Biological Conservation 147 (2012) 243–254

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Testing a novel spatially-explicit dynamic modelling approach in the scope of the laurel forest management for the endangered Azores bullfinch (*Pyrrhula murina*) conservation

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ARTICLE INFO

Article history:
Received 29 July 2011
Received in revised form 23 November 2011
Accepted 6 January 2012
Available online 31 January 2012

Keywords:
Azores bullfinch
Habitat management
Invasive plant species
Laurel forest conservation
Spatially dynamic modelling
Stochastic dynamic methodology

ABSTRACT

The Azores bullfinch (*Pyrrhula murina*) is an endemic bird of São Miguel island (Azores Archipelago, Portugal), currently threatened by two of the major causes of biodiversity loss worldwide: invasion of native habitats by exotic plants and habitat destruction by land use changes. The aim of this research was to develop and test a novel spatially explicit modelling framework that predicts the Azores bullfinch responses to alternative realistic scenarios of native forest management. This was done by integrating Multi-Model Inference statistical analysis, Stochastic-Dynamic Modelling and Geographic Information Systems under a common framework relating bird population trends to changes in the surrounding habitats. Overall, in the next 25 years, the Azores bullfinch breeding population was predicted to increase around 19% as a consequence of habitat management actions already implemented ("LIFE Priolo" project) or around 27% in the context of realistic future habitat restoration scenarios. These results represent, respectively, a supplementary increase of more 6% or more 13% in the Azores bullfinch abundance when compared with the trends simulated for the scenario without management. Nevertheless, those actions seemed to be relatively ineffective in promoting the expansion of the species from the actual restricted favourable area, essentially due to local forestry dynamics and on-going plant invasion processes. This novel integrative approach provides a promising baseline to support ecological models with increased realism and predictive power, making the outputs more useful and intuitive to decision-makers and environmental managers.

1. Introduction

There is a worldwide recognition that the current biodiversity crisis is one of the most serious environmental problems ever faced by mankind (Hickman et al., 2004). In this context, the invasion of natural ecosystems by exotic plant species is one of the biggest threats to biodiversity worldwide (Vitousek et al., 1997; Lake and Leishman, 2004). In enclosed and isolated areas, such as islands, ecological interactions between native and invasive species can assume more drastic consequences because ecosystems exhibit limited resistance and resilience and, therefore, higher susceptibility to invasion (Elton, 1958; Caujapé-Castells et al., 2010). Additionally, the relatively small size of animal populations on islands, particularly in the case of birds, increases their extinction risk (Clavero et al., 2009), frequently expressed in the loss of the most sensitive species and/or in important changes at the level of species assemblages and trophic chains (Thibault et al., 2002; Wal et al., 2008; Tylianakis et al., 2010).

The Azores bullfinch (*Pyrrhula murina*, Godman, 1866) is a narrow endemic bird of São Miguel island (Azores, Portugal), currently threatened by the habitat destruction by land use changes and invasion of the native laurel forest by exotic plants (Ramos, 1996a; Vitousek et al., 1997; Theoharides and Dukes, 2007). Listed until very recently as one of the only two 'Critically Endangered' bird species that breed in Europe (BirdLife International, 2009, 2011), the distribution of the Azores bullfinch is limited, due to severe habitat constraints, to the last available fragments of native laurel forest in the eastern part of the island (Ramos, 1996a). This habitat type has long been cleared for pasture and afforested mainly with the exotic Japanese Red Cedar [*Cryptomeria japonica* (L. fil.) D. Don)], but other

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doi:10.1016/j.biocon.2012.01.009

recently introduced exotic plants have become aggressive invaders (Dias, 1996; Ramos, 1996a; Silva and Smith, 2004). The Australian cheesewood (*Pittosporum undulatum* Vent.), Kahili ginger (*Hedychium gardneranum* Sheppard ex Ker-Gawl.) and lily-of-the-valley tree (*Clethra arborea* Aiton) represent the main plant invaders driving native biodiversity losses in the Azores laurel forest (Heleno et al., 2009). The key driver of exotic plant invasion in the island is the increasing expansion of human activities, which create new opportunities for invasive species, namely through the alteration and degradation of autochthonous ecosystems, converting heterogeneous native communities into a more impoverished and homogenized structural composition (Heleno et al., 2009, 2010).

One of the great challenges in ecological integrity studies is to predict how anthropogenic environmental changes will affect the ecology of species and the composition of biotic communities in disturbed ecosystems (Kareiva et al., 1993; Andreasen et al., 2001). Ecological studies have been improved by creating dynamic models that simultaneously attempt to capture the structure and the composition in systems affected by long-term environmental disturbances (Jørgensen, 1994, 2001). When properly developed and tested, and when applied with insight and with respect for their underlying assumptions, such dynamic ecological models are capable of simulating conditions that are difficult or impossible to understand otherwise (Jørgensen, 2001).

In support of technical and political decision, modelling can be very useful as an investigative tool to forecast the outcome of alternative scenarios, guiding current management options from predicted future targets. In this perspective, the stochastic dynamic methodology (StDM) has been proposed as a sequential modelling process developed to predict the ecological status of changing ecosystems, from which management strategies can be designed (Cabral et al., 2007). The StDM is based on the premise that the general statistical patterns of ecological phenomena are emergent indicia of complex ecological processes that do indeed reflect the operation of universal rules or mechanisms (Santos and Cabral, 2004). During the last decade, the StDM framework has been extensively and successfully tested in several types of ecosystems affected by gradients of change (e.g. Silva-Santos et al., 2008; Santos et al., 2010) and in the scope of wildlife conservation (e.g. Santos et al., 2007; Silva et al., 2010). To improve the applicability of this framework, the StDM can be coupled with Geographic Information Systems (GISs) to produce simulations that allow the interactive creation of spatially dynamic ecological patterns. When applied as a multi-scale approach to address the effects of alternative management scenarios, such a "spatially explicit StDM" can be run at different levels simultaneously, considering stochastic phenomena that characterize real ecological processes.

To our knowledge, such integration of stochastic-dynamics models and spatial analysis tools has not been developed and tested as a robust management and decision-support tool. Therefore, the main goal of this research was to illustrate the potential of this new approach in the scope of the practical implementation of conservation actions for endangered species, using the Azores bullfinch as a test species. This paper discusses the applicability of this integrative tool to discern and predict the spatial patterns of the Azores bullfinch abundance in its main distribution area, as a response to present and future changes in the laurel forest composition related to alternative habitat management options.

2. Methodology

2.1. Study area

São Miguel is the largest island of the Azores Archipelago (Portugal), located in the eastern group of islands (Fig. 1a). In this volcanic region, situated in the North Atlantic Ocean, the climate is temperate oceanic, presenting low thermal amplitudes and high values of humidity and rainfall. The study area, located in the eastern part of the São Miguel island (Fig. 1b), includes the Special Protection Area (SPA) of Pico da Vara/Ribeira do Guilherme (37°47′N, 25°13′W) (Fig. 1c). This SPA, a mountainous area with altitude ranging from 300 to 1100 m, sloping topography and dense native and exotic vegetation, covers the eastern remaining laurel forest of São Miguel, the stronghold of the Azores bullfinch (Ramos, 1995).

