops	Landscape composition		
pBlFor	Percentage cover broad-leaf forests	• •		
pCoFor	Percentage cover artificial stands			
pMixFor	Percentage cover mix forests			
pPioMo	Percentage cover pioneer mosaics			
pUrb	Percentage cover urban areas			
MPAR	Mean perimeter-area ratio	Landscape structure		
MSI	Mean shape index	•		
NumFir	Number fires	Fire regimes		
SOS	Time of the start of growing season (GS)	Phenological metrics		
MOS	Time of the mid of GS	-		
EOS	Time of the end of GS			
LOS	Length of GS			
INT	Normalized Difference Vegetation Index (NDVI) integral during GS	Productivity metrics		
AMP	Amplitude of NDVI values during GS			
MAX	Maximum NDVI during GS			

European Natura 2000 Network and the National Protected Areas Network. Conservation status (the level of protection for nature conservation purposes) was used as a proxy of conservation value. Each map was classified into four classes, from 1 (no conservation status) to 4 (highest conservation status). For the nationally protected areas available in the region (one national park and three natural parks), conservation status was extracted from the corresponding management plans by the National Agency for Nature Conservation and Forestry (ranging from 1 no protection to 4 – maximum protection). For the Natura 2000 network, we used the following scores: 1 – no protection, 2 – special protection area (SPA; EU Birds Directive), 3 - special area of conservation (SAC: EU Habitats Directive) and 4 - simultaneously SPA and SAC. For each cell, the conservation status was computed from the percentage of the cell occupied by each class (weighted mean) (e.g. Alagador et al. 2011). Finally, the two maps were combined to obtain a conservation value area map.

Step 2 - species distribution modelling

Species distribution models are increasingly used to test the importance of key environmental drivers of invasive woody plant species distributions (e.g. Guisan & Thuiller 2005; Vicente et al., 2010) and to predict areas of potential invasive woody plant species distributions under current conditions and future environmental change scenarios (e.g. Peterson et al. 2008; Vicente et al. 2011). Accordingly, SDMs are particularly useful to support management decisions in preventing expansions of invasive woody plant species (Araújo & Peterson 2012; Vicente et al. 2013a,b). We applied the combined predictive modelling framework developed by Vicente et al. (2011) to predict current and future distributions of A. dealbata, using 277 presence-absence records (163 presences and 114 true absences at 1 km² resolution; for more information see Appendix S1). Separate models were fitted using either 'regional' or 'local' predictors at 1 km² resolution (for more details see Environmental Predictors and Predictor Classification). The final model was obtained by spatially aggregating the binary projections from the two partial models: The combinations of predicted presence and absence (both for regional and local model outputs) were classified as one of four types: suitable regional conditions and local habitat (A), only suitable local habitat (B), only suitable regional conditions (C) and unsuitable regional conditions and local habitat (D) (for more details about model evaluation and presence-absence reclassification, see Appendix S1). BIOMOD (Thuiller et al. 2009) was applied to fit an ensemble of models (Araújo & New 2007) using the nine available modelling techniques in the R BIOMOD package (for more information, see Appendix S1).

Combined predictions of species distributions were mapped over the full geographical extent of the study area. To produce projections of species distribution into the future, regional climate variables obtained from climate change scenarios were used and utilized with the same modelling procedures used. Local variables (e.g. fire regime related, NDVI, phenology) were not available for future scenarios due to the complex mechanisms, drivers and predictors behind these processes, therefore we considered them static through time. Finally, expected changes in the distribution of the target species due to climate change were determined in each cell, based on differences between current and future species distributions: no change, colonization, extinction, deterioration or improvement of conditions for the species (Vicente *et al.* 2011).

Step 3 – current and future potential invader impact on conservation value areas map

To identify spatial conflicts between conservation value areas and invasion, we overlaid predictions and projections derived from combined SDMs with the conservation value map, which allow a refined detection of present and future conflict areas (see Fig. 1).

We created spatial projections of current and future impacts of the distribution of the invasive species, A. dealbata over the conservation value in the study area. For this purpose, we used the conservation value maps from Step 1 and species distribution predictions from Step 2 (Vicente et al. 2011, 2013b). The ranking of conservation impacts was obtained from mean summing scores considering the consistency of predicted species' presences and absences from different models (from Step 2, types A, B, C or D) and their overlapping with areas of high conservation value (from Step 1: high, medium, low, or no value). The process resulted in six categories: (a) highest concern – where the species has suitable regional conditions, local habitats are available (type A), and the conservation value is high or medium; (b) probable impacts with low conservation relevance - where the species has suitable regional conditions, local habitats are available (type A), but the value of conservation areas is low; (c) possible but uncertain impacts with conservation relevance - where the species has only suitable regional conditions or local habitats available (types B or C), and the value of conservation areas is high or medium; (d) possible but uncertain impacts with low conservation relevance - where the species has only suitable regional conditions or local habitats available (types B or C), and the value of conservation areas is low; (e) lowest concern - where the species is predicted to be absent (type D); and (f) without impacts - the area has no conservation value even if the species is predicted to be present (types A, B or C).

