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Applying species distribution models in conservation biology

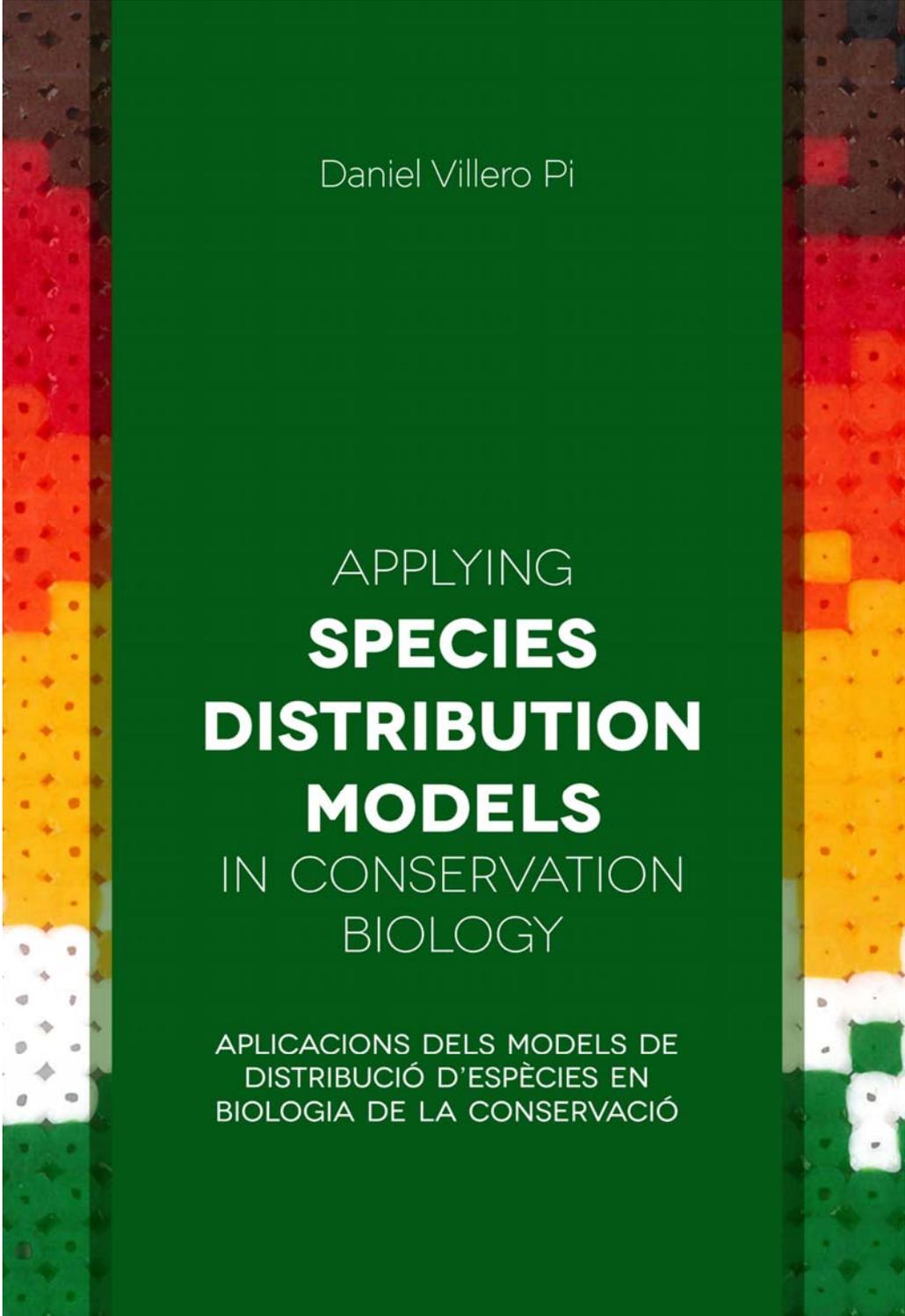
Aplicacions dels models de distribució d'espècies en biologia de la conservació

Daniel Villero Pi

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Daniel Villero Pi

APPLYING
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DISTRIBUTION
MODELS
IN CONSERVATION
BIOLOGY

APLICACIONS DELS MODELS DE
DISTRIBUCIÓ D'ESPÈCIES EN
BIOLOGIA DE LA CONSERVACIÓ



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Centre Tecnològic Forestal de Catalunya/CEMFOR
i Departament de Biologia Evolutiva,
Ecologia i Ciències Ambientals

Applying species distribution models in conservation biology

*Aplicacions dels models de distribució d'espècies
en biologia de la conservació*

*Memòria presentada per Daniel Villero Pi
per optar al grau de doctor per la Universitat de Barcelona*

Daniel Villero Pi

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Dr. Albert Montori Faura

Barcelona, Juny 2016

*A la Magda,
i al Manel, la Carme i en Ramon
per seguir gaudint plegats de les coses boniques
i de tots els temps del món*

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Summary

This work is at the crossroads where conservation problems, arising from biodiversity and environmental crisis, meet the difficulties of applying research outcomes in conservation practice, framed in a sustained decline of resources for biodiversity conservation due to an entrenched economic and social crisis. The overall aim of the thesis is to deepen in the use of species distribution models (SDM) to improve decision-making processes in biodiversity conservation. With the ambition to build bridges between research and conservation practice, the thesis proposes to stay closer to real contexts of decision making and contribute to boost effective species conservation strategies. Concerning methodological issues, the thesis emphasises the importance of information sources of species distribution, since it's a key aspect of the quality of SDM outcomes, and also one of the most controversial sections of conservation budgets. To meet these objectives, the thesis include six chapters organised in three thematic blocks. The first block include various examples of SDM application to different conservation backgrounds (Chapters I, II, III, IV and V). Complementarily, the second block explore how to boost SDM outcomes to inform conservation practice (Chapter IV and V). Finally, the third block examines uncertainties of different information sources of species distribution to develop SDM (Chapter VI). The thesis highlight SDM as key tools to improve decision-making in different conservation backgrounds, playing critical roles in almost all steps of the decision-making processes, especially in dealing with decision uncertainties. It also emphasize that an effective implementation of SDM to solve conservation problems has to match SDM goals to specific questions arising from the decision-making process, and also to promote utilisation of SDM outcomes through active communication and clear, valuable and useful information products. These two conditions are also sufficient for an effective knowledge-transfer from other scientific developments to inform and improve conservation practice.

Resum

Aquest treball es situa en la cruïlla on conflueixen els problemes de conservació, derivats de la pèrdua de biodiversitat i la crisi ambiental, amb els problemes d'implementació de solucions efectives, relacionats amb les dificultats d'aplicar els resultats de la recerca en la pràctica de la conservació, tot plegat emmarcat dins un context més general de crisi econòmica i social que es tradueix en una reducció progressiva dels recursos destinats a la conservació de la biodiversitat. L'objectiu general de la tesi es aprofundir en la utilització de SDM (models de distribució d'espècies) per millorar els processos de decisió en conservació de la biodiversitat. Amb l'ambició de bastir ponts entre la recerca ecològica i la conservació sobre el terreny, la tesi es planteja anar una mica més enllà dels exercicis teòrics i apropar-se a contextos reals de presa de decisions per fer contribucions més efectives a la conservació de les espècies. Pel que fa als aspectes metodològics, la tesi posa l'accent en la importància de les fonts d'informació sobre distribució d'espècies, atès que es un aspecte clau de la qualitat dels resultats dels SDM i alhora un dels apartats més controvertits en els pressupostos públics destinats a la conservació. Per donar resposta a aquests objectius, la tesi consta de sis capítols estructurats en tres blocs temàtics. En el primer bloc es desenvolupen exemples d'aplicació de SDM en diferents contextos de conservació (Capítols I, II, III, IV i V). De forma complementària, el segon bloc explora com potenciar els resultats derivats dels SDM per informar la pràctica real de la conservació (Capítol IV i V). Finalment, el tercer bloc examina la incertesa de diferents fonts de dades biològiques per desenvolupar SDM, tenint en comte diferents àmbits d'aplicació (Capítol VI). Al llarg dels diferents capítols s'ha posat de manifest que els SDM son eines clau en la millora de les decisions de problemes de conservació diversos, i amb implicacions en quasi totes les etapes dels processos de decisió, i especialment en la quantificació de la incertesa relacionada amb cadascuna de les etapes. També s'ha posat de relleu que l'aplicació efectiva de SDM en processos de decisió passa per ajustar els objectius dels SDM a les preguntes plantejades en el context particular del problema de conservació, i també per promoure la utilització dels resultats obtinguts amb SDM a traves d'una comunicació activa i de productes espacials clars, útils, accessibles i ben ajustats al problema de conservació. Aquestes dues condicions son igualment vàlides per la transferència efectiva d'altres desenvolupaments científics per la millora de la pràctica de la conservació de la biodiversitat.

Introduction¹

Where conservation should be done?

Conservation biology is a discipline aimed at solving pressing problems based on partial and biased knowledge of species and ecological processes (Pullin, 2002). As other "crisis" disciplines, as emergency medicine or firefighting, professionals have to use their intuition to make decisions and provide solutions with high degrees of uncertainty (Pullin et al., 2004; Soulé, 1985). In addition, the impact of these decisions beyond conservation -e.g. protected areas definition in the context of regional development policies, or control of invasive species to avoid impacts on the primary sector- implies that decision-making processes are always governed by strong external pressures related to administrative and political agendas (Whittaker et al., 2005). However, global climate change and biodiversity loss pose serious challenges for Conservation Biology in 21st century (Brook et al., 2016; Sodhi et al., 2008; Vitousek et al., 1997). These challenges can only be faced improving conservation practice with more useful and applied science (Convention on Biological Diversity, 1992).

The *where*, *when* and *how* conservation should be done are key and complementary questions to be addressed in conservation (Redford et al., 2003). *Where* and *when* questions address spatial and temporal definition of priorities, while *how* emphasises the development and implementation of strategies to achieve conservation objectives. To answer these questions significant financial investments are required, and these are multiplied when extending the conservation focus to taxonomic groups with bigger gaps of knowledge. But far from enough, financial resources would not seem to increase for covering all investment needs (James et al., 1999). Rather contrary, present and future social and economic crisis offer pessimistic prospects for conservation biology. Given the scarcity of financial support, critics with the conservation status quo are increasingly getting arguments to defend the need to improve the implementation of effective conservation strategies (*how* questions) against the accumulation of information to support them (*where* and *when* questions). This criticism is based on the evidence that the success of conservation strategies is more influenced by social, economic and political factors, rather than the lack of knowledge about species ecology

¹ This chapter translate the original introduction written in catalan (**see Appendix**).

(Knight et al., 2010). This controversy points out an existing tension between different approaches to deal with serious and growing conservation challenges arising in the next few decades. Faced with these challenges, the implementation of new analytical tools in decision-making processes, developed in the field of ecological research, opens up new possibilities both to optimize the use of available information, as well as to improve the efficiency of conservation actions (Sutherland et al., 2004).

Answers to *where* question provide good examples of the impact of new tools in the implementation of conservation actions. Until recently, definition of protected areas has been a good example of subjectivity in decision-making (Pressey et al., 1994). This vision, however, has changed with the progressive development of systematic conservation planning tools (Bedward, M. et al., 1992; Groves et al., 2002; Jennings, 2000; Margules and Pressey, 2000), applied to support the definition, location and extent of protected areas within structured and dynamic decision-making processes based on scientific evidences (Margules and Pressey, 2000; Wilson et al., 2007). These tools allow to optimize resources needed to develop improved conservation strategies, based on a more efficient use of species primary information (Ferrier et al., 2002; Margules et al. 1994), but also information on the impact and severity of environmental pressures (Pressey and Bottrill, 2008), and the social, economic, political and cultural issues around the conservation problem (Knight et al. 2006), as well as the costs and benefits of various alternative actions and the opportunities and constraints to implement them (Cowling et al., 2008; Knight et al., 2008, 2006; Naidoo and Ricketts, 2006).

Among these new tools, species distribution models have been recognised for its great application potential in conservation. These methods, developed in the framework of the niche theory, provide a deeper understanding of the environmental factors determining species distributions, and are especially suited to contrast ecological and evolutionary hypotheses, and forecast (or hindcast) predictions in space and time (Araújo et al., 2005; Thuillier et al., 2005). Conservation applications are not limited to improve knowledge of species current distributions, but also empower to examine processes of contraction, expansion and fragmentation of species distributions at large spatial and temporal scales (Garcia et al., 2014; Whittaker et al., 2005; Willis et al., 2007), and also at smaller scales closer to conservation practice (Richardson et al., 2010; Sebastian-Gonzalez et al., 2011; Starfield, 1997).

Theoretical basis of species distribution models

The term “niche” to describe abiotic (temperature, rain, etc.) and biotic (competition, predation, etc.) conditions within which a species can survive and reproduce, first appeared in scientific literature in a Joseph Grinnell paper published in early-20th century (Grinnell, 1917, 1924). At the same time, Charles Elton (1927) amended this definition, mentioning that the “niche” is referred to the role of species in ecological communities, with emphasis on the biotic conditions and its impact on the configuration of ecological communities, and diminishing the role of abiotic conditions. Some years later, George Evelyn Hutchinson (1957) formalized niche theory, opening the doors for modern ecology (Leibold, 1995; Vandermeer, 1972). In his theory, Hutchinson differed *fundamental niche* - environmental conditions within which a species could survive and reproduce in the absence of interactions with other species- from *realized niche* -environmental conditions within which a species actually lives, taking into account interactions with other species (Figure 1).

More recently, the neutral theory (Hubbell, 2001) has questioned the role of niche to explain species observed occurrence and abundance patterns. This theory argues that stochastic population events (i.e. birth, death, immigration and emigration), and not niche differences among species, determine communities' composition at local scales, based on the assumptions that all species are essentially identical in terms of birth, death, dispersal and extinction rates, and they all have a limited dispersal abilities (Figure 1). This debate has been a main target of ecological research since the beginning of the 21st century, being the substrate to a more holistic overlook where niche theory and neutral theory represent opposite ends of the same process along which ecological communities are observed (Gaston et al., 2008; Kelly et al., 2008; Leibold and McPeck, 2006).

In this theoretical framework, the development of species distribution models has a key role to confront species distribution and abundance patterns of species to the hypothesis proposed by neutral theory (Chown and Gaston 2005; Hubbell, 2005; Kelly et al., 2008). These analysis have also benefited from the integration of some aspects of the neutral theory to species distribution models, such as dispersion limitations (Brotons et al., 2011; Smith and Green, 2006; Snyder and Chesson, 2003) or stochastic demographic processes (Carnicer et al., 2007;-Sebastián González et al., 2011; Tilman, 2004). Further, species distribution models have allowed to gain a deeper understanding of other aspects of the niche theory, for example co-occurrence

patterns in ecological communities and competitive exclusion (Helmus et al., 2007; Kraft et al., 2007 ; Webb, 2000).

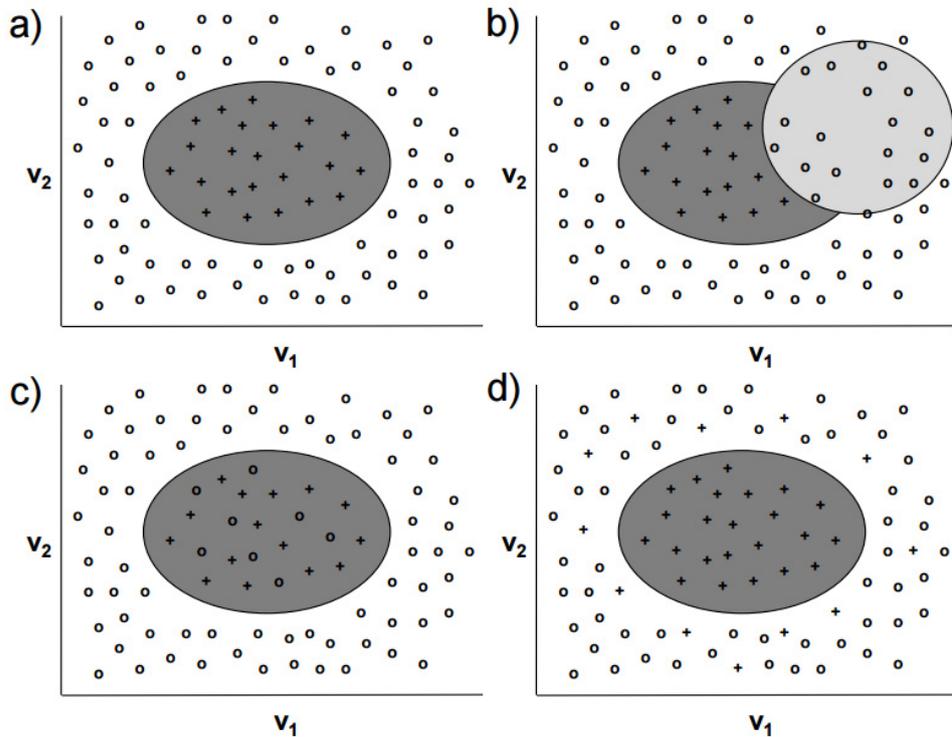


Figure 1. Various plausible relationships between the fundamental niche, shown here by dark grey shading, and the actual distribution of species, shown here as hypothetical instances of species presence (+) or absence (o). For simplicity, the niche is assumed to be a simple function of two environmental variables, v_1 and v_2 : (a) the species occupies its entire fundamental niche; (b) the presence of a superior competitor (light grey shading) excludes the species from part of its fundamental niche, leaving it to occupy the realized niche; (c) dispersal limitation means that the species is unable to reach all environmentally-suitable areas; (d) continued migration from areas of suitable habitat (sources) allows the species to persist in areas of unsuitable habitat (sinks). Source: Pulliam, 2000.

Species distribution models (henceforth SDM) refers to a heterogeneous set of numerical methods intended to relate biological information on species distribution and environmental information to build spatially explicit predictions of species distribution in a geographical area of interest (Guisan and Zimmermann, 2000). These methods, initially based on linear regressions and discriminant analysis (Franklin, 1995), have been boosted by the emergence of new modelling algorithms (Guisan and Thuillies 2005; Wintle et al., 2005), simultaneous to the rapid emergence of geographic information systems and large environmental databases (Gillespie et al., 2008;

Shanmughavel, 2007), all framed in the technological acceleration process experienced for the last two decades (Figure 2). The availability of robust and detailed information on climate, topography and habitat for all marine and terrestrial environments has generakized SDM applications to study all kind of organisms (Hawkes et al., 2007; Kaschner et al., 2006; Wiley et al., 2003). Advances in these methods are reflected in numerous papers, essays and books establishing a general framework for modelling species distribution (Elith and Leathwick, 2009; Franklin, 1995; Thuillier and Guisan 2005; Guisan and Zimmermann 2000; Mackey and Lindenmayer, 2001; Wintle et al., 2005), links with ecological theory (Austin, 2007, 2002, Hirzel and Le Lay, 2008), modelling methods (Guisan et al., 2002; Pearce and Boyce, 2006), biological information and scale models (Graham et al., 2004; Rushton et al., 2004), modelling ecological communities (Ferrier and Guisan, 2006) and conservation applications (Burgman et al., 2005; Ferrier et al., 2002; Franklin, 2010; Rodriguez et al., 2007), among many other issues.

A critical consideration in SDM is defining what niche component is analysed (Pulliam 2000). Some methods are based on a statistical correlative approach to establish relationships between a set of abiotic variables and species observed current distributions. Given that the current distribution of the species is not determined solely by abiotic factors, but also involved interaction with other species and/or dispersion limitations, correlative methods are proxies to predict species *realized niche* (Guisan and Araújo, 2006; Guisan and Zimmermann, 2000; Soberón and Townsend Peterson, 2005). Other methods use a mechanistic approach to predict species *fundamental niche*, based on direct measurements of the physiological response of species to environmental conditions. Additionally, these methods may also include biotic interactions to move toward species *realized niche* (Austin, 2002; Pearson and Dawson, 2003).