2.2. Sampling strategy

The species occurrence data used in this study were obtained from the "Atlas do Priolo", an exhaustive snapshot survey of the Azores bullfinch during the breeding season of 2008, conducted throughout the study area to estimate the population size and range size (see Ceia et al., 2011a, for detailed methods). The original sampling grid used in the "Atlas do Priolo" was composed by 307 point-counts, located on the vertices and centre of each correspondent UTM unit. Thereafter, this sampling design was superimposed by a new grid so that all point-counts were located in the middle of the grid squares but not on edges, allowing linking the records of bullfinch local abundance with the habitat characteristics of each point-count exclusive surrounding area (Fig. 2a).

Ninety Azores bullfinch's records (heard or seen) were obtained during the point-counts. Due to the extensive set of point-counts where the species was not detected (259 out of 307), data from additional transects between point-counts were used to confirm absences. The point-counts with false absences were excluded from the database and not used in the model calibration.

2.3. Land cover mapping and habitat classes

To assess environmental factors with potential influence in the Azores bullfinch distribution and abundance, several parameters of the study area were considered within a 50 ha area, centred by each point-count (study unit) (Fig. 2a). The information for the 17 habitat classes considered (Table 1) was obtained from aerial cartography and the respective areas (m^2) were calculated taking into account each study unit habitat composition. Land cover information was based on a pre-existent map covering the central area of the SPA (see Botelho et al., 2008 for details) and completed for the whole study area by photo-interpretation (reference scale 1:23 000) in a GIS environment (ArcMap9.3®; ESRI, 2009). The land cover mapping was validated in the field through direct observation of land cover features and respective boundaries.

Habitat classes were then derived from the land cover map. Laurel forest, which appears to be critical for the Azores bullfinch (Ramos, 1996a), was discriminated in relation to the degree of invasion by the main exotic invasive plants, such as *C. arborea* and *P. undulatum*, since forest invasion was considered a key factor for the loss of habitat quality. An additional heterogeneous class, that includes other exotic plant species, was established in order to complete the pertinent land cover combinations with regard to invasion forest processes. The laurel forest class (*laurel_forest*; Table 1) was characterized by areas up to 75% cover dominated by laurel forest species. Mixed habitats of laurel forest with *C. arborea*, *P. undulatum* and other exotics were categorized, in terms of invasion degree, by percentages of dominant or dominated species (*laur_clethra*, *laur_pitt*, *laur_other_exotics*, *cl_dom_laur*, *pitt_dom_laur*, *other_exotics_dom_laur*; Table 1).

Since plantations of *C. japonica* represent a dominating element of the local landscape with a variable role, in terms of habitat quality for the Azores bullfinch, through their exploitation cycle, we sub-categorized this class by maturation periods (*cryp_young*, *cryp_adult*, *logging*; Table 1). Mature *C. japonica* plantations are dense

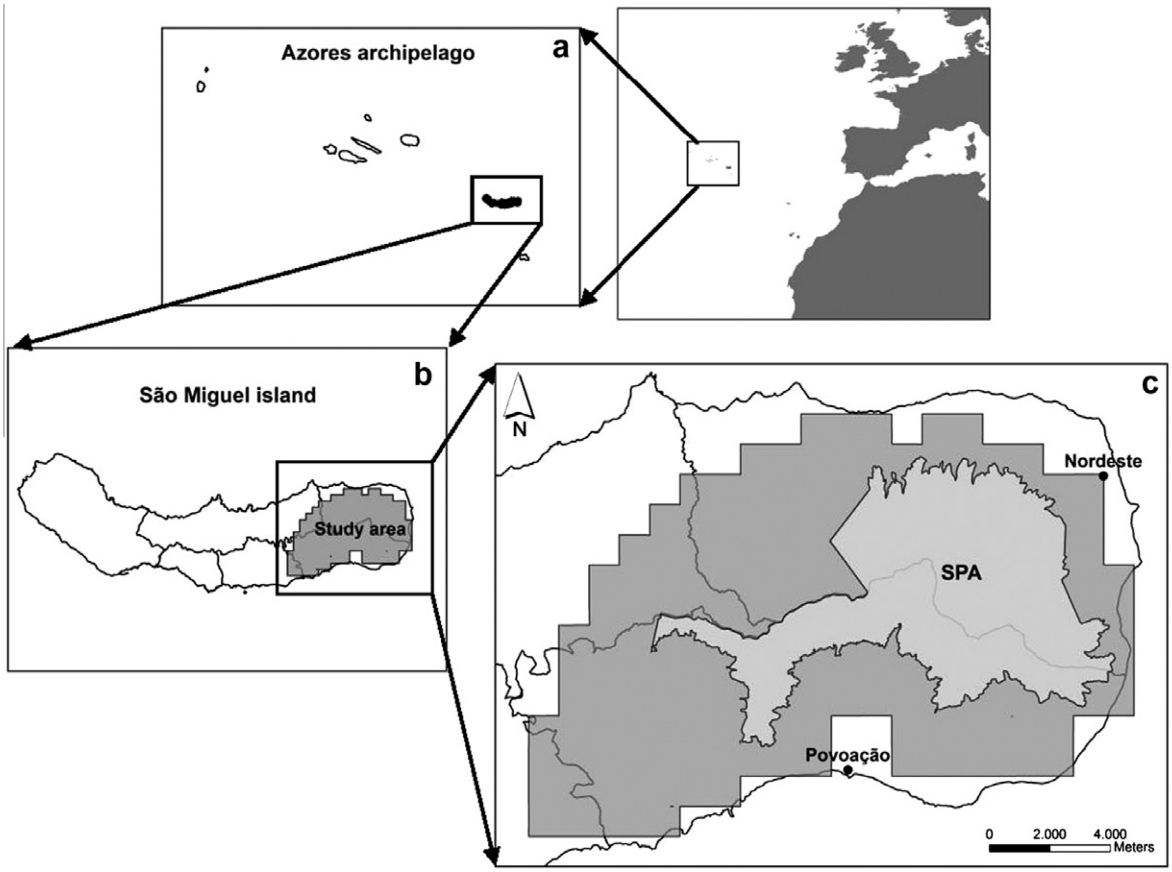

Fig. 1. Location of the study area (a) in the Azores Archipelago, (b) in the São Miguel island, and (c) in the Special Protection Area of Pico da Vara/Ribeira do Guilherme.

and mono-specific woodlands (often without an herbaceous/shrub layer) thus not providing suitable habitat for the Azores bullfinch (Ramos, 1996a; Ceia et al., 2009). Conversely, young plantations (<10 years) and logging areas allow the development of an herbaceous/shrub layer that are used by the species (Ramos, 1996a; Ceia et al., 2009).

Landslides (*landslides*; Table 1) were discriminated as a habitat class as they represent typical events in the area (Valadão et al., 2002; Gil, 2004), removing large portions of soil and natural vegetation (Wilcke et al., 2003; Walker and Shiels, 2008). Moreover, in invaded areas they may represent an opportunity for alien species expansion (Arévalo et al., 2005; Heleno et al., 2010). Pastures were combined with the active raised bogs from highlands, becoming a single habitat class (*pastures_and_meadows*; Table 1), since large continuous open areas are not used by the Azores bullfinch (Ramos, 1996a; Ceia et al., 2011a). Paths and roads were included in order to evaluate impacts of the anthropogenic direct disturbance on the species occurrence (*pathways_and_roads*; Table 1). The water body of Furnas Lake was classified together with other infrastructures (*other_areas*; Table 1) that represent unsuitable areas with low ecological value for the Azores bullfinch occurrence (Ramos, 1996a).