Step 4 – connectivity maps

The connectivity of predicted suitable areas for *A. dealbata* was calculated using the connectivity index developed by Randin *et al.* (2009), based on current and future climate species distribution projections derived in Step 2. We considered values of species presence with: (i) suitability of one for the response type A; (ii) suitability of 0·5 for response types B and C; and (iii) suitability of zero for response type D. The connectivity index attains a maximum value of 1 when all cells surrounding a focal suitable cell belong to class A.

Step 5 – definition of monitoring objectives

Monitoring networks were identified through hierarchical assessments in the previous steps coupled with area network selection. Area network selection was performed using a nested design. At any hierarchical stage sampling was done from a pool of areas selected to be part of the network in the precedent stage. We defined two types of networks based on different priorities: (i) one that prioritizes monitoring of invasive species in currently established in European Natura 2000 Network and the National Protected Areas Network (protected area networks, PAN) and (ii) one that prioritizes monitoring of invasive species at the regional scale including the north of Portugal (Regional Networks, RN).

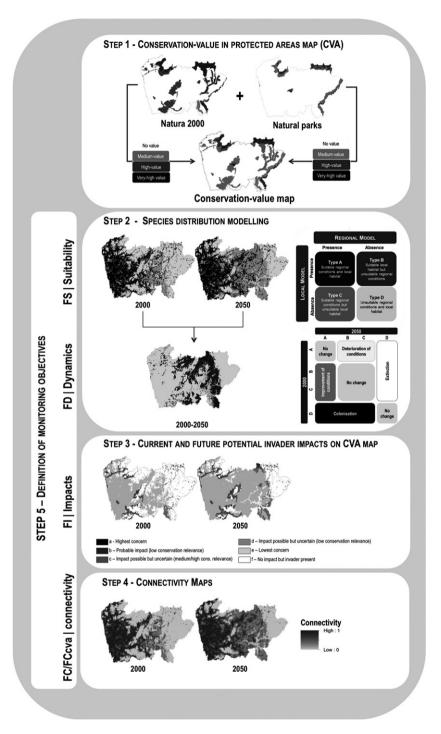


Fig. 1. Framework for identification of optimal monitoring networks. Step 1: mapping areas of high conservation value; Step 2: Modelling distribution of Acacia dealbata, for current and future scenarios using a combined modelling approach resulting in four predicted responses: (A) suitable regional conditions and local habitat, (B) only suitable local habitat, (C) only suitable regional conditions and (D) unsuitable regional conditions and local habitat. Step 3: Depending on local conservation values and species responses, a potential invader impact map is developed matching Step 1 and Step 2. Step 4: Assessment of connectivity of suitable environments for A. dealbata both in current and future times; Step 5: A hierarchical scheme to target monitoring networks for A. dealbata (FS - Predictions of species occurrence based on regional and local-scale environmental suitability; FI - Impacts of environmental suitability over protection/conservation value of areas, FD - Predicted changes in suitability conditions from current to future time 2050, FC - Regional-scale environmental suitability defined in terms of connectivity, FCcva - Regional-scale connectivity in protected areas).

SELECTION OF THE MONITORING NETWORKS

The outputs from steps 1 to 5 in the analytical framework (Fig. 1) were used as inputs for selection of cost-effective monitoring networks (objectives PAN and RN) based on a top-down hierarchical decision process (Fig. 2). Selection criteria were applied in a sequential manner leading, in each step, to a smaller number of monitoring areas to which further selection criteria were then applied (see also Araújo, Williams & Turner 2002). The criteria used for network delineation were as follows:

FS | Suitability - Predictions of species presence and absence based on regional- and local-scale environmental suitability: The goal was to promote a balanced representation of the four suitability types (A, B, C and D; Fig. 1 - Step 1). We used a multivariate Wallenius' non-central hypergemotric sampling process (Appendix S4) to resample a near-uniform FS class distribution from a pool of areas with severe bias on FS class representation.