These considerations are in the basis of the applications of SDM, expressly when used to predict the species distribution outside the environmental conditions used for their development; methods that capture *fundamental niche* should offer better extrapolations than those that capture the *realized niche* based on particular environmental conditions (Pearson and Dawson, 2003). However, the application of mechanistic methods involves some conceptual limitations related to partial estimates of *fundamental niche*, i.e. physiological response to environmental conditions can vary at population (phenotypic plasticity) and evolutionary (niche shifts) scales, and predictions not necessarily are a good reflection of species distributions, i.e. species ranges represent only part of the species fundamental niche (particularly areas colonized by dispersion processes). To these conceptual limitations must be

added the complexity and high cost to parameterize and validate mechanistic models, which nowadays has strongly conditioned the widespread use of these methods (Webber et al., 2011).

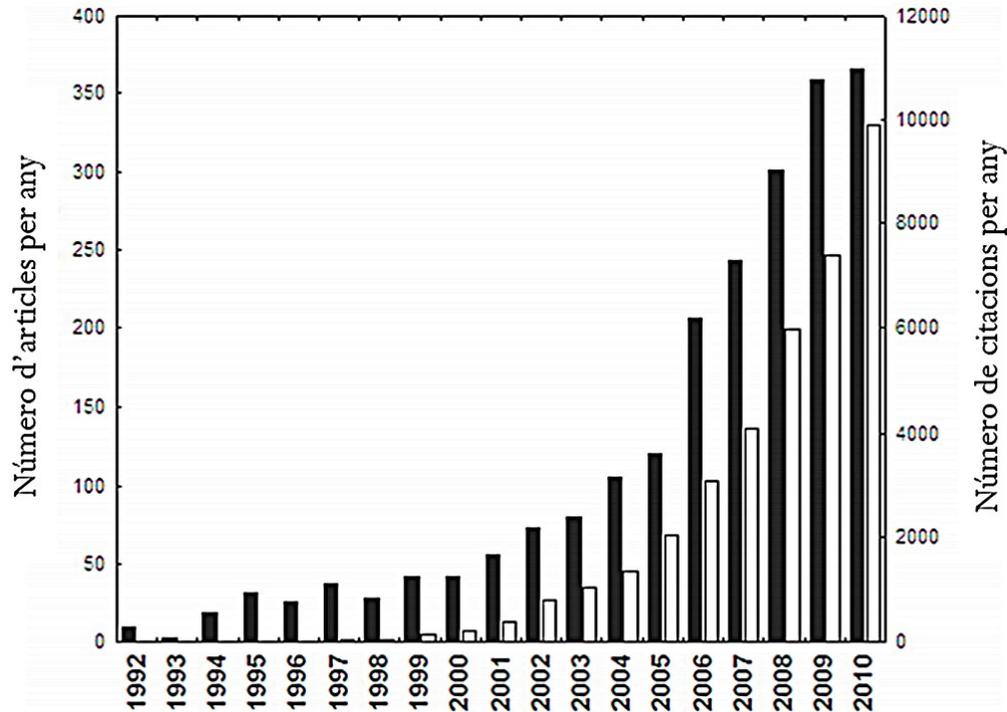


Figure 2. Number of published SDM related articles in the ecological literature (black bars) and number of citations received by these articles per year (white bars) during the period 1992–2010..

Source: Brotons, 2014

Regarding correlative methods, one of the most common criticisms point out that these methods yield lightly accurate predictions that do not necessarily capture causal relationships between species and environment, avoiding all theoretical foundations (Hirzel and Le Lay, 2008). That feature is closely related to the use of SDM to answer two different key questions. On one hand, quantitative ecology and evolutionary biology use SDM to *explain* causal factors determining species distribution (Graham et al., 2004b; Leathwick and Austin, 2001; Mac Nally, 2000). On the other hand, the increase in demand for applications related to spatial planning and biodiversity conservation has promoted the use of SDM to *predict* species distributions (Ferrier and Wintle, 2009; Franklin, 2009; Guisan et al., 2013) based on species-environment statistical relations but with strong ecological criteria, especially on the selection of predictor variables and interpretation of model outcomes.

In conservation practice, the use of correlative models to predict species distributions improves knowledge of species current distribution. These applications are effective when predictions are based on SDM built with reliable biological data correlated with appropriate environmental predictors, according to species ecology (Guisan and Zimmermann, 2000; Tulloch et al., 2016). Further, SDM also allow to predict species distribution into new geographical or temporal scenarios, historical or future. In these applications new environmental conditions must be properly analysed, especially when representing new environmental conditions beyond the environmental ranges used to model development. Besides the inherent risks of the projection or extrapolation of SDM to new environmental conditions, related to the lack of data to validate predictions, its application contradicts the assumption that species are in equilibrium with the environment to, one of the main SDM assumptions. However, correlative SDM are still one of the few methods to analyse environmental change impacts on species distribution, justifying that are in the forefront of ecological research (Brotons, 2014; Elith and Leathwick, 2009).

Implementation of species distribution models in conservation

Spatially explicit predictions obtained with SDM provide an unquestionable added value respect to simple distribution data used traditionally to report species distribution, with a high potential for prioritising conservation actions (Ferrier et al., 2002 ; Franklin, 2009; Jetz et al., 2012). Improved knowledge of species distribution provides insights of determinant ecological factors and, based on SDM robust predictive capabilities, achieves predicted distributions for different conservation applications (Tulloch et al., 2016). Examples of applications include the improvement of sampling strategies for rare or endangered species (e.g. Siqueira et al., 2009; Guisan et al., 2006; Marcer et al., 2012; Pearson et al., 2007; Raxworthy et al., 2003; Thomas et al., 2004), identifying priority areas and designing networks of protected areas (e.g. Arcos et al., 2012; Fajardo et al., 2014 ; Hermoso et al., 2015; Pawar et al., 2007; Wintle et al., 2005), orientation of recovery plans or species reintroduction and ecological restoration (e.g. Angelieri et al., 2016 ; Clavero and Hermoso, 2015; Fei et al., 2012; Gastón and Viñas García, 2013). Also, SDM can be extrapolated to new geographic and temporal scenarios to assess the risk of invasive species (e.g. Ficetola et al., 2007; Jiménez-Valverde et al., 2011; Roura-Pascual et al. , 2007) or to predict -or explain retrospectively- potential impacts of climate change (e.g. Ficetola et al., 2010; Runge et al., 2015) or land-use changes (e.g. Jetz et al., 2007; Martin et al., 2013; Regos et al., 2015; Vallecillo et al., 2009).

However, most of these assessments published in peer-reviewed journals consist of scientific analyses in pursuit of ever-more precise information on, and efficient techniques for, prioritizing elements in a conservation framework, lacking real-world conservation contexts of application (Guisan et al., 2013; Rodriguez et al., 2007). Far less scientific attention has been devoted to practical approaches for developing strategies that make effective use of SDMs through inclusive decision making processes, to improve prospects for implementation and, ultimately, successful conservation efforts (Addison et al., 2013; Guisan et al., 2013; Knight et al., 2006).

The lack of SDM applications to solve real conservation problems is part of a more general implementation crisis of scientific developments that goes beyond conservation science, and that was classified for the first time in economics and social psychology disciplines (Pfeffer and Sutton, 1999). In conservation biology, the difficulty of translating the results of research has implications at different levels, from strategic planning (e.g. ineffective plans based solely on scientific knowledge and without the participation of key institutions in the process planning) to develop conservation actions on the ground (e.g. proposed effective conservation actions but infeasible in social or economic terms) (Knight et al., 2006; Prendergast et al., 1999; Salafsky et al., 2002).

Many authors point out that these difficulties are rooted in dissimilarities between scientists and conservation practitioners, referred to core differences on funding sources, work planning, career aspirations or reward structures (Cook et al., 2013; Guisan et al., 2013). These differences determine distant standpoints when facing the same conservation problem, often further away misconceptions from both scientists and conservation practitioners about real conservation management questions (Knight et al., 2008; Laurance et al., 2012), and about the utility (or even the existence) of valuable research insights (Addison et al., 2013; Pullin et al., 2004), respectively. To reverse this situation, some authors pose the need to promote "translators" that facilitate information flows between scientists and decision makers, embodied by intermediate organizations, individuals, groups or consortia (Cash et al., 2003; Guisan et al., 2013; Schmolke et al., 2010; Soberon, 2004). Also, these authors propose the structured decision-making framework (Gregory et al., 2012) as a conceptual foundation to approach research developments to conservation practice (Addison et al., 2013; Guisan et al., 2013; Knight et al., 2006).

The structured decision-making framework promotes stakeholder participation in a sequential process starting from the definition of the decision targets until the final implementation of the decision outcomes (Addison et al., 2013; and Gregory Long, 2009 ; Gregory et al., 2001; Reed,

2008) (Table 1). These processes stimulate the use of a wide range of analytical tools to provide rigorous, transparent and logical solutions. Moreover, there is a good context for the "translators", stimulating the social dimension of decisions, generally ignored in conventional scientific careers (Addison et al., 2013), and maximizing decision efficiency based on improved communication between participants and, hence, enhanced confidence in final decision outcomes.

Table 1. Key steps in a structured decision-making process (Gregory and Long, 2009).

Clarify the decision context	Define the context and scope of the decision, along with budgets and timelines.
Define objectives and evaluation criteria	State key considerations in terms of endpoints or values that could be affected by policies or actions under consideration.
Develop alternatives	Establish a range of well-defined management options, showing diversity in response.
Estimate consequences and identify uncertainties	Make use of best science along with local community and aboriginal knowledge to show anticipated consequences of actions. Include explicit estimates of uncertainty
Evaluate trade-offs	Recognize differences in the importance of objectives and how these will influence preferred choices.
Select preferred option(s), implement and monitor	Document the decision process, implement the selected alternative(s), and monitor to improve the basis for making future decisions.

Objectives²

This work is at the crossroads where conservation problems, arising from biodiversity and environmental crisis, meet the difficulties of applying research outcomes in conservation practice, framed in a sustained decline of resources for biodiversity conservation due to entrenched economic and social crisis. The overall aim of the thesis is to deepen in the use of species distribution models (henceforth SDM) to improve decision-making processes in biodiversity conservation. With the ambition to build bridges between research and conservation practice, the thesis proposes to stay closer to real contexts of decision making and contribute to boost effective species conservation strategies. Concerning methodological issues, the thesis emphasises the importance of information sources of species distribution, since it's a key aspect of the quality of SDM outcomes, and also one of the most controversial sections of conservation budgets. Specific objectives include:

- To evaluate the role of SDM applications to different conservation problems.
- To explore the links between SDM conceptual framework and decision-making processes to enhance the use of model outcomes to inform conservation practice.
- To examine the use of different information sources of species occurrence and abundance to develop SDM, and implications on the quality of predictions, as well as the prospects of application.

To meet these objectives, the thesis is divided into three thematic blocks consistent with specific objectives, although some chapters deal with more than one objective and, therefore, are included in different blocks. The first block includes various examples of SDM applications to different conservation backgrounds (Chapters I, II, III, IV and V). Complementarily, the second block explores how to boost SDM outcomes to inform conservation practice (Chapter IV and V). Finally, the third block examines uncertainties of different information sources of species distribution to develop SDM (Chapter VI).

² This chapter translate the original objectives written in catalan (**see Appendix**).

Chapter I. Abundance maps in the Catalan Winter Bird Atlas 2006-2009³

Abstract

The Winter bird atlas of Catalonia 2006-2009 is the result of a collective effort with over 1,000 volunteer collaborators. The work fills the gap of knowledge on birds in winter with detailed information about the spatial and temporal abundance patterns, population estimates and trends, and habitat preferences. The heterogeneity of information sources to feed species distribution analyses has resulted in five types of abundance maps, each with its own calculation methods, graphical representation and interpretation. Hence, there are abundance maps for terrestrial birds, built with SDM and different analytical procedures for common and uncommon species (77 and 74 species, respectively); abundance maps for widespread river birds (5 species), addressed with similar procedures of uncommon terrestrial species; abundance maps of water birds (30 species), based on the annual census of wintering waterbirds; abundance maps of coastal seabirds (16 species), developed with interpolation techniques based on seabirds censuses from the coast; and abundance maps of pelagic seabirds (9 species), developed with SDM based on oceanographic surveys. The publication of this atlas, along with its predecessor, the Breeding Bird Atlas 1999-2002, makes closer a comprehensive view of birds distribution and abundance throughout the year, strengthen the foundations to birds conservation in Catalonia.

³ This chapter cover the methodology of abundance maps from *Winter bird atlas of Catalonia 2006-2009*. The author has written this part of the atlas methods and has performed all concomitant analysis. Manuscript courtesy of the Institut Català d'Ornitologia.

Reference: Herrando, S., L. Brotons, J. Estrada, S. Guallar, M. Anton, **D. Villero**, R. Gutiérrez, G. Gargallo, P. Arcos, J. Bécares, J. Quesada & M. Pla. 2011. Metodologia. En: Herrando, S., L. Brotons, J. Estrada, S. Guallar and M. Anton (eds.) 2011. *Atles dels ocells de Catalunya a l'hivern 2006-2009*. Institut Català d'Ornitologia & Lynx Edicions, Barcelona. 59-112 pp.

Resum

L'Atlas dels ocells de Catalunya a l'hivern 2006-2009 és una obra col·lectiva, amb més de 1.000 col·laboradors voluntaris, que omple el buit de coneixement sobre l'avifauna a l'hivern amb informació detallada per a cada espècie sobre la distribució espacial de l'abundància i la seva variació interanual, la mida de les poblacions i les tendències temporals, així com les preferències d'hàbitat i altitud. La gran heterogeneïtat de fonts d'informació utilitzades per analitzar la distribució de les espècies s'ha traduït en 5 tipologies de mapes d'abundància, cadascun amb els seus propis procediments de càlcul, representació gràfica i interpretació. Les 5 tipologies comprenen mapes d'abundància d'ocells terrestres, basats en SDM i amb diferents tractaments de dades per les espècies molt comunes (77) i poc comunes (74); mapes d'espècies aquàtiques continentals comunes (5), abordats de forma similar a les espècies terrestres poc comunes; mapes d'abundància d'ocells d'aigües continentals (30), basats en els resultats dels censos d'ocells aquàtics hivernants; mapes d'abundància d'espècies costaneres (16), desenvolupats amb tècniques d'interpolació a partir dels mostratges d'ocells des de la costa; i mapes d'abundància d'ocells marins pelàgics (9), desenvolupats amb SDM a partir dels resultats de campanyes oceanogràfiques. La publicació d'aquest atlas, juntament amb el pòsit del seu predecessor, l'Atlas dels ocells nidificants 1999-2002, fa més propera una visió global de la distribució i abundància al llarg de tot l'any dels ocells a Catalunya, establint un marc de referència cabdal per la conservació d'aquest grup d'espècies.

Abundance maps

In recent years there has been an increasing trend in ornithological atlases towards the generation of abundance maps, especially in those atlases that represent a first or a second update of a previous publication (Gibbons et al. 2007). Following on from the second Catalan Breeding Birds Atlas, the new winter Atlas also contains abundance maps, although in this publication they are of a more diverse nature. They essentially consist of two types: those that represent the results of absolute bird censuses carried out in specific areas, and those that rely on statistical inference from a representative sample of a species' population. The first case only concerns maps generated with data gathered during the winter waterbird censuses, which provide results that can be mapped in a very straightforward fashion; for the rest of the species the abundance maps are based on different statistical modelling techniques. Unlike in the Catalan Breeding Bird Atlas, in this new atlas not every species has a single map, and the number of maps per species depends on the extent to which abundances varied during the study period. Thus, in all cases, before creating the maps we calculated the spatiotemporal differences in the abundance of the species during the three winters of the study period.

Spatiotemporal variability of abundance

One aim of the Atlas was to use maps to depict spatiotemporal variations in abundance for all species during the study period. For instance, if a species was more abundant in winter 2008/09 than in the previous two winters, two maps were shown, one for the period in which the abundance showed no relevant fluctuations (winters 2006/07 and 2007/08) and one for the third winter in which the abundance was significantly different (e.g. Goldcrest).

We analysed the variations between the three winters in which the fieldwork was carried out, as well as between the first and the second half of each winter. In addition, we looked for temporal variations in abundance for the whole of Catalonia and at smaller geographical scales. In order to explore such changes we defined 5 major zones corresponding to broad winter weather patterns: Central Catalonia, North Coast, South Coast, Lleida plains and the Pyrenees (see The winter weather in Catalonia).

Statistical analysis

Temporal variations in abundance were analysed using a generalized linear mixed model in which the transect was defined as a random effect, and the winter (2006/07, 2007/08 and 2008/09), the zone and the period (first or

second half of winter) were defined as fixed effects. In addition, to test whether there were significant temporal variations in any particular zone, the interactions *zone*winter* and *zone*period* were introduced. Hence, the model can be formulated as follows:

$$Abundance = zone + winter + period + zone*winter + zone*period$$

where the abundance follows a Poisson distribution.

We also performed a post-hoc analysis based on the minimum square means in order to detect the years or the interactions *zone*winter* and *zone*period* that showed significant variations. We used the entire available sample for most species, although when a species was not detected in a particular zone (at least one observation in all three winters was required), that zone was eliminated from the analysis. All these tests were performed by using the GLIMMIX module of the SAS program (SAS 2000-2004).

The analysis of spatiotemporal variation was performed using data from the intensive sampling (SOCC), the seabird sampling from the coast and the winter waterbirds censuses. At first we thought that the spatiotemporal analysis would give reliable results for those species that were well covered by these three sampling methods, and that the spatial variation for the remaining species could be analysed with the square sampling data. Subsequently, though, tests conducted on these data showed that the frequency of occurrence obtained (between 0/8 and 8/8 for a standard square, see Square sampling) did not have enough resolution to analyse the spatial variations. For this reason we decided to discard this type of analysis for those species poorly covered by the SOCC surveys, seabird samplings or waterbird censuses. In these cases, the species account only has one abundance map, not because there were no spatiotemporal variations, but because the information gathered during the Atles fieldwork was not sufficient for the statistical analysis of variability in this group of species.

The predictive variables were the same for both the intensive and seabird samplings; nevertheless, for the waterbird censuses the model excluded the period effect and its interaction with the zone because for each winter there was only one data set (January census). The dependent variable chosen in each case was the one that was best suited to the different type of data:

1. Intensive sampling

- The dependent variable used was the total number of individuals counted within each SOCC transect.
- We only analysed species that appeared in at least 25 itineraries.

- We only used data from itineraries with a complete series of 6 winter censuses (performed during both periods in all three winters).

2. Winter waterbird censuses

- The dependent variable used was the number of individuals counted in each census area.
- We only used the areas that were surveyed in each of the three winters.

3. Seabird sampling

- The dependent variable used was the maximum number of individuals recorded during the 6 counts of 10 minutes.
- We only analysed the species for which neither the SOCC nor wintering waterbird census provided better data regarding their spatiotemporal variations.
- Only two areas were considered: North Coast and South Coast.

Determining the number of maps

Due to the limited amount of space in the species accounts and to avoid an excessive accumulation of graphic information, the decision was taken to only show possible variations between winters or between periods, and thus we ruled out maps with a combination of winter and period data. To define these differences, we used statistical significance criteria derived from the results of the generalized linear mixed models. For main effects, without interaction, a significance level $\alpha = 0.05$ was applied directly, while for post-hoc analysis a Bonferroni correction was applied. When significant differences between winters were found, the number of maps to be created was determined using the results of the *post-hoc* analysis:

- When significant differences were found between all winters: three maps.
- When significant differences were found between some of the winters the following rules were applied:
 - If there was congruence between the post-hoc analysis: two maps. For example, when $2006/07 \neq 2007/08$, $2007/08 \neq 2008/09$ and $2006/07 = 2008/09$ a map was given for 2007/08 and another for 2006/07-2008/09.
 - If there was no congruence between the post-hoc analysis (for example when $2006/07 \neq 2007/08$, $2007/08 = 2008/09$ and $2006/07 = 2008/09$), three maps were included.
- Once these criteria had been applied we reviewed all the species for which certain zones had been deleted from the statistical analysis due to a lack of

data. We checked the original data matrix to detect possible obvious temporal patterns that had not been statistically evaluated as in the case of the Hoopoe, which was common during winters 2006/07 and 2007/08 on the North Coast area, but not during 2008/09; thus, two maps are shown, one for 2006/07-2007/08 and another for 2008/09.