2.4. The spatially explicit StDM framework

2.4.1. A general overview

The proposed spatially explicit StDM framework is a sequential modelling process initiated by the analysis of landscape and habitat composition (Fig. 2a and Section 2.3), which defines the convenient parameters that contextualize the physical and biotic descriptors at the study unit level. This procedure involves the use of a robust information-theoretic approach based on Generalized Linear Models (GzLMs; Fig. 2b and Section 2.4.2) in order to establish the interaction criteria between the construction of the dynamic model and the resulting stochastic dynamic simulations for each study unit (Fig. 2c and Sections 2.4.3 and 2.4.4).

These simulations, when projected into a geographic space (Fig. 2d and Section 2.4.5) and submitted to an appropriate geostatistical interpolation (Fig. 2e and Section 2.4.5), create an integrative picture, in space and time, of the Azores bullfinch abundance responses to the gradients of habitat changes. Since the dynamics of the species main distribution is driven by the interaction between biophysical and human dimensions, the combined use of such statistical modelling and geostatistical techniques was considered a promising approach to address complex emergent problems, from the individual habitat patch to the whole landscape context.

2.4.2. Statistical analyses

The StDM model construction was preceded by a statistical procedure, for parameter estimation, to test for relationships between dependent and independent variables (Santos and Cabral, 2004). The dependent variable corresponds to the Azores bullfinch abundance, expressed in bird numbers. The independent variables are expressed in the area occupied by each habitat class. In order to avoid multicolinearity, the selected 17 predictors (habitat classes; Table 1) for the Azores bullfinch abundance were tested for pairwise correlation using Spearman's rho correlation coefficient and only predictors with correlation lower than 0.7 (Elith et al., 2006; Wisz and Guisan, 2009) and Generalized Variance Inflation Factor lower than 5 were considered (Neter et al., 1996).

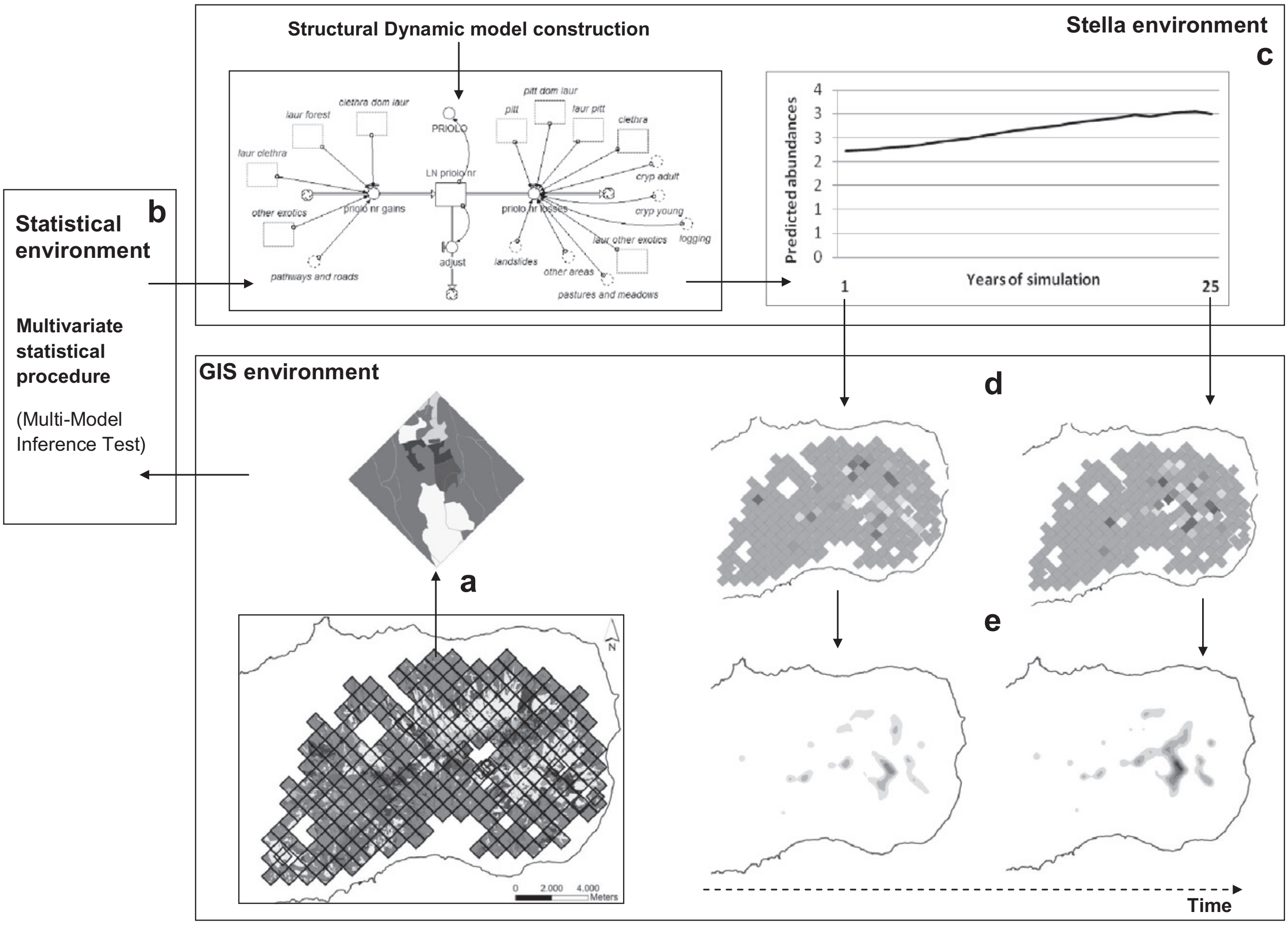

Fig. 2. The spatially explicit StDM framework for the Azores bullfinch abundance (PRIOLO) forecasting: (a) the previous analyses of landscape and main habitats in each study unit; (b) the statistical analysis to define the convenient parameters that contextualize the physical and habitat descriptors at the study unit level; (c) the construction and simulations of the structural dynamic and stochastic dynamic model (StDM) at the study unit level; (d) the projection of the resultant stochastic dynamic simulations into a geographic plane; (e) the final geostatistical interpolation that create an interactive and integrative picture, in space and time, at the regional level.

Rather than a single best model, we fitted a set of competing models and applied Multi-Model Inference (Burnham and Anderson, 2002) to assess how well each model was supported by the data. We used a particular implementation of the Akaike information criterion for small sample sizes (AIC_c; Shono, 2000), as recommended when the ratio between *n* (the number of observations used to fit the model) and *K* (the number of parameters in the largest model) is less than 40 (Shono, 2000; Burnham and Anderson, 2002). To overcome dependence on sample size and allow comparability among models, we calculated the AIC_c difference ($\Delta i = AIC_{c\ initial} - AIC_{c\ minimum}$) for each candidate model to rank the candidate models (Burnham and Anderson, 2002). We applied data dredge statistics (dredge – MuMIn R package; available at http://r-forge.r-project.org) to run Generalized Linear Models (with a Poisson variance distribution and a log link function) with all (valid) combinations of environmental predictors for the test species. We selected all the models with $\Delta i < 2$ as recommended by Burnham and Anderson (2002), and finally we calculated the averaging model to incorporate in the StDM (Fig. 2b and c).

2.4.3. Conceptualization of the dynamic model

The diagram of the model presented in Fig. 3 is based on the relationships detected in the previous statistical procedures, supported by datasets that include the whole regional gradients of the studied habitat changes. Therefore, in a holistic perspective, the partial regression coefficients represent the global influence of the selected habitat variables that are representative of several complex ecological processes in each study unit. Yet, they were not included explicitly in the model, but were related to the Azores bullfinch abundance. These led the interface between the dynamic model construction and the StDM outputs (Fig. 2c).