FI | Impacts - Interactions of environmental suitability and protection/conservation value: From the impact map generated between the A. dealbata potential current and future distributions and conservation value areas, we defined the probability of a given cell to enter in a solution, such that the impact areas of types a, b, c, d, e and f have 0.50, 0.20, 0.15, 0.10, 0.04 and 0.01 probability of being selected, respectively (Fig. 1 - Step 2);

REGIONAL NETWORKS

PA NETWORKS

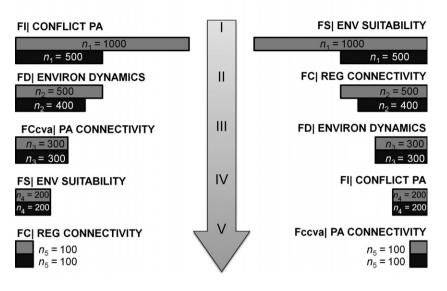


Fig. 2. A five level (I–V) hierarchical framework for the identification of regional and protected area (PA) monitoring networks with n5 = 100 cells, using an array of relevant factors. Cell number at each level, n_i : $i \in \{1,2,3,4\}$, depends on nestedness condition (dark bars for the constrained condition and grey bars for the relaxed condition).

FD | Dynamics – Predicted changes in suitability conditions from current to future time (2050): For the selection process, the highly dynamic areas (those converted to suitability type A or type D from 2000 to 2050) were prioritized. Within the pool of candidate areas (conversions from B, C, or D to A; and A, B, or C to D) for selection the ones defined as dynamic are selected first, and if more areas are needed for selection, the remaining areas are uniformly chosen among the non-dynamic areas;

FC | Connectivity – Regional-scale environmental suitability defined in terms of connectivity: The connectivity index (varying between zero and one) was directly used to set the cell selection probabilities. The higher the connectivity, the higher the probability of a given cell being selected (Fig. 1 – Step 3); FCcva | Connectivity – Regional-scale connectivity in protected areas: It uses the same principle of factor FC but was applied only for areas classified as having conservation value. If the number of cells to select was higher than the number of protected areas available, then the remaining cells were uniformly selected from the unprotected area set (Fig. 1 – Step 3).

Depending on the network type, these criteria were allocated to different hierarchical levels of the decision protocol (Fig. 2). For the regional networks (RN), the top-down hierarchical protocol was settled using factors FI, FD, FCcva, FS and FC, in this order, with regional-scale factors entering at the lowest levels. For the PAN, we ranked factors as FS, FC, FD, FI and FCcva, the objectives focusing on protected areas entering at the lowest levels.

To define the number of monitoring areas selected in each hierarchical step we used two alternative procedures: i) constrained nestedness, whereby the network size at each hierarchical stage was $n1 = 5 \times n5$, $n2 = 4 \times n5$, $n3 = 3 \times n5$ and $n4 = 2 \times n5$, and ii) a relaxed nestedness, using $n1 = 10 \times n5$; $n2 = 5 \times n5$; $n3 = 3 \times n5$; and $n4 = 2 \times n5$, whereby n1 is the number of monitoring areas selected after the first decision step, n2 after the second, etc. The targeted number of monitoring areas (n5) was alternatively 50, 100, 500 or 1000 (n5). The constrained nestedness gives higher weight to the lowest decision level (level V) (R codes in Appendix S5). We identified networks for two periods of time: baseline (2000) and future (2050) conditions.

Finally, we ran the selection algorithm 100 times for each combination of network type, size, nestedness condition and time context. A cost was assigned to each replica using the survey effort index developed by Guerra *et al.* (2013). We also generated 100 random networks of the same network size (*n*5) to define benchmarks to which the generated networks were compared (a procedure with long tradition in conservation planning; e.g. Rebelo & Siegfried 1992; Araújo *et al.* 2011). Indeed, although optimization is, by definition, a process to attain best performances then null models, because our framework is not mathematically driven and entails some stochasticity, it turns out to be relevant testing our results against random generated networks.

NETWORK COMPARISON

For each combination of network type, size, nestedness condition and temporal context, we obtained 100 solutions. Since the resulting frequency distribution of solution sets did not follow a Gaussian distribution, we applied Kruskal–Wallis tests to assess significant differences between network types (regional network vs. random network, PAN vs. random network, and regional network vs. PAN) regarding each one of the five analysed factors. In particular, we assessed the distribution of classes in FS through the Shannon entropy index: $H = -\sum_{i \in (A,B,C,D)} p_i \ln(p_i)$, where p_i represents the fraction of cells of class i in the solution. We described how uniform were distributions of environmental suitability classes within solutions by comparing them with the theoretical maximum entropy value (H/H_{max}) , where $H_{\text{max}} = -4 \times 0.25 \times \ln(0.25) = 1.386$).