Once we had applied the criteria of statistical significance, we created as many abundance maps as the statistical differences dictated. However, we added a final criterion to determine how many maps should be finally shown in the Atles: we calculated the magnitude of change for those species for which statistically significant changes had been detected by evaluating the degree of similarity between the abundance maps calculated for different years or periods. This evaluation was done using an overlap index between the initial abundance maps. This overlap index was calculated as the common area between the two maps divided by their average area. The cut-off for considering an overlap to be low enough to warrant different maps was 0.6, that is, when two abundance maps had an overlapping value of less than 0.6 they were considered sufficiently dissimilar to be shown as different maps. When performing the analysis for possible inconsistencies (e.g. 2006/07 \neq 2007/08, 2007/08 \neq 2008/09 and 2006/07 $=$ 2008/09) the procedure was the same as that specified for the statistical significance criteria.

This second filter was developed to focus attention on the most obvious spatial variations, thereby minimizing the importance of statistically significant low magnitude variations. Following these criteria, we found differences between winters for 11 species, but did not detect important differences between the first and second periods for any species.

Maps generated by statistical inference

Most of the abundance maps produced in the framework of the Atles were generated from niche-based models. These numerical models relate information about the distribution and abundance of species (presence or abundance in known locations) with information on the environmental and/or spatial features present at these locations (Elith & Leathwick 2009). These procedures model relationships between species and environmental variables and predict the presence of species in areas for which there are no sampling data (Guisan & Zimmermann 2000).

Predictions regarding the distribution and abundance of species allowed us to test ecological and biogeographical hypotheses and in general provide a basis for the management of natural resources in fields such as the assessment of species' conservation status, the design of protected areas, management and

habitat restoration, population, community and ecosystem modelling, the analysis of the risks posed by invasive species and the prediction of the effects of climate change on species and ecosystems (Franklin 2009). The Catalan Breeding Bird Atlas (Estrada et al. 2004) was a pioneering ornithological work given its use of similar statistical methods in the generation of abundance maps of species at high resolution within the framework of an atlas project. The numerous applications that these models have generated and the maps they have created are good examples of the robustness of these methodologies and have led to work evaluating the effectiveness of different modelling methodologies (Brotons et al. 2004a), studies of the effect of changes on landscapes (Brotons et al. 2004b, Brotons et al. 2004c, Vallecillo et al. 2008, Vallecillo et al. 2009) and the generation of estimates of conservation value throughout a region (Herrando et al. 2010).

This winter Atles shares with the Breeding Bird Atlas the aim of generating high-resolution abundance maps from habitat models based on species-environment relationships. Nevertheless, one of the most important features of the Atles is its use of a large number of models based on data from pre-existing monitoring programmes. In the case of birds, these type of programmes have been implemented in several other countries, generally with well designed and representative monitoring schemes (Gregory et al. 2005). Their consolidation has opened the door to the use of spatial information extracted from a network of sampling stations as a way of generating high resolution maps, which reflects the convergence of goals between atlas and ongoing monitoring programmes (Jiguet et al. 2005, Brotons et al. 2007).

Thus, to create these high resolution maps, the Atles used as far as possible ornithological information derived from the SOCC (Catalan Common Bird Survey, see Intensive sampling). The SOCC focuses on the monitoring of the most common and conspicuous species, and provides a lot of information on their abundances, which improves considerably the predictions obtained from modelling methods based exclusively on presence or presence/absence data. Nevertheless, given that the less common species are generally poorly represented in the SOCC counts, it was necessary to make use of additional information sources such as the complementary and extensive samplings, the winter waterbird censuses and seabird samplings.

General modelling approach

There are currently numerous analytical methods that combine data from the presence or abundance of species with environmental predictors to generate estimations of their distributions and abundances. The quality of available

sampling data and the ecological questions to be addressed are two key aspects that have to be borne in mind when selecting an appropriate analytical method. On one hand, presence-absence or abundance data allow the use of regression models (GLM, GAM, etc.), Bayesian methods and methods developed in the machine learning and data-mining approaches (ANNs, boosted regression trees, genetic algorithms, etc.) to provide robust predictions (Brotons et al. 2004a, Elith & Leathwick 2009). On the other hand, when there is a lack of information regarding known absences, presence-only data can be modelled with other methods based on the comparison of presence records and the pseudo-absences of environmental background points (e.g. MAXENT, GARP and ENFA); this technique also produces good results that in some cases may actually improve the predictive accuracy of models based on presence-absence methods (Elith et al. 2006).

Of the wide range of available methods for modelling the abundance of species, for the Atles we opted for the maximum entropy modelling approach implemented in the software MAXENT (version 3.3.0f, freely download from www.cs.princeton.edu/~schapire/maxent), because of its flexibility when handling different kind of species data (presence or abundance-only data) and responses. The basic principle of the statistical approach implemented in MAXENT is the estimation of the probability of a distribution with maximum entropy (that is, the most spread out or the most uniform distribution) given a set of conditions (the environmental characteristics of the site where the species is detected) that shows our incomplete information regarding the distribution of the species (Phillips et al. 2006). The MAXENT approach can be compared with the General Linear Model (GLM) approach inasmuch that both methods use environmental predictors (Phillips et al. 2006). Despite these similarities, important differences exist between these methods. GLMs are used to model the probability of occurrence and hence true absence data is required. By contrast, MAXENT models a probability distribution on the basis of the pixels in the study region and pixels without records are not interpreted as absences. Therefore, the units of a MAXENT model cannot be directly interpreted as probabilities of occurrence, but, rather, as habitat indices developed by comparing environmentally similar areas in which a given species has been reported.

This approach based on presence but not absence data seems particularly appropriate for the study period of the Atles. In winter, a low detectability for many species is to be expected and consequently many false negatives occur. Nonetheless, for species with high detectability that are well sampled, the indices of habitat suitability modelled by MAXENT can be interpreted in a similar way to the results of presence-absence models. The general approach of

MAXENT also offers great flexibility and allows for the incorporation of information on the number of detected individuals as a means of giving greater importance to areas where a species is more abundant. It is thus important to remember that a direct comparison between the units of each species map cannot be made and so maps should be interpreted in terms of the type of the model used.

Model types

To model species abundance two main types of models were defined: models generated from abundance data and models constructed exclusively with presence data. Abundance models are derived from the SOCC sampling for common terrestrial species and from coastal and pelagic seabird sampling for common marine species, and data from these projects enabled us to create maps of relative abundance. For species with no reliable abundance data, presence-only data was the most appropriate for modelling species' distribution and to some extent the results can be interpreted as if they were probability of occurrence maps. It is important to note that both types of models actually generate habitat suitability index maps and that we only refer to them with different names in order to facilitate their interpretation.

In all, we used statistical inference to generate abundance maps for 171 species. Relative abundance maps were created from the standardized sampling for species well represented in the SOCC (77 species), seabird censuses from the coast (16 species) and pelagic bird censuses (9 species). In addition, abundance maps were also generated for 5 species of waterbirds using data from both aquatic bird censuses and SOCC datasets. For less common terrestrial species (74 species), we generated occurrence models from the presence-only data at 1 km² resolution, using in most cases data from controlled efforts and also adding non-standardised data for the scarcest species (complementary sampling or data from non-standardised samplings). All these maps were produced with the MAXENT methodology for niche modelling with the exception of coastal seabirds, which, due to the difficulties in setting up relationships between species' presence and environmental variables, were created using spatial interpolation techniques. Finally, it is worth to bearing in mind that for some species classifiable as present on both inland and marine waters (and within the latter group, both pelagic and coastal species), several abundance maps were created using the data that were available.

It was not always easy to determine which methodological approach to follow in each case and the statistical evaluation of the models still needed to

be backed up by expert evaluation. In the case of the Atles, the editorial team had to choose species-by-species the type of model that was believed to be closest to reality. The final model/s chosen for each species are listed in Atlas appendices.

Predictor variables used

The development of ecological niche models depends on the availability of good quality environmental data. Fortunately, over recent years institutions such as the Catalan Government, the Centre for Ecological Research and Forestry Applications (CREAF) and the Catalan Cartographic Institute (ICC) have undertaken a major effort to develop high-quality digital databases with environmental information for the whole of Catalonia. In the Atles we made good use of these databases in order to generate the environmental variables that were used as predictors of species distribution. We transformed the spatial resolution of the original data into two analytical resolutions: 1x1 km and 500x500 m UTM grid cells. These variables (Table I.1) were selected to incorporate the factors known a priori to determine bird distribution at different spatial scales (Wiens 1989). The different groups of variables included in the models were as follows:

1. **Habitat and land-use:** variables describing habitat structure are known to be amongst the best predictors of bird distribution at local spatial scales. We derived habitat and land use variables from the Catalan habitat map (2005) and the SIGPAC (Geographic Information System for Agricultural Plots). The Catalan habitat map was generated from an interpretation of aerial photographs and fieldwork, using the habitats classification of the European Union (European Commission, 1991, CORINE biotopes manual); the SIGPAC was used as a geographical database of land-use as declared by livestock breeders and farmers in compliance with the European Commission Regulation (EC) n° 1593/2000. For a given category, we created a single map representing the percentage of 50 m pixels in each UTM grid cell. We also calculated an index of landscape heterogeneity (Shannon diversity index) and the distance from the nearest forest patch.
2. **Climate and relief:** climatic variables provide valuable information that complements the data obtained from habitat variables. Furthermore, climate and/or altitude may provide a surrogate for a number of environmental characteristics that are difficult to measure and which otherwise would be difficult to include in the analysis. Climatic variables were derived from the Digital Climatic Atlas of Catalonia, whereas elevation and slope variables were obtained from a digital elevation model. In all cases we used average values for each UTM grid cells, apart from slope, to

which we added its standard deviation as a surrogate for relief heterogeneity

3. **Human influence:** the effect of human activities on species ecology is well known. To include variables summarising human impact in the UTM squares we generated variables based on information from geographic databases and population statistics (inhabitants per municipality). From these maps and within each UTM grid cell we calculated the mean distance to selected features (e.g. roads, large cities, etc.) and the proportion of the surface area occupied by artificial habitats (urban, industrial, etc.).
4. **Others:** in order to account for spatial patterns not directly explained by other environmental variables, we also included in the models the mean latitudinal and longitudinal coordinates for each square, and the mean distance to the sea.

Incorporating all the hypothetical factors expected to determine species distribution is a thankless task. Even when the available environmental data is of high quality, as in the case of Catalonia, the essential factors affecting the distribution of a given species are likely to be missing. A good way of accounting for the unknown variables that may be relevant to species distribution is to use measures of spatial autocorrelation, since the presence of a species in a given locality is often not completely independent of whether or not it occurs in surrounding areas (Vaughan & Ormerod 2003). In these cases, the information about the degree of spatial contagion in species occurrence may be used as a surrogate for environmental information that is crucial for the species, but of unknown origin. Historical factors may be important in this context. For instance, recently lost areas of a species' distribution that are still suitable for the species may be difficult to identify if they are environmentally similar to others where the species still occurs (Brotons et al. 2004a). In this case, given that the species would be completely absent from such areas, the use of contagion variables may help us include information about the species' current absence in the model. The Catalan Atlases used two different spatial contagion variables or auto-covariables, as defined in Augustin et al. (1996): mean occurrence probability and mean normalized abundance, obtained, respectively, from occurrence data in the 10x10 km UTM square sampling and abundance data from the intensive sampling. Both contagion variables were calculated using interpolation techniques, which yield values for a series of unknown points on the basis of information available for a set of sampled neighbouring points weighted by different factors such as distance. These interpolations were performed with the AutoMap 'R Package module, using an ordinary krigging and assuming an exponential model for the variogram. It is important to note at this point that the use of contagion variables assumes that

the distribution data used to produce them agrees with the real distribution of the species. In this sense, the contagion variables are very useful in species that are easily detectable in field sampling, but they may bias the results of the models for hard-to-detect species.

Table I.1. Environmental variables used to generate ecological niche models. Unless otherwise mentioned, variables refer to 500x500 m and 1x1 km UTM grid cells. Cartographic sources are specified at the bottom of the table. Numerical punctuation according to non-English usage in which commas indicate decimal signs and full points indicate thousands.

Variables ambientals <i>Environmental variables</i>	Unitats <i>Units</i>	Rang <i>Range</i>
Hàbitat i Usos del sòl / <i>Habitat and Land use</i>		
Avetosa ¹ <i>Silver fir forests</i>	%	0 100
Bosc de pi blanc ¹ <i>Aleppo pine forests</i>	%	0 100
Bosquines de pi blanc ¹ <i>Transitional Mediterranean Aleppo pine woodland-shrub</i>	%	0 76
Bosc de pinassa ¹ <i>European Black pine forests</i>	%	0 100
Bosc de pi pinastre ¹ <i>Maritime pine forests</i>	%	0 98
Bosc de pi negre ¹ <i>Mountain pine forests</i>	%	0 100
Bosc de pi roig ¹ <i>Scots pine forests</i>	%	0 100
Arrossar ¹ <i>Rice fields</i>	%	0 100
Cítrics ² <i>Citrus groves</i>	%	0 48
Fruiters (poma, pera, préssec, etc.) ² <i>Orchards (apple, pear, peach, etc.)</i>	%	0 89
Fruits secs (avellana, garrofers, etc.) ² <i>Nuts (hazels, carob, etc.)</i>	%	0 82
Conreu herbaci secà (sense arrossars) ² <i>Non-irrigated herbaceous crop (not rice)</i>	%	0 682
Conreu herbaci regadiu (sense arrossars) ² <i>Irrigated herbaceous crop (without rice)</i>	%	0 100
Horta ² <i>Market gardens</i>	%	0 64
Oliveres ² <i>Olive groves</i>	%	0 97
Vinya ² <i>Vineyards</i>	%	0 96
Altres boscos caducifolis ¹ <i>Other deciduous forests</i>	%	0 69
Castanyer ¹ <i>Sweet chestnut forests</i>	%	0 99
Faig ¹ <i>Beech forests</i>	%	0 95
Caducifoli jove ¹ <i>Young deciduous forests</i>	%	0 56
Roure ¹ <i>Oak forests</i>	%	0 98
Canyissars ¹ <i>Reedbeds</i>	%	0 84

Variables ambientals <i>Environmental variables</i>	Unitats <i>Units</i>	Rang <i>Range</i>
Congestes ¹ <i>Snow patches</i>	%	0 26
Alzinar ¹ <i>Holm oak forests</i>	%	0 100
Alzinar ¹ <i>Cork oak forests</i>	%	0 100
Estanys ¹ <i>Lakes</i>	%	0 39
Litoral marítim ¹ <i>Coastlines</i>	%	0 100
Dunes litorals ¹ <i>Dunes</i>	%	0 98
Matollars forestals de muntanya ¹ <i>Transitional upland woodland-shrub</i>	%	0 89
Màquia esclerofil·la ¹ <i>Sclerophyllous maquis</i>	%	0 57
Matolls mediterranis ¹ <i>Mediterranean shrublands</i>	%	0 100
Matolls de muntanya ¹ <i>Upland shrublands</i>	%	0 100
Molleres ¹ <i>Peat bogs</i>	%	0 27
Plantacions coníferes ¹ <i>Coniferous plantations</i>	%	0 61
Plantacions pollancre ¹ <i>Poplars plantations</i>	%	0 95
Prats alpins ¹ <i>Alpine grasslands</i>	%	0 100
Prats mediterranis ¹ <i>Mediterranean grasslands</i>	%	0 100
Prats de muntanya ¹ <i>Upland grasslands</i>	%	0 100
Ribera arbustiva ¹ <i>Riparian shrubs</i>	%	0 31
Bosc de ribera ¹ <i>Riparian forests</i>	%	0 69
Rius i llacunes <i>Rivers and lagoons</i>	%	0 100
Roques i penya-segats ¹ <i>Rocks and cliffs</i>	%	0 94
Tarteres ¹ <i>Screes</i>	%	0 91
Distància a la taca de bosc més propera ³ <i>Distance from nearest forest patch</i>	m	0 4040
Índex de Shannon ³ <i>Shannon Diversity Index</i>		0 3
Clima / Climate		
Temperatura mínima anual ⁴ <i>Minimum annual temperature</i>	°C	-2,9 14,0
Temperatura mínima d'estiu (juliol-setembre) ⁴ <i>Minimum summer temperature (July-September)</i>	°C	2,7 20,8
Temperatura mínima d'hivern (gener-març) ⁴ <i>Minimum winter temperature (January-March)</i>	°C	-7,8 7,6
Temperatura mínima de primavera (abril-juny) ⁴ <i>Minimum spring temperature (April-June)</i>	°C	-5,1 12,1
Temperatura mínima de tardor (octubre-desembre) ⁴ <i>Minimum autumn temperature (October-December)</i>	°C	-2,5 15,4
Temperatura mitjana anual ⁴ <i>Mean annual temperature</i>	°C	5 17,3
Temperatura mitjana d'estiu (juliol-setembre) ⁴ <i>Mean summer temperature (July-September)</i>	°C	6,1 25,4

Variables ambientals <i>Environmental variables</i>	Unitats <i>Units</i>	Rang <i>Range</i>
Temperatura mitjana d'hivern (gener-març) ⁴ <i>Mean winter temperature (January-March)</i>	°C	-4,5 10,7
Temperatura mitjana de primavera (abril-juny) ⁴ <i>Mean spring temperature (April-June)</i>	°C	-2,3 15,8
Temperatura mitjana de tardor (octubre-desembre) ⁴ <i>Mean autumn temperature (October-December)</i>	°C	1,8 18,7
Temperatura màxima anual ⁴ <i>Maximum annual temperature</i>	°C	4,0 22,4
Temperatura màxima d'estiu (juliol-setembre) ⁴ <i>Maximum summer temperature (July-September)</i>	°C	9,8 32,2
Temperatura màxima d'hivern (gener-març) ⁴ <i>Maximum winter temperature (January-March)</i>	°C	-1,0 16,7
Temperatura màxima de primavera (abril-juny) ⁴ <i>Maximum spring temperature (April-June)</i>	°C	1,2 21,9
Temperatura màxima de tardor (octubre-desembre) ⁴ <i>Maximum autumn temperature (October-December)</i>	°C	4,2 24,7
Precipitació acumulada anual ⁴ <i>Accumulated annual precipitation</i>	mm	339,5 1.464,1
Precipitació acumulada d'estiu (juliol-setembre) ⁴ <i>Accumulated summer precipitation (July-September)</i>	mm	41,8 474,9
Precipitació acumulada d'hivern (gener-març) ⁴ <i>Accumulated winter precipitation (January-March)</i>	mm	53,1 313,0
Precipitació acumulada de primavera (abril-juny) ⁴ <i>Accumulated spring precipitation (April-June)</i>	mm	95,0 376,6
Precipitació acumulada de tardor (octubre-desembre) ⁴ <i>Accumulated autumn precipitation (October-December)</i>	mm	102,6 424,0
Radiació solar mitjana anual ⁴ <i>Mean annual solar radiation</i>	10kJm ² /year	820 1.732
Radiació solar mitjana d'estiu (juliol-setembre) ⁴ <i>Mean summer solar radiation (July-September)</i>	10kJm ² /year	1.575 2.395
Radiació solar mitjana d'hivern (gener-març) ⁴ <i>Mean winter solar radiation (January-March)</i>	10kJm ² /year	118 1.104
Radiació solar mitjana de primavera (abril-juny) ⁴ <i>Mean spring solar radiation (April-June)</i>	10kJm ² /year	1.085 2.062
Radiació solar mitjana de tardor (octubre-desembre) ⁴ <i>Mean autumn solar radiation (October-December)</i>	10kJm ² /year	407 1.532
Relleu / Relief		
Altitud mitjana ⁵ <i>Mean altitude</i>	m	0 2.886
Pendent mitjà ⁵ <i>Mean slope</i>	%	0 43
Desviació estàndard del pendent ⁵ <i>Std Dev slope</i>	%	0 20
Influència humana / Human influence		
Distància a camins i corriols ⁶ <i>Distance from roads and footpaths</i>	m	69 835
Distància a carreteres de la xarxa primària de transport ⁶ <i>Distance from roads within the main road network</i>	m	80 133.429
Distància a carreteres de la xarxa secundària de transport ⁶ <i>Distance from roads within the secondary road network</i>	m	275 938
Distància a ciutats > 10.000 habitants ^{6,7} <i>Distance from cities > 10,000 inhab.</i>	m	0 84.087
Urbanitzacions ⁸ <i>Out of town residential areas</i>	%	0 100
Zones industrials i comercials ⁸ <i>Industrial or commercial areas</i>	%	0 100
Zones urbanes ⁸ <i>Urban areas</i>	%	0 100
Altres / Others		
Distància mitjana al mar ⁹	km	0