The basic principle of StDM models is given by the balance between gains and losses of a state variable, described by difference equations and resulting from the influences of dynamic environmental variables, which are mediated by the respective partial regression coefficients (Fig. 3a). The StDM state variable represents the Azores bullfinch abundance, intricately linked by its dependence on the selected habitat characteristics, particularly their average abundance induced by the main local environmental conditions (Fig. 3a). These habitat influences were introduced into the StDM state variable either as inflows, based on all positive coefficients of each favourable habitat descriptor, or as outflows, based on the negative partial regression coefficients of the respective habitat detrimental influences (Fig. 3a). Since the output for the Azores bullfinch abundance is composed of a given estimate per time unit, the respective state variable might have a cumulating behaviour over time in response to changes in the environmental conditions of each study unit (Santos and Cabral, 2004). Therefore, to avoid the accumulation of discrete estimates, an additional outflow, the adjust, is incorporated in this state variable in order to ensure emptiness in each time step, through a "flushing cistern" mechanism, before a new step with new environmental influences would begin (Fig. 3a). Although the Azores bullfinch abundances were successively estimated based on the

Table 1
Specification of the habitat classes considered in this study and respective model codes. The mapping of each habitat class was based on previous cover maps from Botelho et al. (2008) and Timóteo (2009).

Habitat classes	Structural classification (percentage of cover)	Model codes
Plantations of *C. japonica* (<10 years)	*C. japonica* (100%)	cryp_young
Plantations of *C. japonica* (>10 years)	*C. japonica* (100%)	cryp_adult
Forest harvest	Logging (100%)	logging
Landslides	Landslides (100%)	landslides
Laurel forest	Laurel forest (>75%)	laurel_forest
Areas of *C. arborea*	*C. arborea* (50–75%)	clethra
Areas of *P. undulatum*	*P. undulatum* (50–75%)	pitt
Areas of other exotics	Other exotics (50–75%)	other_exotics
Laurel forest with *C. arborea*	Laurel forest (50%–75%) *C. arborea* (25%–50%)	laur_clethra
Laurel forest with *P. undulatum*	Laurel forest (50%–75%) *P. undulatum* (25%–50%)	laur_pitt
Laurel forest with other exotics	Laurel forest (50%–75%) Other exotics (25%-50%)	laur_other_exotics
C. arborea dominating laurel forest	Laurel forest (25–50%) *C. arborea* (50–75%)	cl_dom_laur
P. undulatum dominating laurel forest	Laurel forest (25–50%) *P. undulatum* (50–75%)	pitt_dom_laur
Other exotics dominating laurel forest	Laurel forest (25–50%) Other exotics (50–75%)	other_exotics_dom_laur
Pastures and natural open meadows	Pastures, agricultural fields and active raised bogs (100%)	pastures_and_meadows
Pathways and roads	Principal and secondary accesses (100%)	pathways_and_roads
Other areas	Residential and recreational areas, quarry areas, tunnels, water treatment stations and water cover of Furnas' lake (100%)	other_areas

prevalent habitat areas alone, for each breeding season and study unit, the resultant trend was assumed as a valid indication of the population local response throughout the annual dynamics of their main habitats. Moreover, since bullfinch abundances were obtained from a logarithmic transformation (LN priolo nr), a conversion was introduced for a better comprehension of the StDM model simulations (PRIOLO). This conversion was obtained by an inverse transformation (anti-logarithmic), which transform logarithms of bird abundances into values expressed in the original measurement units (Fig. 3a).

2.4.4. Implementation of the dynamic model

The interaction between the Azores bullfinch state variable and structural habitat features, mainly resulting from invasion processes acting through laurel forest and forestry stages of *C. japonica* plantations, represents the main local influences for forecasting the species abundance (Fig. 3b). Additionally, the effects induced by stochastic events and management decisions were also considered as drivers of species prediction, through their direct influence on the surrounding habitat features (Fig. 3c). Therefore, to model habitat dynamics, sub-models were designed in order to reproduce: (1) the invasion of laurel forest by *C. arborea*, *P. undulatum* and other exotics (Fig. 3b), (2) the exploitation cycle of *C. japonica* plantations (Fig. 3b), (3) stochastic events, such as landslide episodes (Fig. 3c) and (4) habitat management actions in order to promote the Azores bullfinch conservation (Fig. 3c).

The invasion rates of the main exotic plants, *C. arborea* and *P. undulatum*, were based on their current extent of occupancy (23% and 33%, respectively) combined with historical data about the time interval since the respective introduction in the Azores archipelago (1960 and 1950, respectively) (Franco, 1984; Dias et al., 2007). To calculate these annual invasion rates (AIR) the following formula was used (Appendix G, Composed variables) (Chaves et al., 2000): $AIR = [(1 + ATIR)\exp(1/ITIY)] - 1$, where ATIR is the actual total invasion rate, given by the exotics current extent at the study area divided by their potential spread area, limited by the respective altitudinal ranges of tolerance (Ramos, 1996a; Schaefer, 2003; Silva and Smith, 2006) and ITIY is the invasion time interval, given by the number of years counted from the beginning of the invasion process firstly reported in the Azores archipelago (Franco, 1984; Dias et al., 2007).

The cycles of *C. japonica* exploitation were modelled to reproduce forestry stages of plantation, maturation and forest harvest as a steady state along the simulation period, since economic forestry cycles imply new plantations when an area is harvested (Decreto Regulamentar Regional no. 13/99/A de 3 de Setembro de 1999, Artigo no. 7; DRRF, 2007). The only exception to this cycle occurs inside the SPA, where the existent plantations are considered for conservation purposes and the forest logging is interdicted (Gil, 2004).

Landslides were incorporated in the model as optional deterministic or stochastic events. When selected, stochastic landslides are restricted to conditions of precipitation, random generated according to climatic data for São Miguel island (Azevedo, 2005), slope and altitude (Gil, 2004). Although the selection of the landslides running mode can be done by switching a toggle option between 0 and 1 for deterministic or stochastic calculations, respectively, in order to reduce uncertainty of the results and for demonstration purposes, only the deterministic option was used in the selected simulations.

Finally, management actions were included into the model in order to simulate control/removal of exotic plants and reconversion of *C. japonica* stands by plantation with native flora. The model is prepared to incorporate several different options concerning types of management, such as periodicity and/or intensity of removals and the target habitats to manage (depending on the degree of invasion).

The overall structural-dynamic variables, combined with environmental constants regarding the positional characteristics of each study unit (Fig. 3a), allowed the simulation of the ecological consequences of laurel forest invasion and human/natural induced changes on the Azores bullfinch local abundances. The time unit chosen was the year and the simulation period was established for 25 years. This period was considered suitable to capture the changes in the study area, namely those induced by invasion processes and/or by the long term environmental management actions and to perceive the Azores bullfinch responses in such contexts.