Given that the spatial arrangement of a monitoring network affects financial costs, we also assessed the cost to survey each solution, using a monitoring effort map developed by Guerra *et al.* (2013) (see Appendix S3 for a detailed description).

For each combination of network type and size, we assessed differences in the five factors (FS, FD, FC, FCcva and FI) between the two nestedness conditions and the two time periods. Because these data sets do not satisfy Gaussian assumptions we used nonparametric Mann–Whitney–Wilcoxon tests.

We ranked each monitoring network based on the five analysed factors. This assessment was done separately for the regional and PAN s. We used the concept of Pareto dominance (Clark 1990), in which a solution is said to dominate another if it is not inferior to the second in all the objectives and if it is better in at least one them (Fig. S1). The set of non-dominated solutions has a dominance degree of one. To obtain the remaining dominance degrees, the non-dominated sets were deleted and the analysis was repeated until all the solutions were assigned to a dominance degree. We used the NDS function in the EMOA package (https://cran.r-project.org/web/ packages/emoa/index.html) in R software to give the ranking order of each network solution based on Pareto dominance.

We used univariate zero-truncated Poisson models to assess significant differences in Pareto dominance between network types, time periods and nestedness conditions. Analyses were performed for each network size class and for all size classes as a whole, using the VGLM function from the VGAMR package (https:// cran.r-project.org/web/packages/VGAM/index.html). We assumed a Gaussian distribution of the intercept estimators and therefore z-values were transformed into P-values for assessments of statistical significance.

Results

PREDICTED DISTRIBUTION, IMPACTS AND DYNAMICS UNDER CLIMATE CHANGE

The areas with suitable regional and local conditions for A. dealbata (response class A), and the areas with suitable regional conditions alone (C), were predicted to increase in the future. Conversely, the areas predicted to have local suitable habitats alone (B) and the areas with unsuitable regional and local conditions (D) were predicted to decrease (Table S3). All spatial combinations expressing impacts (types a-d) between A. dealbata and conservation value areas were also forecasted to increase by 2050, whereas the areas classified as of lowest concern (E) were predicted to decrease (Table S4). Spatially, the higher impacts will potentially take place in the western part of the study area, particularly along the western limits of protected areas, where the high protection value coincides with suitable conditions for the invasive species (Fig. 1). Acacia dealbata was forecasted to expand significantly in both protected and non-protected areas.

Current connectivity among populations was higher in the whole study area than inside the protected areas, but the latter is predicted to slightly increase by 2050.

MONITORING NETWORKS FOR ACACIA DEALBATA

The monitoring networks identified through the proposed hierarchical approach significantly differed, for each of the factors analysed, from equal-sized random networks (Table 2). Although costs were not used as a factor guiding the hierarchical framework, the costs obtained among the targeted networks were substantially lower (P < 0.001) than the costs from random networks. Importantly, the optimization performance of our framework was positively validated as the factors related to the lowest levels in the hierarchical procedure (protected area connectivity in PAN; regional connectivity in RN) presented the largest differences to the random networks.

Geographically, the averaged centroid for PAN occurred at higher latitudes and eastern longitudes than the average centroid resulting from random networks (P < 0.001); for RN the opposite pattern was generated, with network centroids at lower latitudes and longitudes than random networks (P < 0.001) (Fig. 3).

Broadly, the factors that most differentiated network types were regional connectivity, FC, and entropy (i.e. the balanced representation of suitability classes, FS), with higher values for RN. Comparing network costs, PAN depended on generally higher survey efforts than RN and, as expected, protected area connectivity, FCcva, was higher for PAN. RN targeted areas with higher predicted impacts of invasion than PAN, although the impacts (FI) entered into higher levels in the hierarchical decision process, and therefore, it was settled a more distal goal to drive the RN design. This result is derived from the (significantly positive) correlation between FI and the lowest factor (i.e. the more relevant one in defining the network purpose) entering RN selection, FC (Table S5).

PERFORMANCE OF MONITORING NETWORKS

Nestedness conditions also determined network performance for the factors included in the analysis (Table S6). Within PAN and RN, constrained nestedness resulted in more uniform distributions of environmental classes (i.e. higher entropy), western-most centroids and lower regional connectivity than relaxed nestedness. In RN, differences were less marked and inconsistencies occurred among solutions of different size. In general, constrained nestedness resulted in networks covering stronger impacts in protected areas and more extensive regional connectivity, as well as in lower protected area connectivity and eastern-most network centroids than those generated from relaxed nestedness.