Variabls ambientals <i>Environmental variables</i>	Unitats <i>Units</i>	Rang <i>Range</i>
<i>Mean distance from the sea</i>		194,5
Latitud mitjana ⁹ <i>Mean latitude</i>	m	4.489.562
Longitud mitjana ⁹ <i>Mean longitude</i>	m	260.500
		526.500

¹ Cartografia dels hàbitats a Catalunya, Departament de Medi Ambient i Habitatge i Universitat de Barcelona

² *Sistema de Información Geográfica de parcelas agrícolas (SIGPAC)*, Ministerio de Medio Ambiente y Medio Rural y Marino

³ Mapa de Cobertes del Sòl de Catalunya Versió 1, Departament d'Agricultura, Ramaderia i Pesca i Centre de Recerca Ecològica i Aplicacions Forestals (CREAF)

⁴ Atlas Climàtic Digital de Catalunya, Universitat Autònoma de Barcelona

⁵ Model Digital d'Elevacions Versió 2 (revisada), Institut Cartogràfic de Catalunya

⁶ Mapa Topogràfic de Catalunya 1:50.000 Versió 3, Institut Cartogràfic de Catalunya

⁷ Cens de població de Catalunya 2001, Institut d'Estadística de Catalunya (IDESCAT)

⁸ Mapa de Cobertes del Sòl de Catalunya Versió 3 i Classificació dels usos del sòl a Catalunya 2002, Departament de Medi Ambient i Habitatge i Centre de Recerca Ecològica i Aplicacions Forestals (CREAF)

⁹ Elaboració pròpia, Centre Tecnològic Forestal de Catalunya

For the development of habitat models for pelagic birds, a reformulation of the environmental variables was required using information regarding the ecological requirements of each species. On the basis of a bibliographical study and an evaluation of the accessibility and quality of information available for marine environments, after various attempts we were able to define the environmental variables with the greatest indicator value for bird distribution at sea. Generally, the chosen variables (Table I.2) included a set of static variables (no temporal changes) related to the topography of the marine environment (depth, slope, distance to coast and distance to continental slope), which directly or indirectly characterize the range in which every species moves (Skov et al. 2008). As well, we included a set of temporary dynamic variables derived from time series obtained with remote sensing, directly related to the global productivity of the marine environment. Among these, we included sea surface temperature (SST), chlorophyll-a concentration (Chl-a, a measure of the overall productivity of the environment) and distance from oceanic fronts (a calculation of the distribution of the areas where food is available) (Louzao et al. 2006, Praca & Gannier 2008). The definition of this set of variables was necessarily linked to the offshore seabird sampling data. Thus, we included in the final models 1) the SST and Chl-a during the four three-month periods previous to the ECOMED campaigns, assuming that the overall productivity of the environment is conditioned by SST and Chl-a values of the previous year and 2) the distance to ocean fronts in the same month as the ECOMED sampling took place, assuming that areas where food is concentrated are related to productivity phenomena that determine species' short-term distributions. For a more detailed description of the variables used, see Arcos et al. (2009).

Table I.2. Environmental variables used to generate seabird abundance index maps. Variables are referenced to a resolution of 2.5' pixels. Cartographic sources are indicated at the end of the table. Numerical punctuation according to non-English usage in which commas indicate decimal signs and full points indicate thousands.

Variabls ambientals <i>Environmental variables</i>	Unitats <i>Units</i>	Rang <i>Range</i>
Variabls estàtiques / <i>Static variables</i>		
Fondària ¹ <i>Depth</i>	m	0 -2.541
Pendent del fons marí ¹ <i>Slope of seafloor</i>	%	0 18,2
Distància a la costa ² <i>Distance from coast</i>	m	0 133.730
Distància a la plataforma continental ¹ <i>Distance from continental shelf</i>	m	-67.489 120.135
Variabls dinàmiques / <i>Dinamic variables</i>		
Temperatura del mar en superfície ³ <i>Sea surface temperature (SST)</i>	°C	7,9 30,5
Concentració de clorofil·la (Chl-a) ⁴ <i>Chlorophyll-a Concentration</i>	mg/m ³	0,1 34,4
Distància a fronts oceànics ⁵ <i>Distance from oceanic fronts</i>	minuts	0 1,4

¹ Model Global de Rellu (ETOPO2v2c), *National Oceanic and Atmospheric Administration (NOAA), USA*: <http://www.ngdc.noaa.gov>

² Derivada de la línia de costa global, NOAA: <http://shoreline.noaa.gov>

³ Terra-MODIS Sea Surface Temperature [11 º day], NOAA: <http://oceancolor.gsfc.nasa.gov>

⁴ Aqua-MODIS Chlorophyll, NOAA: <http://oceancolor.gsfc.nasa.gov>

⁵ Elaboració pròpia a partir de distància a principals fronts de temperatura, Centre Tecnològic Forestal de Catalunya

Abundance models based on the SOCC

As discussed in previous sections, abundance data can improve the MAXENT habitat suitability indices when the effort between sampling units is comparable and unbiased. Habitat suitability indices derived from abundance data can be interpreted as indicators of relative abundance, although we must always remember that the result is a species-dependent value and so the maps of different species cannot be directly compared. Thus, we used the counts obtained from the SOCC to develop abundance maps for 77 common terrestrial species.

The analysis unit for abundance models obtained from SOCC intensive sampling was a 1-km linear stretch, and the data used came both from the Standard and the Expanded SOCC types (see *Intensive sampling*). The abundance data entered into MAXENT did not match the number of individuals detected in the field and did not correspond to any absolute density estimate. Given the results of the preliminary tests, in order to prevent bias in

the models produced by large numbers of individuals, the results of the field counts were standardized by natural logarithms (final values between 1 and 9, with different ranges according to the species); as well, for very abundant species with a natural logarithmic value over 5, ranges were reclassified into categories from 1 to 5. In order to minimize geographical bias towards areas with a greater number of sampling units (e.g. wetlands or highly populated areas), we used a subsample consisting of a single transect for every UTM 10x10 km square; only in those squares in which transects sampled different and underrepresented habitats were two transects included. The final subsample included 405 transects (from the original total of 523) and a total 1,215 stretches. This was the general subsample used for most species, although for 6 species closely associated with a particular habitat (urban or wetland), the complete sample was used to avoid data-loss in environments in which the general bias was not applicable.

At first, we developed three models for every species, one for each winter (2006/07, 2007/08 and 2008/09). As two censuses were carried out in each winter, we chose the census that had the maximum abundance over the whole transect and, if both were the same, we used the census in which the species was detected in most stretches. We calculated the average of the results of the three models developed initially for each winter according to the guidelines given in the analysis of spatiotemporal variations (see *Spatiotemporal variability of abundance*). In this way one final map could be obtained for the whole study period (average of three winters) for 69 species (those with non-existing or irrelevant spatiotemporal variations in abundance); we also generated two maps (one corresponding to the average of two winters) for 4 species (Hawfinch, Goldcrest, Redwing and Hoopoe), and three maps (one for each winter) for the 4 species which showed exceptional differences between the three studied winters (Siskin, Yellowhammer, Crossbill and Fieldfare).

MAXENT models were produced at 500x500 m resolution and only linear and quadratic functions were incorporated for defining relationships with predictive variables. Moreover, for the majority of species, contagion variables were incorporated since they improved the predictions of the models (see *Predictor variables used*). Specifically, the average standardized abundance (SOCC data) was used for 49 species, the mean probability of occurrence (square sampling data) was used for 23 species, and for 5 species no contagion variable was used.

To evaluate the predictive strength of these models we used the Spearman correlation coefficient (non-parametric) between the standardized abundance values and the habitat quality values predicted by the models (Phillips et al. 2009). Then we went beyond this statistical evaluation of different models to

a second level of assessment based on expertise criteria. This second evaluation was based on the characteristics of the species (mainly detectability, uncontrollable sampling bias and previously known distribution data) and was useful for defining, firstly, the types of contagion variables that had to be used and, secondly, which cases the modelling based on SOCC did not give consistent enough results. In the latter case, we then had to enlarge the sample, reject the relative abundance model and generate a model with extensive sampling + SOCC.

Abundance models from extensive sampling + SOCC

For the less common species for which it was not possible to create a model based only on SOCC data, or for those whose models were rejected by the expert evaluations, we developed ecological niche models with presence data derived from extensive sampling and SOCC sampling, both with controlled effort. If the data gathered by these methods were not sufficient, data from less standardized methods were added: firstly, data from extensive non-standardized sampling (outside census data, see *Square sampling*) (29 species) and, secondly, when this sample was still not enough for the calibration of the models, we added data from complementary sampling (see *Complementary sampling*) (9 species).

Given that we could not test the possible spatiotemporal differences with data from the square sampling (see *Spatiotemporal variability of abundance*), for these species a single habitat model was developed using all the data collected during the three winters of fieldwork. Models were computed to a resolution of 1x1 km using the MAXENT default parameters, but limiting the response to environmental variables to linear and quadratic functions. In this case, the lack of abundance data dictated that the evaluation of the models be carried out by a cross-validation procedure in order to quantify in a consistent way the predictive effectiveness of the models based on presence data (Guisan & Zimmermann 2000). This predictive effectiveness was estimated with the AUC statistics (Area Under the Curve) of the ROC curve (Receiver Operating Characteristics). This procedure consisted of dividing the data into two different groups, one for calibration that included 70% of squares and a second for evaluation with the remaining 30%. The calibration data were used to generate ecological niche models. Testing data was used to measure quantitatively to what extent the predictions of these models fitted the independent observations not used to generate them. The statistical evaluation was complemented by expert assessment, following the same criteria described for models developed only with SOCC data; when a model failed the assessment, we proceeded to create a new model once the cause of

the bias and a mechanism for its resolution had been identified. For instance, in species that are hard to detect (e.g. nocturnal raptors), local knowledge determined the existence of obvious geographical biases towards certain areas. To reduce these biases in the species concerned (7 species), we proceeded to create a sub-sample of the dataset including a single presence data for every UTM 10x10 km square. Additionally, for some species accurately represented in the extensive sampling (14 species), the contagious variable derived from these samplings (see *Predictor variables used*) improved the predictions of the models.

Finally, it should be noted that when MAXENT works with presence data collected by means of standardized sampling efforts, the habitat suitability index approaches the probability of occurrence of the species (Phillips & Dudik 2008). In this sense and in order to help in their interpretation, these models are all referred to as ‘probability of occurrence models’. Therefore, in these cases this probability should be interpreted as an abundance unit, but with a lower capacity for identifying variations in the higher part of the abundance range of the species than the models of relative abundance obtained from the SOCC quantitative data.

Abundance models from waterbird sampling + SOCC

For wetland species for which the winter waterbird censuses did not cover their entire distribution (5 species, see *Censuses of wintering waterbirds*), MAXENT ecological niche models were developed combining data from the winter waterbird censuses and from the SOCC. To do so, it was first necessary to improve the geographical resolution of the data from the winter waterbird censuses (for example, sampled localities were of variable size) given that it was not possible to directly combine these results with the more spatially accurate data from the SOCC. For this purpose we assumed that a species detected in a census location was found in all the UTM 1x1 km squares covered by that location, an assumption of little relevance at the scale (Catalonia) in which the analysis was carried out. To minimize bias towards larger polygons with more 1x1 km UTM squares with observations, a subsampling of all data was carried out, which included a single presence record for every 10x10 km UTM square.

According to the results of the analysis of the spatiotemporal variations (see *Spatiotemporal variability of abundance*), we eventually developed for each species a single ecological niche model with data collected from the three Atles winters. The models were calculated to a resolution of 1x1 km using the default MAXENT parameters, but limiting the response to environmental variables in linear and quadratic functions. The model obtained for every species was

assessed using the same cross-validation process and expert criteria as the models developed from the extensive sampling + SOCC.

Abundance models based on seabird sampling from the coast

Counts of seabirds from the coast provided data for abundance maps for 15 species covering the whole Catalan coast. The difficulty in identifying and obtaining appropriate environmental variables for predicting the abundance of coastal birds from niche-based models led us to use interpolation techniques to generate abundance maps for these species. These techniques offer a direct way of estimating abundances at a point of unknown value given available information from nearby points. The estimates were obtained by weighting known values with several factors such as the distance to other points with information. A classic example of modelling the relative abundance of birds with these techniques is the Swiss Breeding Bird Atlas (Schmid et al. 1998). However, interpolation has significant limitations concerning its sensitivity to errors in sampling campaigns and the assumption that the environmental conditions in sampled areas do not differ from those in the rest of the territory. However, it was the homogeneity in the environmental conditions at census stations (points located on the coast with excellent visibility over the sea) that motivated the application of interpolation techniques for developing abundance models for coastal seabirds.

In a similar way to the MAXENT models derived from SOCC data, the relative abundances obtained in censuses of coastal birds were also standardized in order to prevent bias caused by exceptionally high counts. To this end, we used the same criteria as those used to standardize data obtained in the SOCC sampling (see *Abundance models based on the SOCC*).

Following the results of the analysis of spatiotemporal variations in abundances (see *Spatiotemporal variability of abundance*), a single interpolation with standardized abundance data corresponding to the three Atlas winters was developed for every species. The interpolations were computed at a resolution of 500 m extending up to 5 km offshore to facilitate its depiction. The method used was the ordinary krigging with a basic parameterization, assuming an exponential model for the variogram. To obtain the same legend of relative abundance as used for the models of terrestrial birds, the range of values for the estimates derived from krigging were reclassified to between 0 and 1.

Finally, we proceeded to evaluate the results using the Spearman correlation coefficient for the standardized and the relative abundances derived from the interpolations (see *Abundance models based on the SOCC*) and expert opinion.

Models based on sampling of pelagic birds

The models for pelagic seabirds included in this Atlas were developed within the framework of the LIFE Project Important Areas for Seabirds in Spain (IBA) (LIFE04NAT/ES/000049, 2004-2009), which provided additional information on the identification and delimitation of marine IBAs off the Spanish coastline (Arcos et al. 2009). Pelagic seabird habitat models were developed from quantitative data collected from oceanographic campaigns carried out in Spanish territorial waters during the breeding and wintering periods. In the Atlas we only included models developed in the Mediterranean Sea with data from ECOMED wintering campaigns (see *Sampling of seabirds on the continental shelf*) for 9 species.

These models were also created using the MAXENT methodology and in order to calibrate them bird counts were processed in a similar fashion to the data obtained from the SOCC counts. Abundance data were standardized and 6 abundance categories were determined: 1 for a single individual, 2 for 2-5 individuals, 3 for 6-10 individuals, 4 for 11-25 individuals, 5 for 26-100 individuals, and 6 for more than 100 individuals. These intervals were defined by expert opinion and looked to find a balance between the majority of censuses, during which there were only a few observations of isolated individuals or small groups (90% of the censuses were of less than 10 individuals), and the small percentage of censuses that counted large groups of birds around fishing boats. Data for developing models was completed using observations from outside the imaginary censusing strip within the n° 1 abundance category.

For every species we obtained a final model, which was the result of the average of two annual models corresponding to the ECOMED campaigns carried out during the winters of 2006 and 2007. Work resolution was fixed by the resolution of environmental information, which was about 2.5 minutes (4,630 m). To develop these models we also used the default parameterization of MAXENT, limiting the response to environmental variables to linear and quadratic functions. The predictive ability of the models was checked with the statistic AUC (Area Under the Curve) of the ROC curve (Receiver Operating Characteristics) (see *Abundance models from extensive sampling + SOCC*). To calculate the AUC, a cross-validation process between years was used. Thus, the abundance pattern in 2006 was assessed with the sample used for calibrating the abundance annual model of 2007, and vice versa. The AUC was calculated using the non-parametric Wilcoxon statistic (Wintle et al. 2005) with abundance samples converted into presence-absence data.

Zoning of maps generated with MAXENT

The maps generated by statistical inference have a legend with 10 categories that indicate the degree of habitat suitability, which can be understood as relative abundance values or probability of occurrence values, depending on the model used. None of the maps provides direct information regarding the presence or absence of the species at a given point, a question that can be resolved using the mapping zones to identify cut-off points or thresholds that convert maps with continuous suitability habitat values into maps with binary presence/absence values or into maps with more areas hierarchically prioritised according to their relevance for the species.

A number of subjective or objective methods can be used to define cut-off points (Liu et al. 2005). For the Atlases we applied an objective method developed as part of the work on the identification of areas with suitable habitat for species within the IBA Secans de Lleida and Cogul-Alfés (Bota et al. 2008), and then successfully applied in the selection of marine IBAs in Spain (Arcos et al. 2009). This method combines two simple and effective approaches with strong ecological components in order to separate, firstly, the presence and absence areas for the species (in terms of the prevalence of the data used in the model development) and, secondly, to define three levels of importance for the species based on the average of suitability values within the area of presence. Thus, for all species, the threshold below which the absence areas for species are defined (zone 0) corresponds to the average tenth percentile of the data used for developing the models (i.e. 10% of the data with the lowest suitability). The average mean of the values within the areas of presence provided a second threshold below which the first level of suitability for the species was defined (zone 1); that is, areas under the average suitability within the distribution range. The third threshold was defined as the mean of the values that were above zone 1. This threshold marked the boundary between the second level (zone 2) and the third level (zone 3) of suitable areas for the species (Figure I.1).

This zoning fulfilled two purposes: firstly, in the analysis of the spatiotemporal variations in abundance that dictated the number of maps to be created for each species, the zoning allowed us to estimate the overlap between years (considering only zones 2 and 3) for the yearly abundance models derived from the SOCC (see *Spatiotemporal variability of abundance*); secondly, the population sizes of common terrestrial species were estimated (see *Population estimates*) from bird densities (ind/km²) calculated in each of these zones according to their total area (km²).

Final generation of abundance maps from statistical inference

Once calibrated and evaluated, the models obtained from different data sources were represented as maps with continuous values between 0 and 1 expressing the habitat suitability index. MAXENT plotted directly the logistic suitability values derived from models on a raster map of Catalonia at a resolution of 500x500 m for those models derived from the SOCC, 1x1 km resolution for the remaining terrestrial birds, and 2.5 x 2.5 minute resolution for models derived from pelagic seabird censuses. Models of coastal seabird species obtained with krigging were also represented on a raster map of the Catalan coast at 500x500 m resolution.