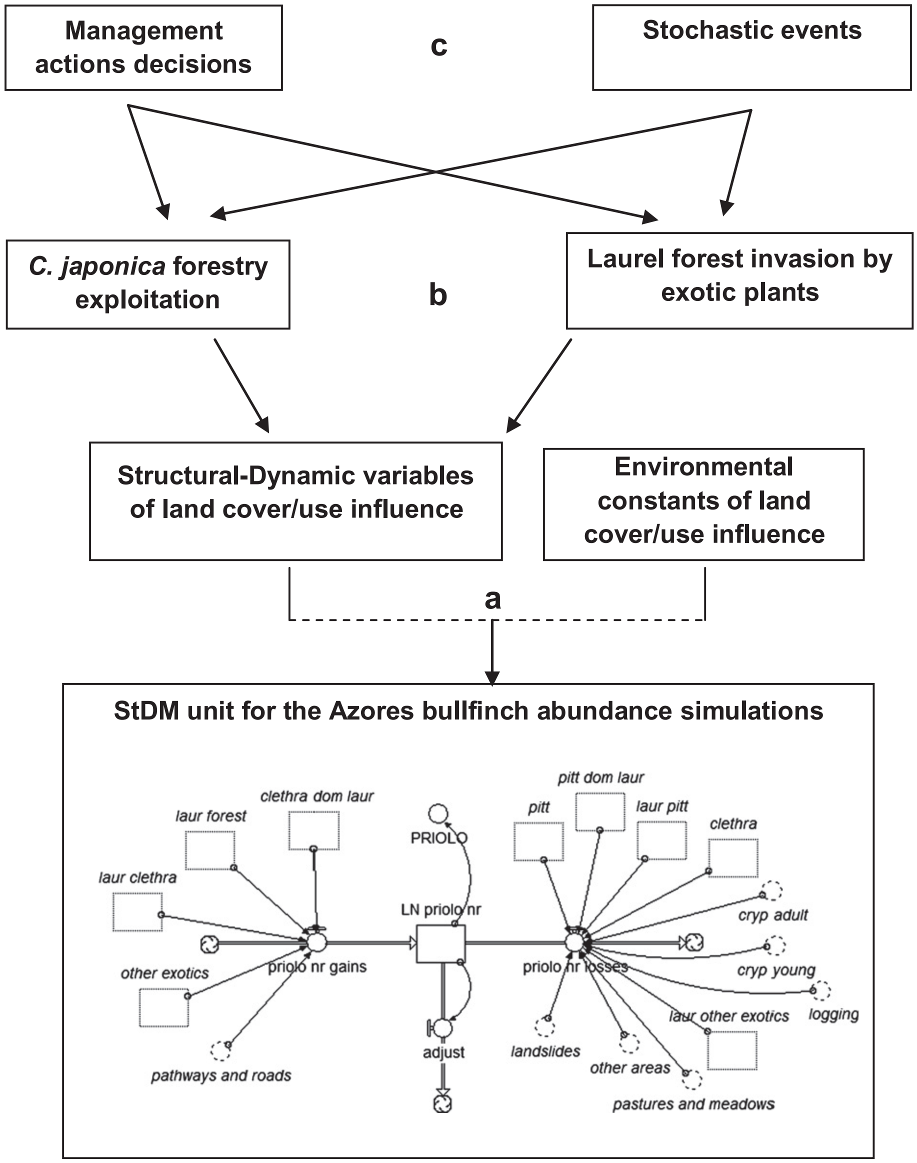

Fig. 3. Conceptual diagram of the StDM model used to estimate the Azores bullfinch abundances (PRIOLO) in São Miguel island. The model is composed by different dynamic sub-models and their interactions at the study unit level: (a) the overall structural-dynamic variables and environmental constants with influence in the StDM simulations of the Azores bullfinch abundances; (b) influences of the land cover/use dynamics; (c) influences of the management options and stochastic events.

For the development of the structural dynamic and StDM models the software STELLA 9.0.3® was used. The original conceptual diagram of the overall model and full explanation of processes, parameters and equations included in the model construction are available online as electronic Supplementary material.

2.4.5. Spatial dynamic projections

Dynamic trends of the Azores bullfinch abundance were initially simulated for each study unit (Fig. 2c). To create the spatial dynamic projections of the overall study area, every study unit was characterized according to the known initial land covers/uses and the resultant areas were included into the model in order to estimate the respective local abundances of Azores bullfinches. This spatial representation of multiple StDM simulations enabled us to create geographical projections of the bullfinch density for the whole study area. Although the selected spatial units capture the main combinations of the principal habitats that characterize the study area, each output only represents a preliminary independent contribution for the global pattern of the Azores bullfinch spatial occurrence, abundance and density (Fig. 2d). Since the dynamic projections neglect spatial relationships among individual study units, a kriging GIS interpolation method (Cressie, 1990; Sherman, 2011) was applied to project and integrate those population attributes for the overall study area (regional scale), by incorporating spatial autocorrelation among abundances per study unit (Zhang and Murayama, 2011) (Fig. 2e). Simple kriging interpolation was selected taking into consideration the type of data that resulted from the StDM (i.e. with continuous, non-discrete distribution and the absence of normally distributed data) and the expected spatial relations between study units (Walker et al., 2008). For every scenario and time selected, this procedure included the adjustment of the semivariogram by a sensitivity analysis of the most relevant model parameters (i.e. nugget, partial sill, lag size and anisotropy) (Dormann, 2011). Finally, we tested the fitting of the interpolated results (in relation to the modelled data) by cross validating the predictions of the spatial model with the results from the StDM simulations for each study unit, extracting a set of spatial indicators related to the distribution, densities and temporal variation of the Azores bullfinch predicted abundances.

The interpretation of the spatial changes in the bullfinch main distribution was based on the use of contour surfaces and the corresponding predicted abundances (Fig. 2e). In order to compare the spatial dynamic variation of species abundances, expressed in densities and their main distribution area, two time frames of the dynamic simulations were selected, the first year ($t = 1$) and the 25th year ($t = 25$), from which the respective spatial projections were carried out (Fig. 2c, d and e).

2.5. Management scenarios

The "LIFE Priolo" project, with active management actions implemented between 2003 and 2008 in the main area of the Azores bullfinch distribution, aimed to promote the recovery of its population through the protection and restoration of native laurel vegetation. In order to evaluate the effectiveness of this EU funded program, two initial scenarios were considered to compare the species response to the "LIFE Priolo" management actions and assuming the lack of those interventions in the study area. Furthermore, to get a realistic representation of new future scenarios, with logistically viable efforts in the Azores bullfinch recovery, some localized interventions were simulated in seven study units (around 2% of the study area). The main objective of such management scenarios was to evaluate the range of areas where habitat restoration can be more effective, by comparing the Azores bullfinch response to periodic actions in the previously "LIFE Priolo" managed areas or throughout new potential areas in the western part of the species distribution.

Management actions were simulated on a realistic time scale, starting in the Azores bullfinch reproductive season of 2015 (June–August), 7 years after the ending of the "LIFE Priolo" interventions. The periodicity chosen to repeat management effort was of 10 years, with an average intensity of 50% for exotics removal in each study unit. This assumption takes into account the viability of such effort, in terms of availability of funds, logistics and/or difficulties of terrain access, reflecting the proportion of area effectively managed, in each study unit, by the "LIFE Priolo".

The selected density breaks criterion, for the spatial projections representation, was based on classes expressed in bird numbers per study unit area (in hectares). The resulting total abundances were extrapolated from the simulation results, considering the estimate of 1064 individuals (Ceia et al., 2011a) as the reference value for our initial simulation of the Azores bullfinch population size.