When comparing time periods, a more balanced representation of suitability classes (i.e. higher entropy) was obtained in the RN defined for current time than for 2050 networks (Table S7). For the remaining factors (including survey cost), networks defined for 2050 reached significantly higher values. PAN designed from current conditions reached higher connectivity compared to 2050 networks. For the remaining factors, 2050 networks covered higher values than 2000 networks.

When analysing the network performance considering their performance in respect to the five analysed factors together (FI, FS, FC, FCcva and FD), RN of smallest size tended to outperform similar-sized PAN (i.e. more networks with low dominance degree, Fig. S2); the networks obtained with the relaxed area selection protocol dominated the networks designed with the constrained area selection approach; and small-sized (n5 = 50) networks for current time outran networks designed for 2050 conditions (Table 3).

Finally, among the 100-solution sets, the networks with the minimum costs save up to 18% of the average monitoring resources compared to the average of the other solutions in the corresponding set (Tables S8 and S9).

Table 2. Kruskal-Wallis results comparing network types for several factors

G: (5)	50		100		500		1000	
Size (n5) Factors	K	Dir.	K	Dir.	K	Dir.	K	Dir
Protected area networ	k (PAN) vs. Ran	dom networ	k					
Cost	0.270***	_	0.272***	_	0.318***	_	0.402***	_
Entropy	0.392***	_	0.435***	_	0.315***	_	0.375***	_
PA impact	0.935***	+	0.975***	+	0.998***	+	0.980***	+
Connectivity	0.625***	+	0.660***	+	0.755***	+	0.830***	+
PA connectivity	0.665***	+	0.785***	+	0.830***	+	0.800***	+
Centroid (long)	0.435***	_	0.53***	_	0.575***	_	.600***	_
Centroid (lat)	0.238***	+	0.335***	+	0.122	NA	0.172*	+
Range (long)	0.390***	_	0.378***	_	0.655***	+	0.735***	+
Range (lat)	0.090	NA	0.075	NA	0.835***	+	0.940***	+
Regional network vs.	Random network	ζ						
Cost	0.440***	_	0.477***	_	0.645***	_	0.690***	_
Entropy	0.742***	_	0.827***	_	0.765***	_	0.718***	_
PA impact	0.997***	+	1.000***	+	1.000***	+	0.970***	+
Connectivity	0.977***	+	1.000***	+	1.000***	+	1.000***	+
PA connectivity	0.562***	+	0.720***	+	0.762***	+	0.660***	+
Centroid (long)	0.782***	_	0.9375***	_	0.935***	_	0.978***	_
Centroid (lat)	0.338***	_	0.455***	_	0.6075***	_	0.465***	_
Range (long)	0.672***	_	0.7425***	_	0.255***	+	0.518***	+
Range (lat)	0.118	NA	0.085	NA	0.805***	+	0.930***	+
Regional network vs.	PAN							
Cost	0.200***	_	0.280***	_	0.438***	_	0.525***	_
Entropy	0.622***	_	0.658***	_	0.628***	_	0.650***	_
PA impact	0.395***	+	0.402***	+	0.408***	+	0.225***	+
Connectivity	0.675***	+	0.810***	+	0.898***	+	0.768***	+
PA connectivity	0.160***	_	0.185***	_	0.292***	_	0.338***	_
Centroid (long)	0.455***	_	0.538***	_	0.580***	_	0.558***	_
Centroid (lat)	0.415***	_	0.515***	_	0.615***	_	0.520***	_
Range (long)	0.342***	_	0.392***	_	0.448***	_	0.273***	_
Range (lat)	0.180***	_	0.138***	_	0.080	NA	0.100*	NA

K: test value; Dir.: direction of the comparison (+, the first network has significantly higher values than the second; –, the first network presents significantly lower values than the second); NA, not applicable. P < 0.001: ***, P < 0.05: *.

Higher savings occur for the smallest monitoring networks (n5 = 50 and n5 = 100: approximately 10% to 18%) when compared with the largest one (n5 = 500 and n5 = 1000: approximately 4% to 5%) but in both cases, minimum cost solutions were able to attain the average representation of the remaining factors from the 100-solution sets (Tables S8 and S9). With the exception of the connectivity factors (FC and FCcva) that were quantified additively across the monitoring sites, for the remaining factors (quantified as representation proportions within the networks), there was no substantive differences with network size variation (both for the minimum cost networks and for the mean values across network sets).