Many authors consider that the maps generated by habitat modelling techniques are a reflection of the potential distribution of the species rather than an approximation to their real distribution (Guisan & Zimmermann 2000). As mentioned above, environmental variables not included in these models (e.g. historical processes or habitat fragmentation) make niche-based models predict the presence of species in places where they are absent. To ensure that the Atlas maps showed as accurately as possible the real distribution of the species and not merely its potential distribution, we applied a filter that excluded all predictions falling outside the distribution range of the species (Pearce et al. 2001). In this case, the distribution range was defined as the UTM 10x10 km squares where the species was detected plus neighbouring squares; these latter squares were incorporated so as to include residual areas located on the borders of a species' distribution, where the species may have gone unnoticed during sampling. Nevertheless, expert criteria determined that this filter could not be applied for a group of species with low detectability since it was based on false absences in data from UTM 10x10 km squares. In these cases, we either applied no filter (e.g. Quail and Woodcock) or the filter was only applied to a few well-sampled squares with particular ecological conditions (e.g. the Ebro delta was filtered for Eagle Owl and Stock Dove).

Finally, to improve the maps, values were softened by replacing the value of each pixel by the average of 9 values consisting of the pixel itself and the 8 pixels that surround it. To give a greater weight to the original value, this operation was performed by twice increasing the original resolution of the rasters (i.e. every 500 m pixel was divided into 4 250 m pixels) so that a third of the values used to calculate the average value corresponded to the value of the original pixel. This smoothing is based on the basic assumption that the habitat suitability for a species varies linearly between two adjacent localities, which seems to be valid at the spatial scale of this atlas

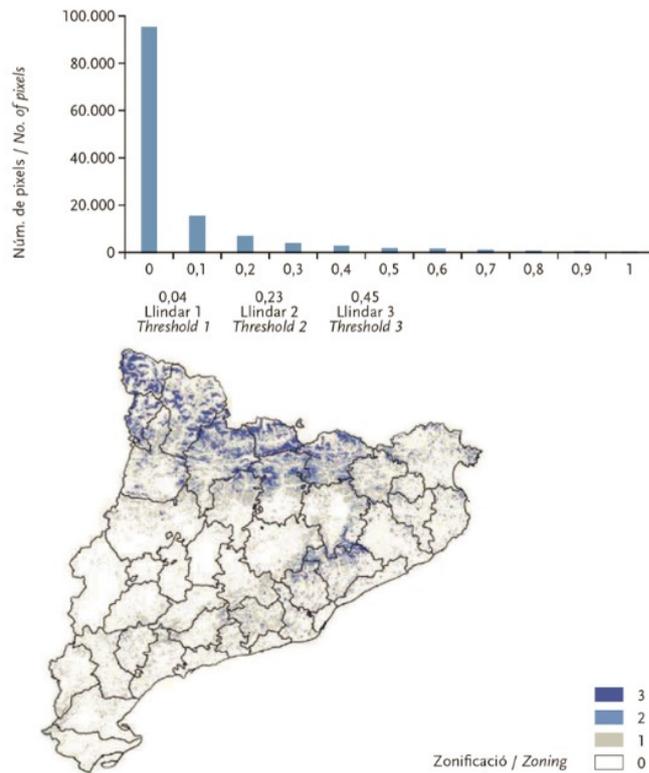


Figure I.1. Histogram of probabilities of occurrence and thresholds for the abundance model of the Goldcrest in winter 2006/07 and map of zones resulting from this classification. See main text for more information. Numerical punctuation according to non-English usage in which commas indicate decimal signs and full points indicate thousands.

Abundance maps from absolute censuses

Maps of waterbirds

For wetland species for which the wintering waterbird censuses combined optimum census quality with suitable geographical coverage, we opted to develop absolute abundance maps without applying any statistical inference procedures. In all, maps of this type were created for 30 species.

The main difficulty in preparing these maps was that census localities were large and that the precise place of observation for a particular record was not known. To minimize this problem with the resolution, we defined the 1x1 km UTM squares of each location and determined the number of individuals for each of these squares by dividing the total number of individuals in the locality by the total number of squares. In the 1x1 km UTM squares that were shared by more than one census location, an abundance value corresponding to the average of the estimated values for each location contained in the square was taken.

The locations used are listed at the end of the Atles and show the final results of the censuses (see Atles appendices). The exception is the Ebro delta, which was divided up into the different areas used during the censuses: Alfacada, rice fields of Aldea, Amposta, Balada, Buda, Canal Vell, Deltebre, Encanyissada, Fangar, Serralló, la Tancada, Través and Vilacoto, the Fangar and Alfacs bays, Buda and Sant Antoni, Canal Vell, Deltebre, Garxal, Illa de Gràcia, Encanyissada and Tancada lagoons, Malicciós, Olles, Platjola, Punta de la Banya and the Ebro river itself.

When generating the final maps and deciding how many should be shown for each species, we took into account spatiotemporal variability in species abundance (see *Spatiotemporal variability of abundance*). To maximise the similarity with the procedure used for calculating the overlap between years in the maps derived from statistical inference, the overlap calculation in this case was performed using only presence data and not abundance data for the species at each location.

Finally, to improve the appearance of the maps, values were softened by replacing the value of every pixel by the average of 9 values consisting of the 8 surrounding pixels and the pixel itself in a procedure that was identical to that used for the statistical inference maps (see *Final generation of abundance maps from statistical inference*), which gave 500x500 m resolution maps.

Interpretation of abundance maps

In terms of interpretation, the 4 different abundance models created for the Atles correspond to maps of probability of occurrence and maps of relative abundance. Moreover, there are also absolute abundance maps derived from the censuses of wintering waterbirds (Figure I.2).

The maps of probability of occurrence provide an estimate of the relative probability of presence based on a habitat suitability index with values between 0 and 1 for every land unit of 500x500 m within the species' range. The logistic format of models produced by MAXENT allow us to interpret the resulting maps in a similar way to estimates for the probability of presence of species, subject to the environmental variables included in the models (Phillips & Dudik 2008). This probability provides quantitative information about the abundance of the species, although the characteristics of the analysed information (presences) limit the discriminatory capacity of these maps in terms of variations in abundance (Estrada et al. 2004). This assumption seems to be justified since abundance patterns are often closely related to the probability of occurrence of a species in the samplings (Robertson et al. 1995). These maps were coloured with the same colour palette as used in the Catalan

Breeding Bird Atlas (Estrada et al. 2004) to show the spatial variation of the probability of occurrence of the species. The lowest probability of occurrence corresponds to values shown in light and dark blue, with intermediate values in yellow and orange, and the highest values in red.

The maps of relative abundance for terrestrial (resolution 250x250 m) and marine species (resolution 2.5x2.5 minutes) also offer a habitat suitability measure (from 0 to 1) within the species' range. Given that these estimates are improved by the models developed with normalised abundance data, it is assumed that the suitability index calculated with quantitative information for every location can be used as a reliable estimator of relative abundance. This assumption is based on the fact that species are often more abundant in the most suitable habitats and hence the incorporation of more precise information about species abundance in the best habitats allows for a better representation of their relative abundance.

The relative abundance shown on the maps of coastal species (resolution 500x500 m) corresponds to an estimate derived directly by interpolation of mean standardized values within the coastal distribution range of the species, subsequently reclassified in values between 0 and 1. Abundance maps were coloured with different palettes for terrestrial species and for marine species (pelagic and coastal). The abundance maps of terrestrial species use a similar colour to that used for the probability of occurrence maps, with the exception that blue tones are replaced by green ones. Thus, the spatial variation of abundance is depicted with light and dark green for low relative abundances and maroon and red for high relative abundances. Maps of pelagic and coastal species use a monochromatic palette that ranges from yellow for the minimum relative abundance values, through different shades of orange and red, to maroon for maximum relative abundances. Finally, the maps for wintering waterbird censuses are the only ones that have a legend with absolute abundance categories (between 0 and 5,000 individuals/km²). This is the only case for which direct comparisons between species can be performed.

It is important to emphasize the fact that the direct comparison of maps must be done with care, since the estimates of probability of occurrence and relative abundance depend on intrinsic factors in all species. Thus, the same probability of occurrence, for instance, could be interpreted differently in two species with different detection probabilities and thus may indicate very different probabilities of real presence.

Summary of the types of abundance maps used in the Atles

In all, 5 types of abundance maps were created for the Atles, each with their own particular calculation procedures, graphical representation and interpretation.

Abundance maps of terrestrial birds were created from ecological niche models with MAXENT software; for common species (77) we only used SOCC data, while for the less common species (74) we used both Square sampling data and SOCC data and, in some cases, data from non-standardized samplings (complementary data). In the maps for these species, expert opinion regarding detectability was vital both when incorporating contagion variables into the model and when filtering the final map on the basis of presence data in 10x10 km UTM squares (Figure I.2).

The species associated with the sea or inland water bodies receive special attention in the Atles. Their abundance maps were created using different protocols for birds frequenting coastal (16), pelagic (9) or continental aquatic (30) habitats. In the first case, interpolation techniques were used based on the bird surveys conducted from the coastline; in the second case the results of oceanographic campaigns and MAXENT were used; in the final case, the results of censuses of winter waterbirds were directly plotted onto a map. Finally, a few very common aquatic species (5) were also modelled in a similar way to uncommon terrestrial species (Figure I.2).

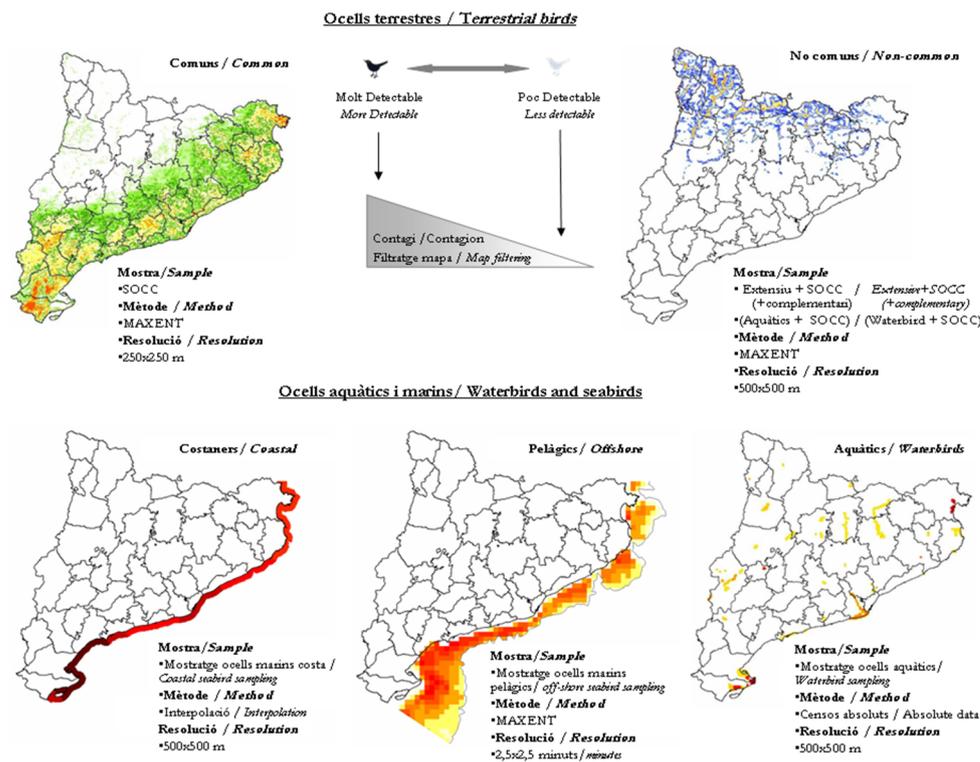


Figure I.2. Diagram showing the characteristics of the 5 major types of abundance maps in this atlas. Numerical punctuation according to non-English usage.

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Chapter II. The role of historical trajectories of land use change on protected forest bird species in d'Aigüestortes and Estany de Sant Maurici National Park⁴

Abstract

We assessed the spatial patterns of two endangered forest bird species (capercaillie and black woodpecker) during the last 50 years in protected areas with different protection histories, by the study of forest processes in the context of socio-economic and land use changes of the second half of the twentieth century. Species distribution models (SDMs) were developed based on contemporary species data and forest predictors, and projected to 1950's forest conditions. Recent and past forest structure and extent were derived from 100 m resolution canopy cover estimates obtained by image reclassification of aerial photographs taken in 1956 and 2009. Forest composition was based on the current distribution of the three dominant forest types in the study area: subalpine and montane coniferous forests, and montane deciduous forests. We used forest canopy cover changes to assess encroachment and densification processes. In the analysed period, we observed minor changes in the total extent of species suitable areas (gain of surface area of 5% for capercaillie and less than 3% for black woodpecker), but increases in surface area were noticeable in areas ranked as optimal suitability for capercaillie (12% improved areas) and black woodpecker (16% improved areas). The spatial patterns of forest bird species expansion showed a good match with

⁴ This chapter translate the original spanish paper published in the book *Proyectos de investigación en Parques Nacionales 2010-2013*. The author has written the manuscript and has performed all the analysis. Manuscript courtesy of the Organismo Autónomo Parques Nacionales.

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forest expansion in the Pyrenees, suggesting that landscape-scale forest processes due mainly to land abandonment have played a more important role than climate in driving endangered forest bird species dynamics over the last decades. Consideration of ecologically meaningful processes for species (i.e. forest maturation) when modelling species to historical environmental conditions might contribute to a better understanding of baseline species distributions and its actual response in the face of global change, and may become a valuable tool for improving future conservation strategies at a regional level.

Resum

Amb l'objectiu d'analitzar les trajectòries històriques dues espècies protegides (gall fer i picot negre) dins d'àrees protegides amb diferent grau de protecció, es va estudiar la dinàmica forestal de la segona de la segona meitat del S.XX en un context d'importants canvis socioeconòmics i d'usos del sòl. L'extensió i estructura del bosc es va calcular a partir d'estimes de fracció coberta (FCC) basades en ortoimatges capturades el 1956 i el 2009. La composició del bosc es va inferir a partir de la distribució actual dels tres tipus dominants de masses forestals: boscos de coníferes de l'estatge subalpí i montà, i boscos caducifolis de l'estatge montà. Els canvis en FCC entre els dos períodes van permetre analitzar els processos de colonització i densificació per als diferents tipus de bosc. Per analitzar els impactes d'aquests processos en la disponibilitat d'hàbitat per espècies d'aus forestals, es van desenvolupar models de distribució d'espècies basats en dades biològiques i forestals actuals, que posteriorment van ser projectats a les condicions forestals de la dècada de 1950. Els resultats obtinguts mostren que les últimes dècades totes dues espècies han experimentat un augment dels hàbitats disponibles, que ha estat especialment important per als hàbitats més bons, amb més d'un 10% d'increment en la superfície d'hàbitat òptims per a totes dues espècies. Els patrons espacials d'aquesta expansió han coincidit amb l'augment de les masses forestals als Pirineus, suggerint que els fins ara els processos forestals relacionats amb l'abandonament rural han jugat un impacte més important en las dinàmiques d'aus forestals protegides que el canvi climàtic. Així doncs, l'anàlisi conjunta de la distribució de les espècies i els canvis en les condicions ecològiques rellevants per les espècies, a més de contribuir al coneixement de les trajectòries històriques de les espècies, permet comprendre millor la resposta de les espècies als canvis en les condicions ambientals, el que, en un context de gestió d'espècies protegides, pot esdevenir una eina molt valuosa per orientar les futures estratègies de conservació a escala regional.

Introduction

Natural systems are spatially and temporally dynamic. Change and disturbance of these systems at a given time are ecological properties such as stability and persistence (Pickett et al., 1989, Platt & Connell 2003). In a context where environmental changes seem to be accelerated by human activities, understanding of species (and their habitats) dynamics, both spatial and temporal, appears as an ongoing challenge (Brook et al., 2008). Human impacts on ecosystems are causing a fast modification of the ecological processes and species distribution on a global scale (Pimm et al., 1995). These impacts include climate change (Thomas et al., 2004), invasive species (Walther et al., 2009) and natural habitats destruction and fragmentation, often associated with significant threats to many species (Andren 1994; Villard et al., 1999). Despite the general validity of these patterns, in many regions with long-standing human influences on natural systems, traditional primary activities related with extensive agricultural and pastoral landscapes with low intensity disturbances, appear to have been fully incorporated into ecological dynamics. In some of these areas, the persistence of current biodiversity patterns might even be closely related to the maintenance of such traditional activities (Blondel and Aronson 1999).

Among these, Mediterranean mountain areas stand out prominently (Lavorel et al., 2005). Understanding and quantification of the historical impact on natural systems of protected areas is essential for dosing management strategies of these areas. Reducing the impact of traditional activities in protected areas of high natural value can increase instability of natural systems and make it more sensitive to other disturbances that does not always favour biodiversity (Brawn, 2001), ecosystem functions or goals outlined in the founding statutes of protected areas. The problem is complex, since the current status of protected areas is the result of historical trajectories that have been undergone in particular historical contexts.

This study aims to assess a methodology intended to understand the impacts of global change in mountain landscape context, confronting a modelling process to examine the response of species in different temporal scenarios. This methodology should allow species distribution models parameterization and their projection to retrospective historical habitat scenarios, to analyse changes in habitat suitability from the mid-20th century in the Catalan Pyrenees. Concretely, we examine the consequences of changes in subalpine and montane forests since the mid-20th century in the dynamics of two forest birds species, the capercaillie (*Tetrao urogallus*) and the black

woodpecker (*Dryocopus martius*), and assess the implications of different protection regimes with similar trajectories of land use.

Methods

Study area and target species

The study area is located at the western Catalan alpine region, covering a total area of 1,882 km², bounded by three overlapped protected areas, Aigüestortes i Estany de Sant Maurici National Park, Alt Pirineu Natural Park and Natura 2000 network (Figure II.1). Aigüestortes i Estany de Sant Maurici National Park comprise 400 km² divided in two distinct protection zones, core areas (35%) and peripheral areas (65%). Since its creation in 1955, natural resources exploitation (except traditional cattle) is strictly prohibited inside the National Park, while traditional activities consistent with nature conservation (e.g. forestry) are allowed in peripheral areas. The Alt Pirineu Natural Park was established in 2003, although it includes areas managed as game reserves since 1966. This Natural Park has a surface of 760 km², mostly public ownership (municipal commons 80% and Catalan government 10). Finally, approval of Natura 2000 network in 2006 involved the designation of two Special Areas of Conservation within the study area, Aigüestortes (560 km², 71% overlapped with the National Park) and Alt Pallars (773 km², 86% overlapped with the Natural Park), both tagged as Special Protection Areas for birds. Hence, the history of natural resources exploitation in recently protected areas (those outside the National Park) since the mid-20th century is parallel to that of non-protected Pyrenean rural areas (44% of the study area), with generalized farmland abandonment in the hill slopes, related to strong depopulation trends, and a sharp decline in livestock due to the crisis on the transhumance system (García-Ruiz & Lasanta 1990; García-Ruiz et al. 1996).

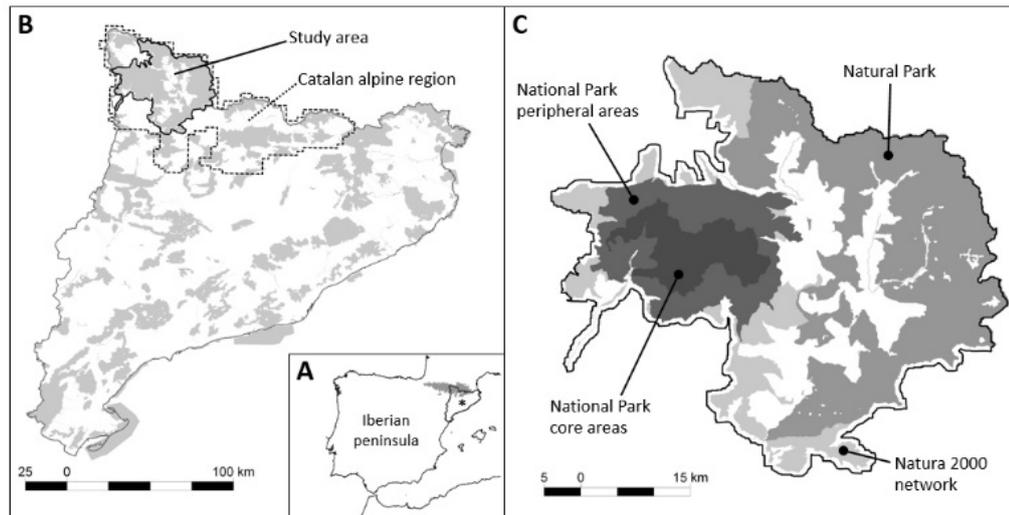


Figure II.1. Location of study area: (A) Catalonia (*) and the alpine region (shaded) in the Pyrenees mountain range, according to the European biogeographical regions (ETC/NPB 2008); (B) study area and alpine region in Catalonia, showing the Catalan network of protected areas (shaded); (C) protected areas inside the study area (greyscale shading, unprotected areas in white), including Aiguestortes i Estany de Sant Maurici National Park (core and peripheral areas), Alt Pirineu Natural Park and Natura 2000 network.