3. Results

3.1. Effects of habitat patterns on the Azores bullfinch local abundance

After the multi-model selection and inference, the abundance of the Azores bullfinch was found to be positively related with laurel forest, laurel forest with *C. arborea*, *C. arborea* dominating laurel forest, other exotics, pathways and roads. Conversely, the species abundance was negatively related with laurel forest with *P. undulatum*, laurel forest with other exotics, *P. undulatum* dominating laurel forest, *C. arborea*, *P. undulatum*, *C. japonica* adult, *C. japonica* young, logging, landslides, pastures, meadows and other areas (Table 2).

3.2. Spatially dynamic simulations of outcomes from management scenarios

3.2.1. Effectiveness of previous habitat management actions

Assuming land cover/use dynamics as the key driver of bullfinch habitat composition and structure through time, simulations were performed for the several management scenarios described above. To evaluate the effective consequences of the "LIFE Priolo" management actions, the scenario 1 was created assuming the lack of management interventions in the area. To attempt this, study units subjected to management actions, from 2003 to 2008, were represented assuming the preceding land cover characteristics, allowing the dynamic model to project the natural trends of invasive plant species in the hypothetical absence of management actions (Fig. 4, scenario 1). In contrast, scenario 2 recreates habitat improvements carried out in the project and predicts the future consequences for bullfinch total abundances, densities and main distribution area, assuming the end of the project as the starting point for simulations (Fig. 4, scenario 2).

In both scenarios changes are expected in the spatial patterns of bullfinch density, with an increase in the number of individuals at the core of the main distribution area, which appeared to maintain the requirements as favourable breeding area (Fig. 4, scenarios 1 and 2, t_1 vs. t_{25}). Considering the consequences of the "LIFE Priolo" actions (scenario 2), throughout the following 25 years, the spatial

Table 2
Average results of information-theoretic-based model selection based on the Akaike information criterion for all models with $\Delta i < 2$ [$n = 254$; deviance = 189.2; coefficient of determination (R^2) = 42.55; adjusted coefficient of determination (R^2adj.) = 40.49; small-sample bias-corrected form of Akaike's information criterion (AIC_c) = 326.1] and the respective multi-model selection and inference parameters for all the independent variables selected as relevant to estimate the Azores bullfinch abundances: variable coefficient (Coefficient), variable importance (Importance), variable standard error (SE), variable adjusted standard error (SE adj.) and variable *z*-value (*z*). The specification of all variable codes is expressed in Table 1.

Variable codes	Coefficient	Importance	SE	$SE_{adj.}$	*z*
(Intercept)	6.37exp−01	–	6.57exp−01	6.57exp−01	0.97
cryp_adult	−2.24exp−06	0.78	1.65exp−06	1.65exp−06	1.36
cryp_young	−6.76exp−07	0.26	1.47exp−06	1.47exp−06	0.46
logging	−1.47exp−06	0.31	2.87exp−06	2.88exp−06	0.51
landslides	−6.66exp−06	0.95	3.90exp−06	3.88exp−06	1.71
laurel_forest	2.00exp−06	0.54	2.41exp−06	2.41exp−06	0.83
clethra	−6.42exp−08	0.03	7.45exp−07	7.43exp−07	0.09
pitt	−1.09exp−05	1.00	3.23exp−06	3.22exp−06	3.37
other_exotics	2.65exp−07	0.15	1.11exp−06	1.11exp−06	0.24
laur_clethra	1.89exp−07	0.06	9.37exp−07	9.35exp−07	0.20
laur_pitt	−5.48exp−06	0.25	1.42exp−05	1.41exp−05	0.39
laur_other_exotics	−3.53exp−07	0.05	2.50exp−06	2.49exp−06	0.14
cl_dom_laur	1.29exp−06	0.40	1.92exp−06	1.92exp−06	0.67
pitt_dom_laur	−1.51exp−05	0.90	1.08exp−05	1.08exp−05	1.40
pastures_and_meadows	−1.04exp−05	1.00	1.97exp−06	1.97exp−06	5.29
pathways_and_roads	6.14exp−05	1.00	2.76exp−05	2.74exp−05	2.23
other_areas	−2.63exp−05	1.00	1.74exp−02	1.73exp−05	1.51

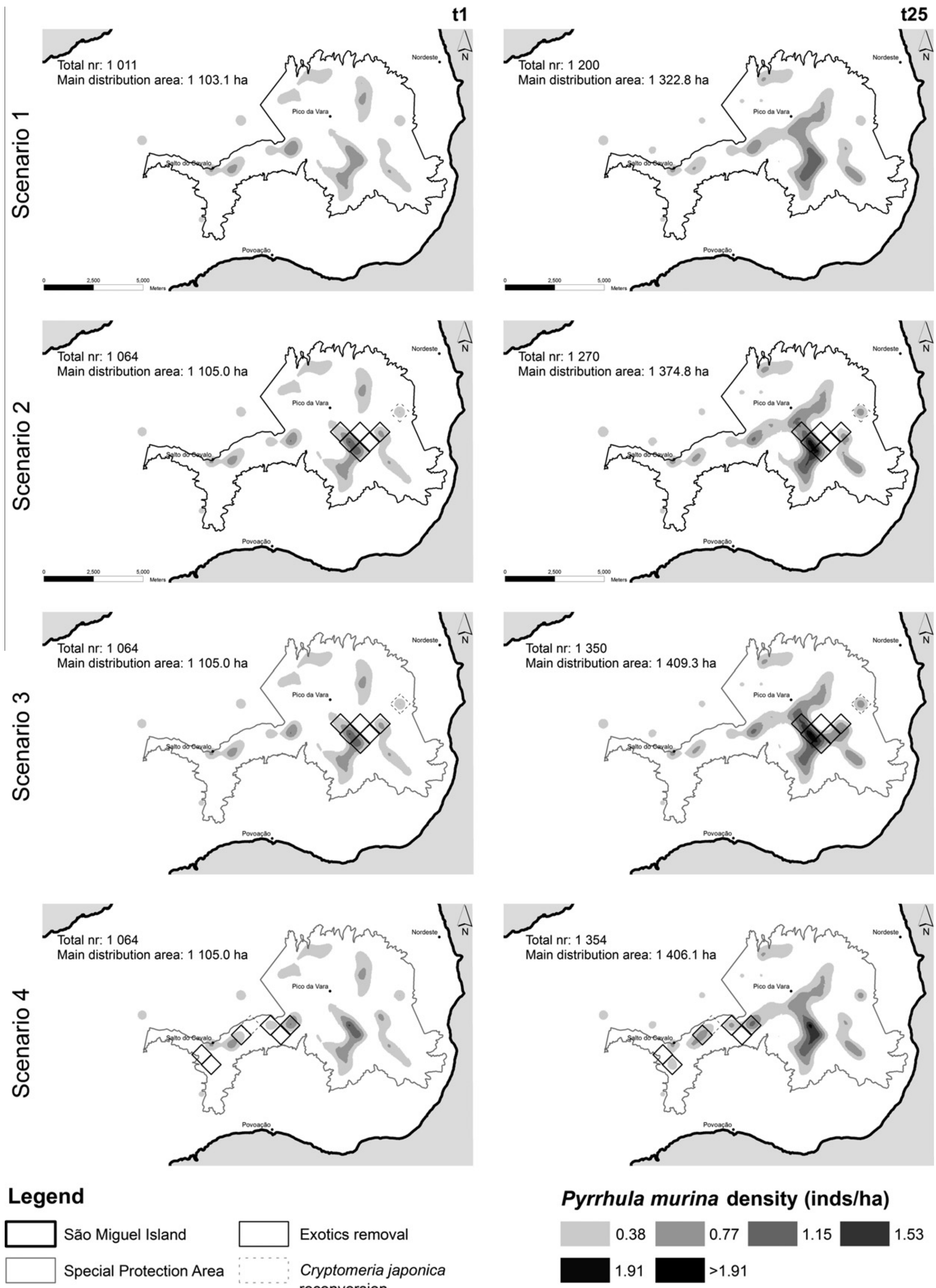

Fig. 4. Spatial representation of the Azores bullfinch responses without or with the "LIFE Priolo" management actions (scenarios 1 and 2, respectively) and facing future management actions in the "LIFE Priolo" areas or in new potential locations in the western part of the species distribution (scenarios 3 and 4, respectively). The Azores bullfinch main distribution area, total abundance and densities were calculated considering a continuous distribution function based on a simple kriging and its temporal variation from $t = 1$ to $t = 25$. The main distribution area was calculated based in the aggregation of the point-counts where more than 0.19 bird/ha was predicted, which correspond to at least one bird recorded per point-count.