Discussion

EFFECTIVE MONITORING AND MANAGEMENT OF INVASIONS UNDER GLOBAL CHANGE

Climate change and invasive alien species are widely recognized as pressing environmental and socio-economic challenges. Despite mounting evidence that global change drivers are strongly interconnected, climate change and invasive species are still often treated as separate problems, and their interactions tend to be ignored (Pyke et al. 2008; Walther et al. 2009). In times with environmental impacts of climate change and invasive species increasing globally, failure to address their dynamic linkages will likely exacerbate their negative impacts on several aspects of the environment, the economy and society (MA 2005; Petitpierre et al. 2016). Monitoring the responses of invasive species to climate change becomes critical for the design of effective biodiversity conservation strategies, but monitoring is an expensive endeavour. As such, careful planning of monitoring schemes and networks is of vital importance if they are to be implemented within the context of scarce conservation budgets (Amorim et al. 2014).

Invasive woody plant species have received much attention owing to their impacts on ecosystems and their services (García-Llorente *et al.* 2011; Wilson *et al.* 2014). The effective eradication of established populations is often not economically viable (Simberloff *et al.* 2013), with prevention being often the most cost-effective option (Chornesky *et al.* 2005; Genovesi & Monaco 2013). How-

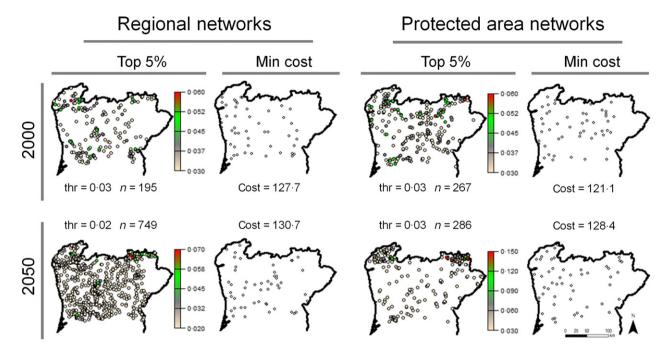


Fig. 3. Maps of the 100 cells-sized solutions obtained with relaxed nestedness conditions. Maps represent the two types of networks (regional and protected area networks) defined for two time periods. Top 5% maps represent the top 5% of cells that were selected at least one time among the 100 runs. In top 5% maps, circles represent cell frequency selection: higher frequencies are highlighted with darker grey colour. thr: minimum frequency among the top 5% set. n: number of top 5% cells. Minimum cost maps represent the minimum cost solutions and their respective cost (cost).

Table 3. Pareto dominance distributions of monitoring networks obtained varying network type, nestedness conditions and time periods using a zero-truncated Poisson model

Size	Intercept	Effect size	P-value
Protected an	ea vs. regional netw	orks	
50	0.195	-2.733	***
100	-2.603	-0.756	
500	-24.656	0.000	
1000	-4.607	1.498	
All	-1.013	-2.212	***
Constrained	vs. relaxed nestedne	ess	
50	0.209	-0.958	***
100	-0.143	-1.091	***
500	-0.887	-2.624	***
1000	-4.607	-16.531	
All	-0.418	-1.170	***
2000 vs. 205	0 networks		
50	-0.539	0.639	***
100	-20.138	19.842	
500	-24.656	0.000	
1000	-23.658	18.359	
All	-23.658	18.359	

Intercept: intercept parameter in the Poisson model; Effect size: effect of the second network compared to the first one; Empty cells: non-significant P-values. P < 0.001: ***.

ever, establishment of new invasive populations or species cannot be discarded, and monitoring will facilitate early detection thereby helping containing or even eradicating new invasions as they arise.

However, selecting areas for the monitoring of invasive woody plant species based on multiple considerations involves several challenges. First, accurate predictions on the spatial distribution of the invasive woody plant species - both today and in the future - are critical. Over the last few years, SDMs have been widely used to predict the expansion of invasive alien species and their potential impacts on biodiversity and ecosystem services (e.g. Kleinbauer et al. 2010; Vicente et al. 2013a,b). Increasing attention has been devoted to the study of invasions across spatial scales, to determine which processes drive invasions at each relevant scale (Pauchard & Shea 2006; Seipel et al. 2012). Recent methodological advances in SDMs (e.g. Vicente et al. 2011, 2014) have contributed to more informative spatial projections of species distributions. Additionally, ensemble modelling provides more robust species forecasts when compared to single-method SDMs (Araújo & New 2007), thereby reducing an important variability in the models (e.g. Araújo et al. 2005a; Garcia et al. 2012). Similarly, frameworks that integrate predictions of different downscaling approaches into a single consensus map allow the use of SDMs in a spatial resolution more compatible with local conservation and management needs (e.g. Araújo et al. 2005b; Fernandes et al. 2014).