Forest changes from since the mid-20th century

To describe changes in forest extent and structure from 1950's to 2000's, we processed 527 orthoimages taken in 2009 (ICC, 2012) covering the whole Catalan Alpine region, and 122 grey-scale aerial photographs taken in 1956 covering the study area. Following Améztegui et al. (2010), each 2009 and 1956 image was semi-automatically reclassified into a 2 m resolution binary raster with 'tree' and 'non-tree' cell values, and all the 2009 and 1956 reclassified images were stitched into mosaics. 2000's and 1950's mosaics were upscaled to 100 m resolution canopy cover rasters, performing the ratio of the total number of 'tree' original cells per pixel, expressed as a percentage. Scaling processes were performed individually based on the current distribution of the three dominant forest types in the study area (Land Cover Map of Catalonia 3rd edition: CREAM 2010): i) subalpine mountain pine (*Pinus uncinata* Ram.) forests; ii) montane coniferous forests, dominated by Scots pine (*P. sylvestris* L.) and silver fir (*Abies alba* Mill.) from drier to humid areas; and iii) deciduous forests in shaded slopes, with beech (*Fagus sylvatica* L.) as dominant species accompanied by silver birch (*Betula pendula* Roth.). Following forest canopy cover thresholds compatible with those used by FAO (Shvidenko et al. 2005), cells with forest canopy cover $\geq 10\%$ were classified as 'forested', and 40% canopy cover was used to distinguish 'open forest' ($< 40\%$) from 'closed forest'

($\geq 40\%$). Based on this, we examined changes between current and historical distribution of the three forest types described above. To reduce orthorectification errors, we only considered as colonized those cells not classified as forest in mid-20th century ($< 10\%$) and with an increase higher than 10% in the study period. Forest densification was based on identifying those areas previously classified as open forest that have evolved to current closed forests.

Hindcasting forest bird distribution to mid-20th century

In order to analyse the distribution changes of capercaillie and black woodpecker, first it was modelled birds current distribution based using species distribution models (henceforth SDMs) based on recent census data and environmental predictors. Once calibrated, SDMs were hindcasted to 1950's forest conditions.

Capercaillie data included 143 lek allocations in the Catalan Pyrenees recorded in a standardized national censuses promoted by the Catalan government in 1995 (Canut et al., 2006). In contrast, black woodpecker datasets were built from the combination of information from two large scale volunteer based bird monitoring programs, the Catalan common bird survey (Herrando et al. 2008; 164 occurrence records) and the web based monitoring tool Ornitho (www.ornitho.cat; 106 occurrence records), reporting 270 occurrence records over a sampled area of 2'015 UTM 1x1 km squares in the Catalan alpine region (~30% of the total area) from 2002 to 2010. In order to obtain a comprehensive set of geographically weighted presence records, we cleaned repeated observations at the same localities and randomly sub-sampled one occurrence record per 1x1 km UTM cell, obtaining an unbiased dataset of 182 occurrence records.

Environmental predictors for model building included nine variables connected to ecological requirements of forest bird species, including forest habitats (6 paired variables for 2000's and 1950's) and relief (3 unaltered variables) (Table II.1) . For specialist forest bird species, forest composition, extent and structure are relevant features for habitat selection at landscape scale (Gil-Tena et al. 2007). These features were summarized for each forest type in two predictors related to open and closed forests areas, based on 'open forest' and 'closed forest' areas derived from 2000's and 1950's canopy cover rasters of subalpine coniferous forests, montane coniferous forests and montane deciduous forests. Open forests extent were defined as the percentage of 'open forest' area around each cell, and was computed from contemporary and historic canopy cover rasters as the average of 'open forest' cells (canopy cover $< 40\%$) in 500 m radius. Closed forests extent were likewise

but based in ‘closed forest’ terms (canopy cover $\geq 40\%$). To complete environmental gradients for forests bird species we selected three relief variables, altitude, slope and percentage of sunny surface, derived from a digital elevation model (DEM) of 30 m resolution and averaged to 100 m resolution analysis.

Table II.1 Environmental predictors used to examine species distribution.

Predictors	Min-Max values	Description
Extent of open forests		
Subalpine coniferous	0-100	Percentage of open forests area around each cell, computed from 2000’s and 1950’s canopy cover rasters as the fraction of ‘open forest’ cells ($10\% \leq cc < 40\%$) in 500 m radius.
Montane coniferous		
Montane deciduous		
Extent of closed forests		
Subalpine coniferous	0-100	Percentage of closed forests area around each cell, computed from 2000’s and 1950’s canopy cover rasters as the fraction of ‘closed forest’ cells ($cc \geq 40\%$) in 500 m radius.
Montane coniferous		
Montane deciduous		
Relief		
Altitude	566-3.052	Vertical distance in meters above mean sea level. Averaged from ICC (2012) 10 m resolution digital elevation model.
Slope	0-343	Percentage of vertical height respect to the horizontal displacement (e.g. $45^\circ = 100\%$). Derived from ICC (2012) 10 m resolution digital elevation model (DEM).
Sunny surface	0-100	Proportion of south aspect around each cell. Computed from an aspect map derived from ICC (2012) DEM.

From the available correlative presence-only methods for predicting species distribution, we chose the maximum entropy modelling approach implemented in the free modelling software MaxEnt (version 3.3.3k: Phillips and Dudik 2004; Phillips et al. 2006) due to its robust predictive performance compared with the highest performing methods (Elith et al., 2006) coupled with acknowledged capacities to address presence-only data limitations (e.g. sample selection bias, lack of information on species prevalence) (Elith et al 2010a). MaxEnt is a general-purpose machine learning method that minimizes the relative distance between two probability densities, one estimated from the species occurrence data and one from the landscape, measured in geographic/environmental terms (Phillips et al. 2006; Phillips and Dudik 2008; Elith et al 2010a). Constraints imposed from occurrence records are solved with regression-like transformations of selected predictors over many features (linear, product, quadratic, hinge, threshold and categorical) allowing potentially complex relationships to be modelled.

SMDs were trained on the full data sets and projected to both current and past environmental scenarios, using MaxEnt default parameters but only

linear and quadratic features, looking for simple models with smooth fitted functions easy to interpret and avoiding the extrapolation of complex functions and interactions (Ref!!!). We applied background restrictions to sampled areas for the Black Woodpecker models, forcing background data with similar biases to those in the presence data (Dudík et al., 2006; Phillips et al., 2009; Elith 2010a). Capercaillie and Tengmalm's Owl were built with no background restrictions, assuming unbiased samples suggested by its survey methods.

Logistic outputs were ranked in three strata of increasing suitability. Among the different methods available to transform model logistic outputs into maps of suitable-unsuitable areas (Liu et al. 2005), we followed Arcos et al. (2012) to define species suitable areas in terms of species prevalence as those areas scored above the average of the habitat suitability estimates from the 10 percentile training occurrences. Then, first, a threshold for high suitable areas was in first place defined as the average mean within suitable areas (Pearson et al. 2007). Secondly, averaged scores within high suitable areas drew the cut-off point for optimal areas. Species thresholds computed from 2000's model outputs were also applied to set the limits of suitable, high suitable and optimal areas for 1950's predicted distributions.

MaxEnt models were evaluated by means of threshold-independent and threshold-dependent measures in order to get a multifaceted view of the quality of the predictions. First, we used the threshold-independent Area Under the [Receiver Operating Characteristic (ROC)] Curve (AUC) of the Receiver Operating Characteristic (ROC) curve (Fielding & Bell 1997; Boyce et al. 2002; Phillips et al. 2009) computed by means of 10-fold cross-validation procedure implemented in MaxEnt. The AUC provides a measure of the model ability to discriminate between occupied and non-occupied sites and typically assumes scores from 0.5 for random predictive discrimination to 1 for perfect discrimination. Scores greater than 0.7 indicate useful predictions and over 0.9 indicates excellent accuracy model performance (Hosmer and Lemeshow, 2000; Swets 1988; Araújo et al. 2005). Despite the limitations of AUC as a performance measure and its responsiveness to absences selection when deals with presence-only data (Lobo et al. 2008), it is, however, a valid measure of relative model performance between models for the same species and study area (Anderson & Gonzalez Jr 2011). Second and complementarily, threshold-dependent metrics included the omission rate, i.e. the proportion of test localities falling outside suitable areas (see previous section for the definition of suitable areas), and the model significance (Anderson, et al. 2002; Phillips et al. 2006; Anderson & Gonzalez Jr 2011). Omission rates were computed from the 10-fold datasets, and one-tailed binomial test, computed from 'MASS'

library implemented in R software, was used to determine model significance (Phillips et al. 2006; Anderson & Gonzalez Jr 2011).

Results

Forest changes

In mid-20th century, coniferous forests predominated in the study area, with subalpine mountain pine forests covering 46,724 ha and montane Scots pine forests occupying 43,310 ha, while montane deciduous forests occupied were restricted to 13,992 ha (Table II.2). Since then, all forests have undertaken remarkable expansion processes, being subalpine coniferous forests which have experienced the major growth in terms of colonization (new 5,191 ha; 11.1% of the area occupied in the 1950's) and densification (25.3% of 1950's open forests densified to closed forests) (Table II.2). These processes were less pronounced in both montane coniferous and deciduous forests, with 5% of new colonized areas, and 14% of densification from open to closed forests. Regarding the location of forest changes, the more drastic changes for all forest types, but specially for coniferous forests, were recorded in non-protected areas, located at lower altitudes and valley bottoms.

Habitat changes for forest birds

Species distribution models showed very good discrimination on held out data for the capercaillie (cross-validated AUC of 0.94 ± 0.02 SD), and just good discrimination ability for the black woodpecker (AUC 0.77 ± 0.05 SD) (Figure II.2). Additionally, mean omission rates reported small fractions of false negatives, as required for good predictions, with 6% for capercaillie and black woodpecker, and binomial omission tests were always significant (Binomial one-tailed test: capercaillie $p < 0.001$, black woodpecker $p < 0.05$). Consistent with the species ecology, models pointed out coniferous forests as the main habitat component for both species, with capercaillie showing greater exclusivity for subalpine mountain pine forests, and black woodpecker preferring montane Scots pine forests, but always emphasizing their preferences towards denser and closed forests (Figure II.3).

Table II.2. Forest changes from 1950's to 2000's. Colonization (Col.), percentage of new forested areas in the 2000's; Densification (Dens.), percentage of open forest and not forested areas from 1950's densified to closed forest in the 2000's.

Forest/Protection status	Forest area (ha)		Open forest (%)			
	1950's	2000's	Col.	1950's	2000's	Dens.
Subalpine coniferous	46'724	51'583	11.1%	18.7%	7.5%	25.3%
National Park	11'526	12'523	9.2%	21.2%	4.4%	27.0%
Natura 2000 + National Park	28'707	31'352	10.1%	17.4%	9.1%	22.4%
Non-protected	6'491	7'708	19.1%	20.1%	6.4%	35.0%
Montane coniferous	43'310	45'719	6.5%	11.4%	7.3%	14.6%
National Park	3'770	3'919	4.3%	11.1%	2.7%	14.5%
Natura 2000 + National Park	26'291	26'853	3.2%	9.9%	8.1%	9.9%
Not protected	13'249	14'947	13.8%	14.5%	7.1%	24.0%
Montane deciduous	13'992	14'336	4.8%	12.8%	12.4%	13.3%
National Park	1'253	1'309	5.0%	16.3%	14.0%	17.0%
Natura 2000 + National Park	7'560	7'629	3.5%	11.4%	14.1%	10.3%
Non-protected	5'179	5'398	6.6%	14.1%	9.6%	16.8%

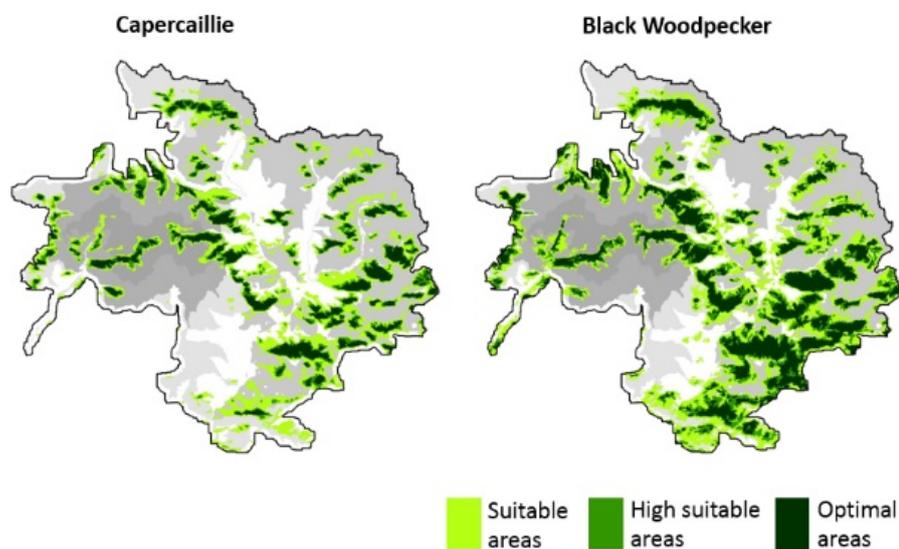


Figure II.2. Ranked predictions for capercaillie (*Tetrao urogallus*) and black woodpecker (*Dryocopus martius*) in the 2000's.

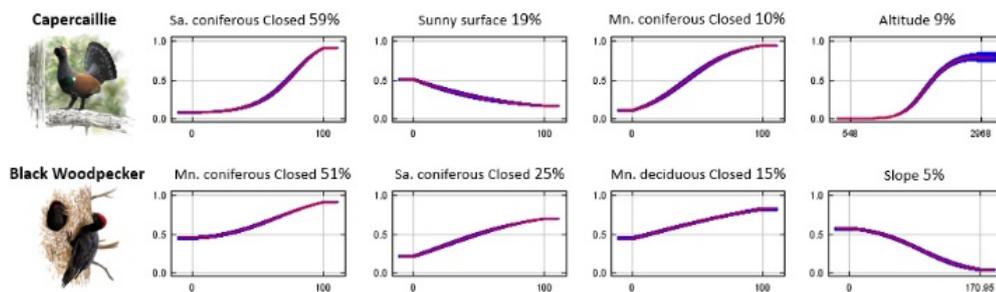


Figure II.3. Partial dependence plots showing the marginal response of the four most important variables (i.e., for constant values of the other variables) for capercaillie (*Tetrao urogallus*) and black woodpecker (*Dryocopus martius*), including the relative contribution of each variable. The y-axes indicate logistic habitat suitability. Sa. Subalpine; Mn. Montane.

SDM projection to past environmental conditions showed small shrinkage of species historical habitat suitability compared to current suitability. Thus, models indicated that capercaillie and black woodpecker increased 5% and 2.6%, respectively, their suitable habitats since mid-20th century (Table II.3). Looking at changes in optimal habitats, increases in surface areas were more important, reaching values of 11.6% in the capercaillie and 16% in the black woodpecker. Additionally, changes in optimal habitats for both species were particularly strong within the National Park, especially when compared to areas within the Natural Park or Natura 2000, where increases in suitable and optimal habitats were slighter (Table II.3).

Table II.3. Species distribution changes from 1950's to 2000's. Species areas in 1950's and 2000's is expressed in hectares, and % change is based on 1950's reference areas.

Specie/Protection status	Suitable áreas (ha)			Optimal áreas (ha)		
	1950's	2000's	% Change	1950's	2000's	% Change
Capercaillie	61,112	64,147	5.0%	17,302	19,313	11.6%
National Park	15,237	15,722	3.2%	3,917	5,208	33.0%
Natura 2000 + Natural Park	38,277	39,894	4.2%	11,247	11,776	4.7%
Non-protected	7,598	8,531	12.3%	2,138	2,329	8.9%
Black woodpecker	116,161	119,232	2.6%	37,326	43,311	16.0%
National Park	14,409	15,398	6.9%	5,483	7,301	33.2%
Natura 2000 + Natural Park	68,359	69,760	2.0%	24,898	27,447	10.2%
Non-protected	33,393	34,074	2.0%	6,945	8,563	23.3%

Discussion

Analyses of landscape historical trajectories has shown no major changes in the total extent of species suitable areas (gain of surface area of 5% for capercaillie and less than 3% for black woodpecker), but increases in surface area were noticeable in areas ranked as optimal suitability for capercaillie (12% improved areas) and black woodpecker (16% improved areas). Outside protected areas, increases and improved habitat availability for capercaillie and black woodpecker were related to colonization and densification processes of subalpine forests of mountain pine, especially in valley bottoms. Within protected areas, and especially in the National Park, forest colonization of valley bottoms was not so relevant because of orographic differences (i.e. protected areas tend to be at higher altitudes) and regulation of human activities. Consequently, most important changes for capercaillie and black woodpecker within protected areas consisted of increases in optimal habitats due to densification (and maturation) processes of forests.

This study show that since the mid-20th century there has been an increase in the quantity and the quality of suitable habitats for the capercaillie and the black woodpecker, both protected species included in the Birds Directive (Annex I) and assigned as priority species in SPAs areas of Natura 2000 sites analysed (Alt Pallars Aigüestortes). But landscape dynamics not only entail consequences in the long term; short term analyses have also shown significant changes in population trends for other bird species affected by forest colonization processes (Herrando et al., 2014). These suggest that both short- and long-term changes in habitat quality and communities composition indicates broader trends occurring at wider regional scales. This fact would explain the tiny differences between species habitat trends within and outside the Protected areas.

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Chapter III. Global warming and long-distance spread of invasive *Discoglossus pictus* (Amphibia, Alytidae): conservation implications for protected species in the Iberian Peninsula⁵

Abstract

Aim *Discoglossus pictus* is a North African amphibian introduced in Southern France early 20th century, spreading southern along the Mediterranean coastal plains up to 170 km. Many studies have demonstrated that *D. pictus* compete against native species with similar breeding strategies, pointing out abiotic conditions as the main driver to tip the balance in favour of one or another specie. Furthermore, recent establishment of *D. pictus* via human-mediated dispersal in the main logistic areas in Barcelona (Spain) makes more feasible a long-distance dispersal scenario to areas inhabited by Iberian-endemic congeneric species. In order to disentangle conservation implications to sensitive native species of the spread of *D. pictus*, we have examined the impact of long-term climate warming on the basis of a niche overlap analysis taking into account abiotic factors.

Location The study area covers the Western Mediterranean region, including distribution ranges of all genus *Discoglossus* species in North-western Africa

⁵ The author has written the manuscript and has performed all the analysis.

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(659'784 km²), Sicily (27'711 km²), and the Iberian Peninsula and Southern France (699'546 km²).

Methods Niche overlap was measured from species environmental spaces extracted in a PCA analysis including climate and relief environmental variables. Current and future climatic suitability for each species was assessed in an ensemble-forecasting framework of species distribution models, built on contemporary species data and climate predictors and projected to 2070's climatic conditions. The extent of the differences in the climatic suitability change between species were examined considering different protection regimes within the actual invaded range of *D. pictus*, and also assuming a long-distance dispersal scenario throughout full distribution ranges of sensitive and endemic species in the Iberian Peninsula.