projection reveals an increase in the Azores bullfinch densities towards the central range of the species occurrence (around 19%), representing an increase of around 6% of the total bird abundance when compared with the scenario without management actions (Fig. 4, scenario 1 t_{25} vs. scenario 2 t_{25}).

3.2.2. Effects of future management actions

The scenarios 3 and 4 were created to evaluate the response of the Azores bullfinch density, total abundance and main distribution to new specific and periodic management actions in its surrounding habitat (Fig. 4). These actions would include the control of invasive species in a 300 ha area (equivalent to six study units), assuming the results achieved by the "LIFE Priolo" project as initial reference, from where intervention actions were selected in order to comprise the removal of *C. arborea*, *P. undulatum* and other exotics. Additionally, the reconversion of a 10 ha of *C. japonica* plantations into laurel vegetation was also simulated in a supplementary study unit. In scenario 3, management actions prevented the reinvasion of the already managed areas during the "LIFE Priolo" project, which included 10 ha of reconverted *C. japonica* into native laurel vegetation, both located in the Azores bullfinch core area of distribution (Fig. 4, scenario 3). On the other hand, in scenario 4 the management actions were transferred, with an equivalent effort as described for scenario 3, to the western area of the Azores bullfinch occurrence (Fig. 4, scenario 4).

The spatial projections obtained for scenario 3 showed evidences of a considerable increase in local bullfinch densities, creating a compact and continuous central area for its main distribution in the next 25 years (Fig. 4, scenario 3 at t_{25}). Regarding scenario 4, the management of selected habitat areas in the bullfinch western area of occurrence seem to improve the spatial connectivity between the east and the west ends of the species range in the next 25 years (Fig. 4, scenario 4 at t_{25}). Although simulation results for both scenarios are similar with respect to the predicted total population size (Fig. 4, scenarios 3 and 4 at t_{25}), with a considerable increase in the number of individuals (around 27%), the final configuration of the main distribution area differs between management scenarios and may provide valuable complementary information with ecological value for decision-makers and environmental managers (Fig. 4, scenarios 3 and 4 at t_{25}). These results represent, respectively, a supplementary increase of more 6.5% in the Azores bullfinch abundance when compared with the "LIFE Priolo" actions (scenario 2) or more 13% when compared with the trends simulated for the scenario without management (scenario 1).

3.3. Global Azores bullfinch population trends

Despite the obtained spatial changes in the Azores bullfinch main distribution, density and population size, between the limits of the projected time interval of 25 years (Fig. 4), the global estimates throughout the simulation period revealed a non-linear variation in the bullfinch population size (Fig. 5). Independently of the scenario considered, the relative high values of total abundance, estimated for the period between the 11th and the 20th year (Fig. 5), seems to represent a transitory window of opportunity for the Azores bullfinch, regarding the cyclic emergence of additional favourable habitats. This dynamic phenomenon is mainly determined by the synchronic logging of several mature *C. japonica* plantations that provides the rapid appearance of "new" favourable areas of openings and young/immature *C. japonica* plantations surrounding by the laurel forest (Ramos, 1995, 1996a). Thereafter, during the maturation process of these young plantation areas, the increasing growth of *C. japonica* canopies induces by competition a gradual decline of the herbaceous cover, losing their importance as additional suitable habitat to the Azores bullfinch. In fact, after the

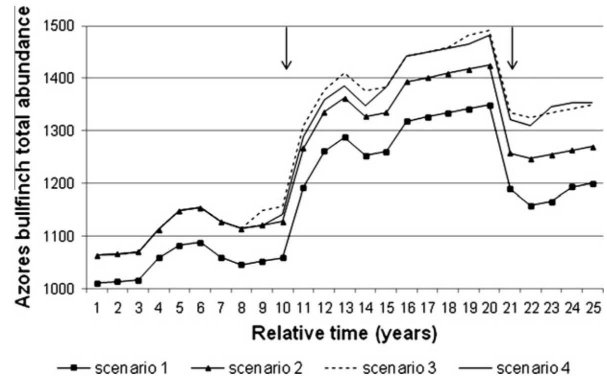

Fig. 5. Model simulation results for the trends of the Azores bullfinch total population size, throughout a period of 25 years, with or without the "LIFE Priolo" management actions (scenarios 1 and 2, respectively) and facing future management actions in the "LIFE Priolo" managed areas or in new potential areas in the western part of the species distribution (scenarios 3 and 4, respectively). The two arrows delimitate the time interval where the population exhibits a transitory rapid increase, mainly determined by the logging of several mature *C. japonica* plantations that provides the appearance of "new" favourable areas of openings and young/immature *C. japonica* plantations.

"favourable period" of the *C. japonica* exploitation, an evident depletive effect occurs in the recuperation trend of the Azores bullfinch total population size (Ramos, 1996a; Ceia et al., 2009) (Fig. 5). Our results showed that the modelling integration of the Azores bullfinch main habitat dynamics, at local and regional levels, is crucial to simulate and understand the global pattern of the species response to the long-term management actions tested.

4. Discussion

4.1. Conservation of the Azores bullfinch under habitat management scenarios

The main spatial patterns concerning the current distribution of the Azores bullfinch, strongly link its presence with laurel forest habitats. The distribution of this bird species is known to be greatly determined by the extent of the SPA, where the large majority of the optimal remnants of laurel forest in São Miguel island are enclosed (Ceia et al., 2011a). Our projected spatial patterns for the initial stage of the simulations are in agreement with previous studies showing higher densities in the eastern range of the Azores bullfinch and areas of lower density towards the western end of the range (Ramos, 1996a; Ceia, 2008). The predicted occurrence discontinuities (see Fig. 4 at t_1) are mainly related with the presence of mature *C. japonica* plantations and pure stands of *P. undulatum*, which are unsuitable habitats to the species (Ramos, 1996a; Ceia et al., 2009). In fact, the bullfinch population size and spatial distribution throughout simulations seemed greatly influenced by the dynamics of the *C. japonica* plantations, stressing the importance of their maturation cycles for the bird's current conditions. Nevertheless, areas that are opened following the timber exploitations can provide important additional food resources, particularly at lower altitudes, due to the emergence of additional favourable mixed habitats dominated by herbaceous cover (Ramos, 1995, 1996a). Moreover, the dynamics of *C. japonica* logging might also attenuate the restrictions to bird's movements, since it is described as a species with large home ranges and longer distance movements during the breeding season (Ramos, 1996a; Ceia, 2008).