Secondly, species' dispersal abilities and habitat connectivity are important to assess the vulnerability of habitats to invasions. Spatially explicit analysis of habitat connectivity greatly improves spatial predictions of invasions (Minor et al. 2009). Surfaces with high connectivity represent potential dispersal corridors, if suitable environmental conditions remain available over time (e.g. Procheş *et al.* 2005; Alagador *et al.* 2012). As shown in our study, temporal dynamics of connectivity will influence species' expansion dynamics as well as the success of control measures.

Thirdly, it is important to consider where invasive species might have the highest impacts. Within conservation areas the establishment of an invasive species can affect unique (often vulnerable) species, ecological communities and processes. At the same time, within conservation areas, management of invasive species is more likely than elsewhere (Foxcroft *et al.* 2013). The establishment of monitoring networks within the area of influence of conservation areas is thus likely to be of greater conservation and social relevance.

Fourthly, to be successful over the long term, the benefits of the information from any monitoring programme must justify the costs. Financial limitations will always restrict the scope of a monitoring programme. Hence, the focus of a monitoring programme must be carefully defined and prioritized, so that the most effective set of indicators is used (Epanchin-Niell *et al.* 2014).

Finally, a key research question is whether or not climate change will be a zero-sum game for invasive species, causing the emergence of new invasive species but also reducing the impact of current invasions (Walther *et al.* 2009). To be sure, climate change must be taken into account when designing long-term invasive woody plant species monitoring networks.

THE ADDED VALUE OF THE NOVEL MODEL-BASED FRAMEWORK

Our approach adds flexibility with regards to previous studies (e.g. Cacho & Hester 2011; Franklin et al. 2011; Hui et al. 2011; Amorim et al. 2014; Wilson et al. 2014). For example, (i) it delivers a large set of optimized solutions with similar cost-effectiveness thereby enabling decision makers to choose from different alternatives depending on their management priorities; (ii) it provides flexibility to include several different inputs and to implement alternative species distributions modelling techniques (e.g. SDMs, coupled dynamic models, process-based models; e.g. Fordham et al. 2013), and (iii) it is general thus being easily applicable to any species, region and associated invasion drivers. Furthermore, although studies have used distinct off-the-shelf spatial conservation prioritization software to identify effective monitoring networks (e.g. Franklin et al. 2011; Amorim et al. 2014), ours is the first to use a model-based and spatially explicit approach for an invasive species, based on SDMs outputs under current and future conditions, along with predictions of surveillance costs and effectiveness, while considering conservation investments already taking place and regional-scale management goals. Finally, the framework embraces multicriteria and multistakeholder goals

(e.g. Hui *et al.* 2011; Genovesi & Monaco 2013; Vicente *et al.* 2013b) and is driven to minimize costs in designing effective monitoring networks.

An important insight from our study is that in equalsize monitoring networks, the coverage of the relevant explaining factors, as well as investment costs, was substantially optimized in our model-based networks (both PAN and RN), when compared with randomly generated networks.

This is especially relevant because in order to have a highly dissimilar set of network options to planners chose from we opted to use a decision framework integrating some stochasticity instead of a full mathematical optimization process. By doing so, we needed to validate network performance in regard to the distinct analysed factors, with especial relevance to network cost, giving that costs were not part of the area selection framework.

In particular, among optimized networks, the proximal factors (protected area connectivity in PAN, and regional connectivity in RN; see Table 2) were best represented. Consequently, these results reinforce the relevance of welldesigned integrative approaches when selecting monitoring sites. Indeed, the design of optimized monitoring programmes fostering cost-efficiency and effectiveness has been advocated (Nichols & Williams 2006) and established as a priority concern for managers. If a flexible framework like the one proposed here is used, a pool of alternative robust solutions can be explored interactively, thus allowing quantitative information to be weighed against qualitative judgements. This brings invasion monitoring closer to management needs while ensuring adaptability under rapid climate and environmental change, being of utmost relevance for preventing the impacts of invasive woody plant species (Pejchar & Mooney 2009; Simberloff et al. 2013). Planning the expenditure of scarce resources by prioritizing areas according to the effectiveness of monitoring networks can contribute not only to the success of invasion control measures, but also to the overall cost-efficiency of management and monitoring actions.