Results Our results show a strong climatic niche overlap between *D. pictus* and sensitive and endemic species in the Iberian Peninsula. Climate change future projections suggest that climatic suitability will increase for all species, both inside and outside Natura 2000 network, with the only exception a moderate and widespread decrease for *Pelodytes punctatus*. However, that positive trends are reversed within Natura 2000 sites where most species are explicitly targeted, jeopardizing the effectiveness of protected areas in the long-distance dispersal scenario.

Main conclusions In the next decades the combined effect of global warming and the spread of *D. pictus* should not pose a risk for most species from the recipient amphibian communities, even if there are new long-distance dispersal events that hypothetically face invasive *D. pictus* to endemic congeneric species. Only non-endangered *Pelodytes punctatus* seems to be negatively affected by synergies between global warming and cohabiting with *D. pictus*. Results also show that Natura 2000 sites explicitly targeted to sensitive species are also the most fragile areas to climate warming, emphasizing the importance of building effective management strategies, based on monitoring species and threats, but also the need to evaluate and adapt site-specific targets to future challenges posed by global change, in order to effectively preserve endangered species.

Resum

Discoglossus pictus és un amfibi nord-africà que va ser introduït al sud de França a principis del S.XX, i que s'ha dispersat seguint el litoral mediterrani fins 170 km en direcció sud. En aquestes àrees, molts estudis han constatat que *D. pictus* competeix amb les espècies natives *Bufo calamita* i *Pelodytes punctatus*, assenyalant les condicions abiòtiques com el principal factor que pot fer decantar la balança a favor d'una o altra espècie. A més, la recent arribada per vies artificials de *D. pictus* a la principal zona logística de Barcelona (Espanya) planteja un escenari de dispersió a llarga distància cap a àrees ocupades per el seu congènere *Discoglossus galganoi*, endèmic de la Península Ibèrica. Amb l'objectiu d'analitzar les implicacions en conservació tant d'espècies natives a la dispersió de *D. pictus*, s'han examinat els impactes de l'escalfament global a llarg termini en base a un anàlisi de solapament del nínxol climàtic entre les espècies afectades. Es van comparar els canvis en la idoneïtat climàtica entre les espècies tenint en compte diferents règims de protecció, tant dins com fora de la zona colonitzada per *D. pictus* a la Península Ibèrica, assumint un escenari de dispersió a llarga distància per tot el rang de distribució de les espècies sensibles. Els anàlisis mostren un fort solapament del nínxol climàtic entre *D. pictus* i les espècies natives. Les projeccions climàtiques de finals del S.XXI indiquen un augment de la idoneïtat climàtica per totes les espècies excepte *Pelodytes punctatus*, amb una lleugera disminució de al llarg del seu rang de distribució actual. No obstant això, aquestes tendències s'inverteixen dins dels espais Natura 2000 on algunes espècies natives es consideren prioritàries, posant en qüestió la efectivitat de les àrees protegides en un context de dispersió a llarga distància. Així, en les properes dècades, la combinació de l'escalfament global i l'expansió de *D. pictus* no sembla que hagi de posar en risc les comunitats natives d'amfibis, fins amb una hipotètica dispersió a llarga distància que porti a *D. pictus* a zones habitades per els seus congèneres endèmics de la Península Ibèrica. Només una espècie no amenaçada, *P. punctatus*, es pot veure negativament afectada per les sinergies de cohabitar amb *D. pictus* en un context de canvi climàtic. Els resultats també posen de manifest que els espais Natura 2000 on les espècies natives es consideren prioritàries son també les àrees més fràgils a l'escalfament global, posant de relleu la importància de vigilar les espècies i les seves amenaces per desenvolupar estratègies més efectives de gestió, i, alhora, la necessitat d'avaluar i adaptar els objectius específics dels espais Natura 2000 davant els reptes que planteja el canvi global per conservar de forma més efectiva les espècies amenaçades.

Introduction

The introduction of invasive species is, after habitat destruction, the second most important cause of biodiversity loss on Earth (Bellard et al., 2016; Mack et al., 2000; Sax et al., 2007). The main problems related to the introduction of invasive species are competition with local fauna, introduction of pathogens and genetic pollution of autochthonous populations (Dodd and Seigel, 1991; Kraus, 2015; Liu et al., 2014; Mack et al., 2000). Guijarro (2001) have estimated that the last 300 years, the 39% of all known extinctions have been driven by invasive species.

Discoglossus pictus is a North African species introduced from Algeria to Europe in Banyuls Sur Mer (Southern France) in early 20th century (Wintrebert, 1908). Currently, the invaded area is extended through a continuous range from Southern France to Northeastern Iberian Peninsula, occupying more than 7'000 km² (Montori et al., 2007) (Figure III.1). Evidences on the progression of *D. pictus* reports an expanding range at a similar rate to other invasive amphibians (Leblois et al., 2000; Llorente et al., 1995; Montori et al., 2007). These studies indicate that populations have moved 60 km West and 140 km South within the Iberian Peninsula, with great prospects for an unbounded progression through bioclimatic favourable regions (Escoriza and Boix, 2012; Franch et al., 2007; Montori et al., 2007; Richter-Boix et al., 2004). Furthermore, unforeseen establishment of *D. pictus* in the main logistic areas in Barcelona (Spain) (Franch et al., 2007) has highlighted the proneness of the specie for human-mediated long-distance “stowaway” dispersal (White and Shine, 2009), while boosting the risk of accelerating range expansion. Ongoing climatic changes at global scale can presumably play a critical role in this acceleration (Kot et al., 1996), especially since future climate conditions for amphibians in the Iberian Peninsula are predicted to approach current conditions found in North Africa (Araujo et al., 2006).

Species interactions between invasive *D. pictus* and native species have been consistently assessed (Escoriza and Boix, 2014; Richter-Boix et al., 2013). Specifically, *D. pictus* shows a strong niche overlap with *Pelodytes punctatus* and *Bufo calamita*, all three species with similar phenology and breeding strategies.

Competition between native and non-native species can drive recipient communities to become less structured (Richter-Boix et al., 2013) and abiotic conditions have been identified as the main driver to exacerbate this process (Escoriza and Boix, 2014). Besides, although neither native species has no serious conservation problems, for both native species there are signs of population decreases in different areas outside the *D. pictus* invaded range (European Red Lists, DG-ENV and IUCN, 2015). Beyond the invaded area, the presence of the Iberian-endemic *Discoglossus galganoi* determines the importance of knowing the limits of potential expansion of *D. pictus*, particularly in a long-distance dispersal scenario based on its ability for long-distance “stowaway” dispersal. That may have implications on the progression of *D. pictus* within the Iberian Peninsula, especially to assess potential impacts for the *D. galganoi* eastern subspecies (*D. galganoi jeanneae*), tagged as “vulnerable” in the Spanish Red List (Pleguezuelos et al., 2002).

In order to disentangle conservation implications to native species of the spread of *D. pictus*, in this paper we examine the impacts of long-distance dispersal scenario and long-term climate warming over the Iberian Peninsula. Our aims are: 1) to assess niche overlap between *D. pictus* and its Western Mediterranean congeneric species, *D. scovazzii*, *D. g. galganoi* (hereinafter *D. galganoi*) and *D. g. jeanneae* (hereinafter *D. jeanneae*), as well as the Iberian native species *Bufo calamita*, *Pelodytes punctatus* and *Pelodytes ibericus*; 2) to predict changes in climatic suitability due to global warming for Iberian native species *D. pictus* in the Iberian Peninsula; 3) assess potential impacts to Iberian native species under different protection regimes, based on Natura 2000 network, under a long-distance dispersal scenario throughout full distribution ranges of native Iberian species. Insights from these investigations are needed to formulate long-term conservation strategies.

Methods

Study area

The study area covers the Western Mediterranean region, including distribution ranges of all genus *Discoglossus* species in North-western Africa (659'784 km²), Sicily (27'711 km²), and the Iberian Peninsula and Southern France (699'546 km²) (Figure III.1).

Protection regimes within the Iberian Peninsula and Southern France were defined on the basis of Natura 2000 GIS databases were (DG-ENV, 2013). In this area, Natura 2000 includes 781 sites covering near 20% of the territory. Among these sites, 189 are explicitly targeted to protect Habitats Directive Annex II species *D. galganoi* (167 sites) and *D. jeanneae* (22 sites). Supplementary conservations targets are also defined in Natura 2000 sites, and under this specification 69 sites extend protection to *B. calamita* (Habitats Directive Annex IV and Bern Convention specie), 66 sites to *P. punctatus* (Bern Convention specie), and 3 sites to *P. ibericus* (Endemic specie).

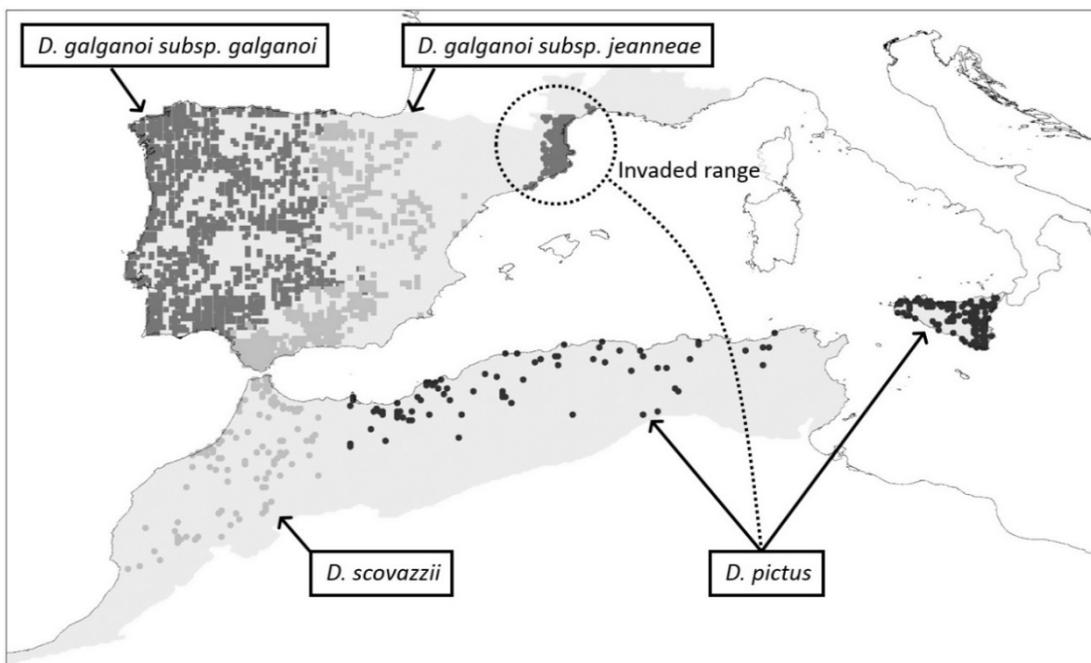


Figure III.1. Distribution of *Discoglossus* congeneric species within the study area (shaded) in the western Mediterranean region.

Species data

Native-range data for *D. pictus* included 76 occurrences from Algeria (presence-only data: non published data from P. Geniez; Mateo et al., 2013) and 115 occurrences from Sicily (among 373 10x10 km atlas cells: Sindaco et al., 2006). Northern Africa databases also provided 113 occurrences for *D. scovazzii* from Morocco (presence-only data: non published data from P. Geniez, Bons and Geniez, 1996) (Figure III.1).

European invaded-range data for *D. pictus* included 59 occurrences from Southern France (presence-only data: Fradet and Geniez, 2004; Lescure and Massary, 2012) and 59 occurrences from Spain (among 7'720 10x10 km atlas cells: AHE, 2016) (Figure III.1). Spanish databases also provided occurrences for *D. jeanneae* (500), *D. galganoi* (860), *B. calamita* (2463), *P. punctatus* (790) and *P. ibericus* (261). Finally, Portugal databases completed the Iberian distribution with 295 occurrences for *D. galganoi* (among 1'166 10x10 km atlas cells: Loureiro et al., 2008).

Environmental data

Five explanatory variables connected to abiotic ecological requirements of amphibians were selected for subsequent analyses. Temperature extremes, annual precipitation and relief are relevant features for amphibian's distribution in the Mediterranean region. These factors were summarized in 2 relief predictors, altitude and slope, and 3 climate predictors, maximum temperature of warmest month (BIO5), minimum temperature of coldest month (BIO6) and annual precipitation (BIO12). Climate and altitude layers were downloaded from the WorldClim database (Hijmans et al., 2005, www.worldclim.org) at 5-minute spatial resolution (~9x9 km), and slope was derived from WorldClim DEM at 30-second spatial resolution.

For long-term climatic suitability analyses, we also downloaded climate layers for late 21st century (averaged climate projections for the 2061-2080 time period) based on Fifth Assessment IPCC report (IPCC, 2014) for both the most optimistic (RCP 2.6) and pessimistic (RCP 8.5) greenhouse gas scenarios. Following recent studies dealing with the impacts of climate change on biodiversity (Naujokaitis-Lewis et al., 2013; Regos et al., 2015), we averaged six different Global Climate Models (CNRM-CM5, IPSL-CM5A-LR, HadGEM2-ES, MPI-ESM-LR, GISS-E2-R and CCSM4) to reduce uncertainties, producing one single layer for each climate predictor and greenhouse gas scenario.

Niche overlap analysis

To search for similarities/dissimilarities in environmental conditions between *D. pictus* and the native species inhabiting the Iberian Peninsula, we conducted a PCA analysis (Broennimann et al., 2011). The two main factors of the PCA were used to visualize in a bivariate plot the variation patterns of native species and invaded species ranges. Environmental spaces were delimited by maximum convex polygons including all species occurrences, and the intersection of spaces between species were used as a measure of niche overlap. The analyses were conducted in R, using the packages *ade4* and *gpclib*.

Climatic suitability changes

Climatic suitability was modelled for all species by running five widely used niche-based modelling algorithms implemented in *biomod2* platform (Thuiller, 2003). These models are: (1) generalised linear model (GLM), (2) generalised additive model (GAM), (3) multivariate adaptive regression splines (MARS), (4) generalised boosting model (GBM), and (5) flexible discriminant analysis (FDA). All models were trained on the basis of species presence-absence samples and current climatic conditions and then projected to future climatic scenarios. Predictive performance of every model was assessed by means of the relative operating characteristic (ROC) curve and the Area Under the Curve (AUC) (Fielding and Bell, 1997), on the basis of a subsampling approach that randomly split a 70% subset of the sample to model building and the remaining 30% for testing predictions. Models were also replicated 10 times using environmental stratified presence-absence subsamples built from available species occurrences looking for a more robust estimate of the predictive performance from the averaged AUC of replicated cross-validations. For presence-only data from Northern Africa and Southern France, this meant to build pseudo-absences on the basis of an environmental stratification of the surveyed areas in each region (Chefaoui and Lobo, 2008). On the other hand, original presence-absence databases from Italy, Spain and Portugal were subsampled in order to balance environmental gradients within the modelling samples (Franklin, 2009). Environmental stratification was based in the WWF Terrestrial Ecoregions of the World (Olson et al., 2001). AUC measure is independent of the threshold at which the model's prediction is considered, and ranges from 0 to 1; AUC scores close to 1 mean perfect model predictions, while AUC scores close to 0.5 indicates predictions no better or worse than random. The potential problems raised by Lobo et al. (2008) on the use of AUC as a measure of model performance were considered as minor here because AUC was used to rank models obtained from the same dataset and within the same geographical area, according to their predictive performance. We applied

an ensemble-forecasting framework by computing a consensus of single-model projections (from models with AUC > 0.7 using AUC values as model weights) using a weighted average approach (Araujo et al., 2007).

To determine the potential range of affectation of *D. pictus* in the Iberian Peninsula, native-range predictions were built on the basis of North African and Sicily databases and projected to new geographical areas in Southern Europe. These models were built using only occurrence data from the native range where the species is in equilibrium with the environment. Here, the agreement between observed and predicted distribution within the invaded range was assessed with AUC computed using invaded-range occurrence samples (Manel et al., 2001).

Differences between current and future predictions of climatic suitability predictions were used to measure changes in climatic suitability, yielding positive changes when future scores were bigger than the current ones, and negative changes in the opposite case. To allow comparisons between species, scale values from current and future climatic suitability predictions were homogenized using standard scores (i.e. difference between raw climatic suitability scores and mean climatic suitability, divided by the climatic suitability standard deviation). This normalization implies adjusting raw scale values (0-1) to a notionally common scale that quantifies the signed number of standard deviations above (or below) the mean. Hence, species-specific misalignments between current and future climatic suitability raw scales should be corrected in order to achieve accurate measurements of climatic suitability changes based on standard scores. Since future forecasts of climatic suitability were based on current climatic suitability models, these misalignments were consistently corrected by using the mean and standard deviation from current climatic suitability predictions to compute future climatic suitability standard scores. Calculations of climatic suitability changes for sensitive species were circumscribed to species occurrence actual data. On the other hand, *D. pictus* computations were not only restricted to occurrence data in the actual invaded range, but assumed a conjectural successful long-distance dispersal scenario, driving the specie to a widespread distribution through the Iberian Peninsula at the end of 21st century, with overlapped ranges with all Iberian sensitive species. This means that we defined the future potential range of *D. pictus* including all different occurrence localities where any of the Iberian sensitive species were recorded. Invaded and potential ranges of *D. pictus* allowed us to examine differences in climatic suitability changes across sensitive species and under different protection regimes, by splitting areas outside and inside Natura 2000, and also Natura 2000 sites were sensitive species where explicitly targeted.

Results

Niche overlap analysis

The main two axes of the PCA accounted for 81% of the total variance: PC1 (45% of variance) was negatively correlated with minimum temperature and precipitation ($r=-0.58$ and $r=-0.53$, respectively), and positively correlated with altitude ($r=0.52$); PC2 (36%) was positively correlated with maximum temperature ($r=0.51$), and negatively correlated with precipitation and slope ($r=-0.47$ and $r=-0.43$). Comparisons of the environmental ranges of *Discoglossus* congeneric species indicate that the environmental conditions in their native ranges are quite similar (Fig. III.2), and suggest that congeneric species could easily occupy broader extensions without the existence of biotic interactions. A similar situation is found when comparing the native and invaded ranges of *D. pictus*, with an invaded range that seems to be a smaller subset of the conditions occupied in the native range. After plotting the occurrences of *D. pictus* in a bivariate plot of the first two factors, only 4 occurrences (3.3% of occurrences) from the invaded range are outside the native environmental space, showing little and “non-significant” niche shifting to new environmental conditions from the invaded area (Figure III.2). Non-congeneric native species also show a strong niche overlap with *D. pictus*, with more than 80% of each species’ environmental space intersecting with the *D. pictus* environmental space within the invaded range.

Long-term climatic suitability changes

Climate ensemble native-range predictions efficiently captured the climate envelope of *D. pictus* (mean.AUC=0.92, SD.AUC=0.01), even when they were compared to the invaded range in southern Europe (mean.AUC=0.83) (Figure III.3). Climate ensemble outcomes from other species also exhibited excellent predictive performance, with AUC bigger than 0.9 for all species except the most widespread *B. calamita* (mean.AUC=0.79, SD.AUC=0.01) and *D. galganoi* (mean.AUC=0.80, SD.AUC=0.02).

We found contrasting amphibian responses to climate change according to the examined greenhouse gas scenario. Climatic suitability changes from the pessimistic scenario showed overwhelmed negative responses for all the species, stressing that against extreme climate warming *D. pictus* invasion might be the less important problem facing native species (Figure III.4). On the other side, the optimistic scenario yielded positive widespread responses for all species to climate warming. Only *P. punctatus* showed a general loss of climatic suitability, including areas inside and outside Natura 2000 network within the

current invaded range of *D. pictus*, but also in the potential range based on the long-distance dispersal scenario (Figure III.4). No major differences were reported within species among *D. pictus* dispersal scenarios and protection regimes based on paired t-tests, except for Natura 2000 sites where *D. galganoi* ($p < 0.05$) and *B. calamita* ($p < 0.05$) were explicitly targeted located within potential range of *D. pictus* (Figure III.4).