Concerning the future patterns of the Azores bullfinch distribution, our results indicated an increasing importance of the central area of the species occurrence, suggesting major ecological restrictions in habitats located towards the edge of its range. The predicted changes in the central area of the species distribution seem to be greatly influenced by the habitat readjustments at mid-altitude, mainly determined by the forestry dynamics of *C. japonica* exploitation and the continuing invasion process by exotic plant species, particularly *P. undulatum*. In fact, the progressive invasion by *P. undulatum*, throughout the next 25 years, may push the species to upper elevations, restricting bullfinch occurrence in the southern boundary of its distribution, which is known to be the hillside most exposed to invasion (Hortal et al., 2010).

Overall, our framework outputs suggest that the sustainability of the Azores bullfinch population may be guaranteed only by suitable laurel forest, which remains in the central area of the SPA, although facing the *C. arborea* invasion. Nevertheless, since mixed laurel habitats with *C. arborea* has been shown to represent an important food resource for the Azores bullfinch in winter (Ramos, 1995, 1996b), the range of this exotic plant expansion inside the SPA (Moniz and Silva, 2003) does not seem to represent the same disruptive effect on the species distribution caused by the *P. undulatum* invasion in the next 25 years (Ramos, 1996a; Ceia et al., 2011b). In this context, despite the apparent changes in the Azores bullfinch distribution, our model scenarios indicate always an increase of total population size in the next 25 years. These projections are in agreement with the latest population trends (Ceia et al., 2011a) and survival modelling estimates (Monticelli et al., 2010), both suggesting some Azores bullfinch resilience or adaptation to habitat invasion by *C. arborea*.

Laurel forest restoration actions, implemented by the ‘‘LIFE Priolo’’ project, allowed the recovery of native plants, leading to a significant increase in the availability of native food resources in the SPA managed areas (Heleno et al., 2010; Ceia et al., 2011b). As a result of these habitat recovery actions, carried out in only 2% of the overall study area, our spatial projections estimated higher Azores bullfinch abundances in restored areas, contributing with a supplementary increase of 6% of the total population size. The analysis of the Azores bullfinch future main distribution patterns, simulated under the management scenarios considered, revealed the concentration of the higher local abundances/densities in restored areas, which may reflect the extent of the available favourable habitats that will satisfy the niche requirements of the species (Brown et al., 1995; Heleno et al., 2010; Ceia et al., 2011b). In this context, a continuous central area of bullfinch densities was always projected for the core of the species actual occurrence. Nevertheless, since similar population size increases were attained when the same management effort is disseminated for the western vicinities of the main occurrence area, the scenario 4 (Fig. 4) may contribute to enhance an additional spatial connectivity between the east and the west ends of the species distribution range in the next 25 years. Despite the higher costs associated to the interventions in new unmanaged areas (e.g. trail opening, high density of invasive plant species, reconversion of *C. japonica* stands by plantation with native flora), habitat improvements at marginal areas of the Azores bullfinch distribution could provide additional optimal breeding areas to the species. Considering that the species is highly susceptible to stochastic or anthropogenic events (Ceia et al., 2011a), this conservation measure would support the Azores bullfinch long-term sustainability, preventing the vulnerability of a confined population against extreme weather events, such as hurricanes in autumn, that might contribute to higher local mortality rates (Ceia, 2008).

4.2. Performance and added-value of the novel spatially dynamic framework

The spatially explicit StDM framework, developed in this study, seems to represent a useful contribution to predict key changes in the Azores bullfinch population trends, namely by quantifying the species abundance/density and its main distribution area under different possible management scenarios. Since the distribution and abundance of the Azores bullfinch seem to be largely determined by habitat structure, the resultant spatial dynamic simulations allowed a better perception of the consequences of the main exotic plants invasion and forestry dynamics, as well as the implications of the management decisions for the present and future conservation of this threatened species. In fact, taking into account the dimension of the managed area (only 2% of the study area), the results of the proposed integrative approach showed that the dynamic outputs and their spatial expression were not indifferent to changes in the bullfinch ecological conditions, including those induced by management actions, at both local and regional scales. Furthermore, the simulated ecological modifications are in agreement with field observations and other studies that investigated the ecological consequences of similar environmental changes (Elton, 1958; Kareiva et al., 1993; Ramos, 1996a; Thibault et al., 2002; Wal et al., 2008; Heleno et al., 2009; Anand et al., 2010; Ceia et al., 2011b). Nevertheless, since Azores bullfinch abundances can be only partly estimated by the habitat structure, this approach also provides a useful starting point, allowing the development of more detailed models, with introduction of other pertinent parameters, interactions and interferences (such as breeding success, carrying capacity and prey/predator cycles) with precise applicability conditions.

When compared to other modelling methodologies, such as Artificial Intelligence (Džeroski et al., 1997), our methodology seems to be more intuitive, namely in mathematical terms, providing simple explanations for the underlying relations between independent and dependent variables and because it is based on linearized methods that allowed a more direct development of testable hypotheses. Džeroski et al. (1997) argued that models produced in the form of rules, based on machine learning approaches, are transparent and can be easily understood by experts. Our integrative application also exhibits these structural qualities while still providing simple, suitable and intuitive outputs, easily interpreted by non-experts (from resource users and managers to senior policy-makers).

Another goal when developing methods for assessing changes in ecosystems is the feasibility of their application, as well as the extent to which results can be applied in other areas and targets (Andreasen et al., 2001). The StDM is easily applicable to other type of ecosystems, communities, guilds and species affected by gradients of changes (e.g., Cabral et al., 2008), where the selection of new scenarios is quick and relatively easy to the end-user. Moreover, the novel spatially explicit StDM upgrade allows not only the direct interpretation of the local dynamic trends of indicator response, but also the visualization of their emergent spatial distribution at a regional scale. The obtained simulation results are encouraging since they seem to demonstrate the reliability of the approach in capturing the dynamics of ecological systems by predicting the behavioural pattern for their key components selected under complex and variable environmental spatial scenarios. Nevertheless, although the first year of our spatial projections recreates realistically the known actual patterns of the Azores bullfinch distribution, if we consider that validation is a fundamental process when showing the relative accuracy of the model response in relation to its applicability (Rykiel, 1996), then a main question remains within the present methodological demonstration: the impracticality of an immediate validation of future scenarios, which can only be done after several years of collecting relevant site specific information in controlled conditions (Glenz et al., 2001; Chaloupka, 2002). Despite this limitation, inherent to a demonstrative study case in progress, the framework presented here offers a unifying approach with the spatial background and the multi-level connections that gives realism to the considered interactions by incorporating a typical ‘‘cascade effect’’ observed in the dynamics of the focal habitats. Therefore, since habitats are characterized by a high degree of heterogeneity in space and time, influenced by many interacting factors and feedback mechanisms, this multi-scale approach is particularly helpful to capture these multi-factor influences under relevant management scenarios.

Acknowledgments

The authors are indebted to all the volunteers who assisted in field work, part of the Azores bullfinch monitoring program included in the project LIFENAT/P/000013 "Recovery of Azores bullfinch's habitat in the Special Protection Area of Pico da Vara/Ribeira do Guilherme". We also thank the LIFE Priolo (LIFE03 NAT/P/000013) project team and the Sociedade Portuguesa para o Estudo das Aves (SPEA) for logistical facilities during fieldwork. Special thanks are addressed to Antoine Guisan, from University of Lausanne, for sharing experience and comments on the statistical analysis implementation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.01.009.

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