LIMITATIONS AND FURTHER PROSPECTS

Accurate predictions of the spatial distribution of invasive woody plant species can be critical for conservation and management purposes (e.g. Foxcroft *et al.* 2013; Vicente *et al.* 2013b; Fernandes *et al.* 2014). SDMs can be used to obtain such spatial distributions, but their potential limitations must be acknowledged (e.g. see for discussion Araújo & Peterson 2012). Missing and biased species distributions and environmental predictors data for modelling have been major topics of discussion (e.g. Broenniman & Guisan 2008; Araújo, Thuiller & Yoccoz 2009; Vicente *et al.* 2011). Including the global distribution of the invasive species in the models is crucial to assess species' potential distributions (e.g. Broenniman & Guisan 2008), thereby reducing the risk of truncating species

response curves related to critical environmental variables (e.g. Thuiller et al. 2004). This is particularly true when models are used to predict future species distributions under scenarios of climate change because of an increased risk of extrapolating beyond the range of predictor values used to calibrate the models (e.g. Pearson et al. 2002; Garcia et al. 2014).

Matching global distributions of species, which are usually at coarse resolutions, with local predictors is often difficult. Of particular concern is the lack of global coverage for some of the variables that are of local importance. Nonetheless, including global information in local modelling can be possible as long as all the predictors can be projected to future conditions (e.g. Gallien et al. 2012; Petitpierre et al. 2016). Although SDM methodologies have been improved in recent years (e.g. Guisan & Thuiller 2005; Araújo & New 2007; Randin et al. 2009), the limitations when modelling early stages of invasion or range expansion into new environmental space not represented in the calibration data set are still not sufficiently comprehended (e.g. Gallien et al. 2012). Nonetheless, our framework constitutes a step forward in the development of decision support systems, especially for new and highimpact invaders, such as A. dealbata, as it allows different monitoring solutions to be combined with information on network performance and expert judgement. These are characteristics of monitoring system demanded by European legislation, and they make monitoring particularly suitable for supporting conservation and management under rapid climate change.

CONCLUSIONS

The recent European legislation on the prevention and management of invasive alien species urges member states to ensure coordination and cooperation and encourages the establishment of a European-wide surveillance system. The framework that we proposed is a step towards such a pan-European monitoring system. Specifically, we have shown that:

- 1. Cost-effective monitoring programmes can assist the optimization of resource allocation and contribute to evaluations of invasion risk that enable the anticipation and success of invasive species control programmes.
- 2. For widespread problematic invasive plant species like A. dealbata in the North of Portugal, detailed predictions of current and future invasion probability highlight that monitoring resources should be prioritized in order to efficiently anticipate and mitigate the impacts of invasions in conservation areas under current and future climate conditions. With our framework, we identified networks that are significantly less costly (P < 0.001) and more effective in representing invasion factors than random, non-guided sets of areas (P < 0.001). Among these, the minimum cost networks were up to 18% less costly than the average costs within the all set of equivalent networks.

- 3. Decision makers have the opportunity to select the pool of sites that best suit their particular objectives and means because the framework encompasses high flexibil-
- 4. By being reproducible, by addressing costs and benefits, and by integrating factors operating at a range of scales, the framework can be used as a tool to support the design of a European surveillance system for invasive species. Indeed, bringing invasion monitoring closer to management needs while ensuring adaptability under rapid climate change should be pivotal principles in the development of such a European system.

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Data accessibility

R scripts: available in Appendix S5 - R codes to reproduce the hierarchical area selection procedures for the two types of monitoring networks.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

- Fig. S1. An illustration of the Pareto dominance analysis.
- Fig. S2. Pareto dominance between pairs of network groups.

- Table S1. Environmental predictors used in the species distribution models.
- Table S2. Scale of influence of predictors.
- Table S3. Areal distribution predicted for *Acacia dealbata*.
- Table S4. Spatial impacts between species occurrence and conservation areas
- Table S5. Correlation matrix for the monitoring networks guiding
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- Table S8. Summary results for the solutions obtained for regional networks.
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- Appendix S1. Study area, test species, sampling design, and model calibration.
- Appendix S2. Phenology and productivity predictors' description.
- Appendix S3. The effort map analysis.
- Appendix S4. The statistical procedure to resample a uniform environmental suitability class distribution from a non-uniform
- Appendix S5. R codes to reproduce the hierarchical area selection procedures for the two types of monitoring networks.