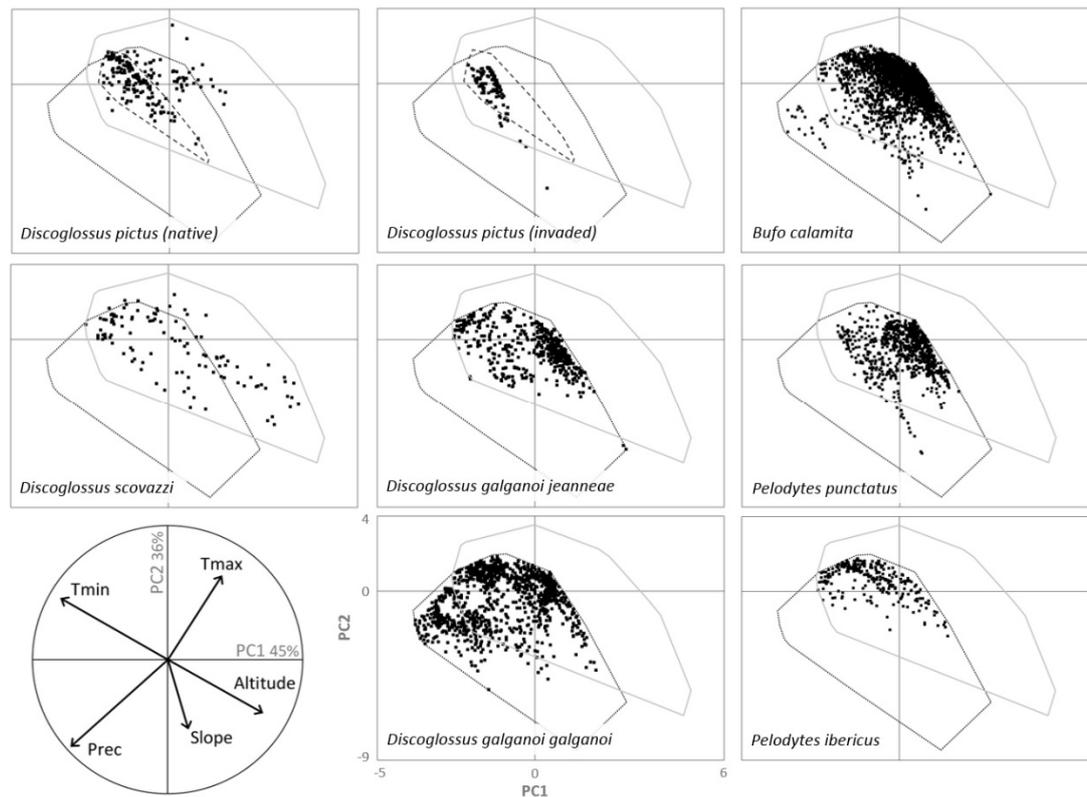


Figure III.2. Environmental space of *Discoglossus* native and invaded (only *D. pictus*) species ranges in a bivariate plot of two principal components. Convex hulls show global climatic space in North Africa (solid grey), Iberian Peninsula and southern France (dotted black) and Sicily (dashed black, only for *D. pictus*). The correlation circle indicates the importance of each bioclimatic variable on the two principal axes of the Principal Components Analysis (PCA), which jointly explain 81% of the variance in the data.

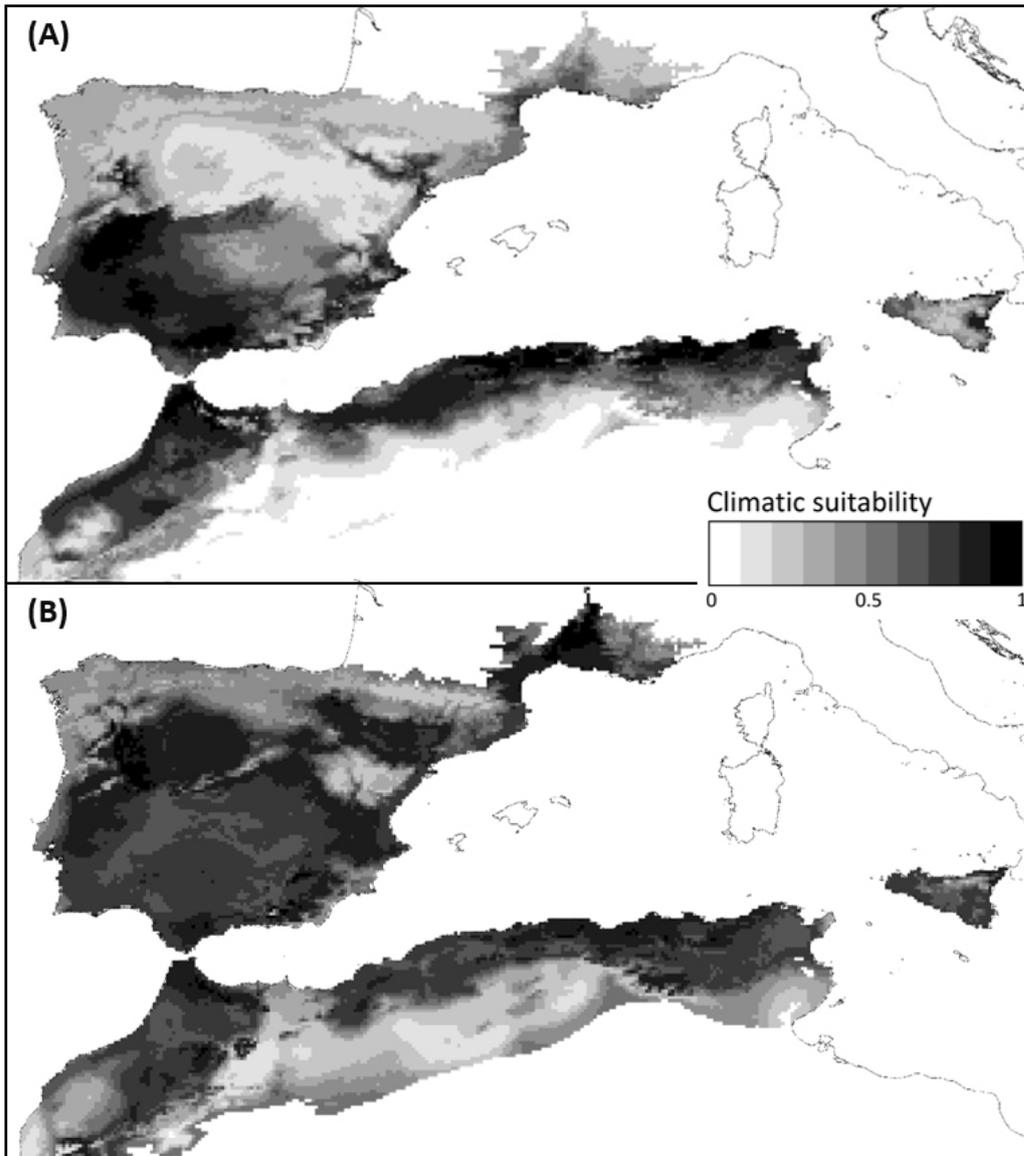


Figure III.3. Current (A) and future (B) climatic suitability predictions for *D. pictus* in Northern Africa and Southern Europe. Future climatic predictions are based on the optimistic greenhouse gas scenario (RCP 2.6).

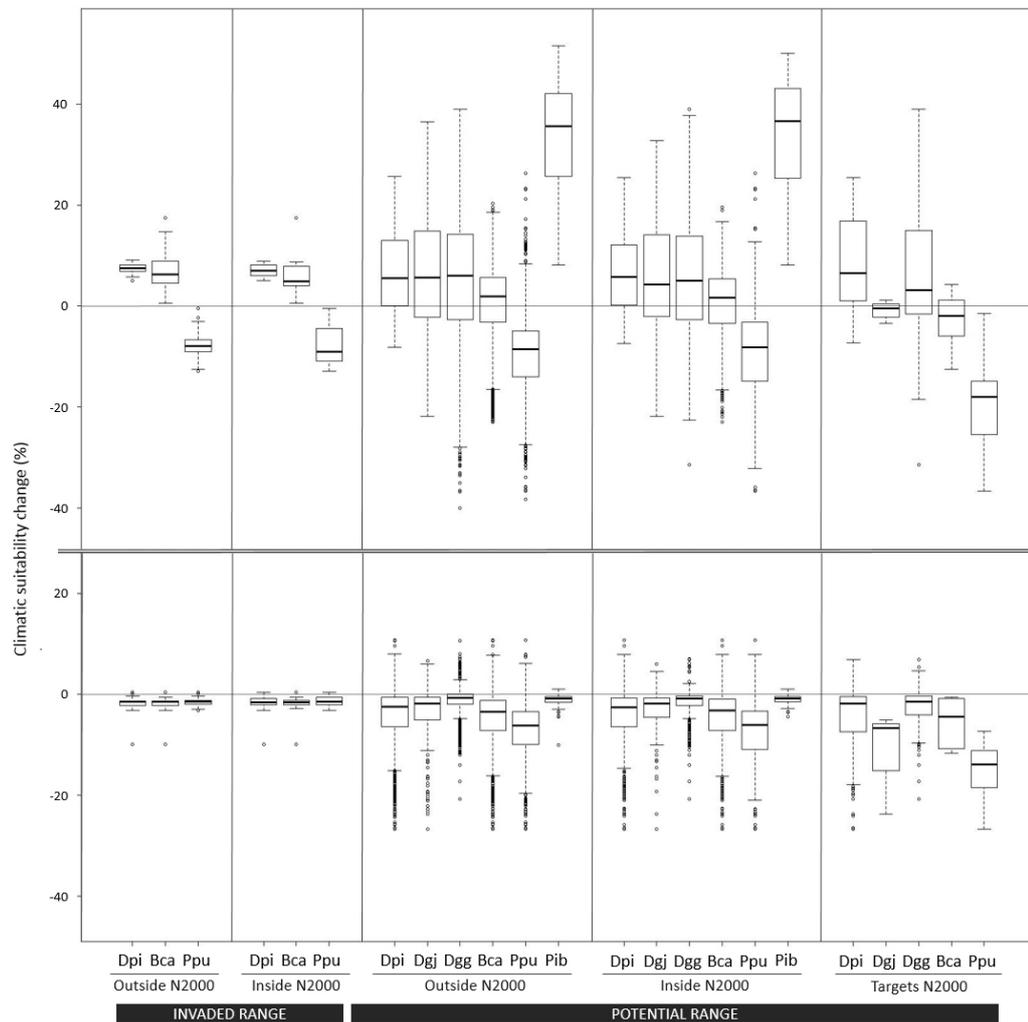


Figure III.4. Species climatic suitability change (%) under optimistic (upper) and pessimistic (bottom) climate warming scenarios, within different *D. pictus* ranges (invaded or potential) and protection regimes, splitting areas inside and outside Natura 2000 (N2000) from those Natura 2000 sites where species are explicitly targeted (Targets N2000). Dpi, *D. pictus*; Dgj, *D. jeanneae*; Dgg, *D. galganoi*; Bca, *B. calamita*; Ppu, *P. punctatus*; Pib, *P. ibericus*. Points show outliers, Lower and upper whiskers indicate the 5% and 95% percentiles, lower and upper hinges indicate the 25% and 75% quartiles, and the central black line indicates the median value.

Discussion

Native-range predictions show that *D. pictus* spread in Southern Europe is following the best environmental paths. Large areas of southern Iberian Peninsula are highly suitable for the establishment of *D. pictus*, and our results suggest that this fact will be exacerbated in the long-term. Several studies have tested the value of niche modelling for assessing the risk of amphibians from other region invading a given area (Ficetola et al., 2010; Urban et al., 2008), highlighting the benefits of using native-range data to assess the geographical potential of invasive species in the face of climate change (Pearson and Dawson, 2003; Roura-Pascual et al., 2004; Van Wolgan et al., 2009). The potential species distribution is projected on the assumption that current niches from native distributions reflect species environmental preferences, which is retained in the invaded new areas (Broennimann et al., 2007; Pearman et al., 2008). However, it's important to note that native-range models were calibrated using a limited set of occurrence data and probably underestimate the potential distribution of *D. pictus* in the Iberian Peninsula and represent conservative predictions of the real potential distribution of the species.

All indications are that *D. pictus* is not at equilibrium with environmental conditions in Europe, with an invasion front expanding at equal rates and similar strategies as other invasive amphibians. In fact, long-distance “stowaway” dispersal has been reported for other amphibians, as *Bufo marinus* in Australia, emphasizing that the magnitude of dispersal through anthropogenic transport should not be underestimated (White and Shine, 2009). Importantly, the proneness to human-mediated dispersion means that the specie is likely to reach most parts of potentially invaded ranges at frequencies high enough to set up new populations if conditions are suitable. The establishment and persistence of *D. pictus* in Barcelona (Franch et al., 2007; Llorente et al., 2015) is a strong evidence supporting this clue. Current climatic suitability predictions show that such areas may exist in southern Iberian Peninsula, albeit separated from the main part of *D. pictus* current invaded range by 200 km of climatically low suitable climates, but with high densities of transportation networks. Hence, high rates of anthropogenically assisted transport may overcome ectotherm limited dispersal abilities (Araújo et al., 2005b), suggesting that *D. pictus* ultimately may be able to colonize any part of the Iberian Peninsula that provides conditions suitable for population persistence (Urban et al., 2008).

To determine the pattern of spread of *D. pictus* the Iberian Peninsula for late 21st century we predicted climatic suitability under optimistic and pessimistic climate warming scenarios. At best, our results indicate that the whole

Mediterranean basin in the Iberian Peninsula may experience an increase of *D. pictus* climatic suitability under optimistic future climatic conditions. On the other hand, the pessimistic scenario shows very bad conditions for the spread of *D. pictus*, but also for the persistence of all native species included in the analyses and, hence, results unhelpful for invasive *D. pictus* risk assessment. It is widely thought that climate change will exacerbate problems with invasive species (Dukes and Mooney, 1999), but the many ways in which changes could affect the ranges of species, and the many complex interactions that could potentially facilitate or hinder shifts, make accurate predictions very difficult (Thuiller et al., 2006). Also, the ways in which climatic variables will interact in the future may well be different from the current situation. Such changes are certain to influence environmental suitability and invasibility in ways other than simply through altered climatic tolerance. However, projections of potential future distributions also need to be interpreted with caution. Our approach is based on the assumption that climate is the major driving factor of species distribution (Franklin, 1998), and that analysis of the climatic preferences of species can therefore be used to predict areas where the species could occur at regional scales. Although climate sets the broad limit of ectothermic species ranges, other factors such as hydrology, disturbance regime, competition and other biotic interactions determine the presence or absence of a species in a particular area and at finer local scales (Willis and Whittaker, 2002). The question is whether such simplifications enable useful projections under climate change. A number of studies have empirically demonstrated that carefully implemented bioclimatic models can recover the broad-scale direction of species range changes under climate change (Araújo et al., 2005a; Elith et al., 2010; Swanson et al., 2012). There are important uncertainties with regards to the magnitude of modelled range changes, as these are contingent on several unmeasured factors. However, evidence shows that models can recover the tendency of range increase or decrease with reasonable accuracy. Thus, one possible approach to limit uncertainty is to interpret model projections conservatively. By quantifying relative climatic suitability changes for each species, we avoid making quantitative inferences about population parameters, such as changes in range, abundance or extinction risk, that are not explicitly modelled (e.g. Brook et al., 2008). Other limitations of this study include uncertainties inherent in climate-change scenarios and the use of coarse resolution GCM anomalies (Pearson, 2006). The coarse resolution of the data used to build models (10×10 km) may also mask some finer-scale variations in the species' ecological requirements that are not detectable at the spatial scale of our analysis. Because the influence of each environmental variable in determining the species' niche is scale dependent,

different degrees of ecological niche variation can arise among populations, depending on the spatial resolution of analyses (Wiens, 1989).

In the next decades the combined effect of global warming and the spread of *D. pictus* should not pose a risk for most species from the recipient amphibian communities, even if there are new long-distance dispersal events that hypothetically face invasive *D. pictus* to endemic congeneric species. Specifically, we show that in an optimistic scenario, at the end 21st century climate conditions are likely to become more suitable for *D. pictus* and native species inside and outside protected areas. Only non-endangered *P. punctatus* seems to be negatively affected by synergies between global warming and cohabiting with *D. pictus*. However, these general trends are reversed for native species within targeted Natura 2000 sites. Hence, explicitly designated protected areas would preserve species worse than unprotected areas, jeopardizing the effectiveness of protected areas in a long-distance dispersal scenario. If true, *D. pictus* long-distance dispersal events stresses the importance of implementation of early detection and monitoring plans within Natura 2000 sites having high suitability. The approach we presented here can provide insights into the basic mechanisms underlying range expansion and can inform efforts to focus the preventive monitoring on the areas that are more at risk (Holt and Gaines, 1992), but also to evaluate and adapt Natura 2000 site-specific targets (Araújo et al., 2011), in order to effectively preserve endangered species.

Ecological impacts of invasive amphibians primarily involve direct changes to single native populations or species, but community-level impacts also logically result from loss of or dramatic declines in native populations (Kraus, 2015). Strong niche overlap between *D. pictus* and native species suggest that climatic suitability changes might involve decreases in the abundance of native species (e.g. Dorcas et al., 2012), in the worst case scenario driving to local extinctions and geographical range contractions (e.g. Cole et al., 2005; Okamoto et al., 2013). But most feasible impacts encompass the simplification and homogenization of amphibian communities due to *D. pictus* establishment (Escoriza and Boix, 2014; Richter-Boix et al., 2013). Regarding the impacts to congeneric species, competitive exclusion between *D. pictus* and *D. scovazzii* in Northern Africa, and between *D. galganoi* and *D. jeanetae* in the Iberian Peninsula, reveals that niche overlap goes beyond abiotic factors and draw clear borders that allow the allopatric coexistence between congeneric neighbours (Garcia-Paris et al., 1999; Real et al., 2005; Veith and Martens, 1987; Vences et al., 2014). Our results don't provide any evidence against this fact.

Amphibians are among the species of highest conservation concern due to their widespread decline worldwide (Blaustein and Wake, 1990; Mendelson et

al., 2006), but the poorly representation in conservation strategies (Buckley and Jetz, 2006) may only be understood by the resiliency of many species to human-dominated landscapes (Crochet, 2004; Ficetola and De Bernardi, 2004; Knutson et al., 2004; Mann et al., 1991). Nevertheless, many studies are showing that global change impacts are able to boost the fragility of the group by the combined effects of global warming, invasive species and emerging diseases (Brühl et al., 2013; Hecnar and McLoskey, 1996; Howard et al., 2002; Pawar et al., 2007; Sodhi et al., 2008; Stuart et al., 2004). These impacts may not be neglected, and an appropriate conservation planning coordinated between conservation and development policies may help to ensure species conservation and communities' integrity.

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Chapter IV. Assessing the location and stability of foraging hotspots for pelagic seabirds: an approach to identify marine Important Bird Areas (IBAs) in Spain⁶

Abstract

Protected areas play a key role in the preservation of biodiversity, but their implementation at sea is lagged behind terrestrial environments, especially in offshore areas. Here we describe the identification of foraging hotspots off the Mediterranean Iberian coast using three Procellariiform species as examples, and assess the stability of these sites. Then, we show how these foraging hotspots contributed to the delimitation of marine Important Bird Areas (IBAs). The whole process consisted of: (1) seabird data collection (extensive boat-based surveys and seabird tracking, conducted in 1999–2010) and compilation of relevant spatial descriptors of the marine environment; (2) species distribution modeling (SDM) aimed at identifying areas with high habitat quality for the different seabird species (3); identification and delineation of the main seabird hotspots, based on models, supported by direct seabird data, and mediated by expert opinion; (4) application of BirdLife International IBA criteria for hotspot validation; and (5) combination of hotspots from different species to set the final limits of the marine IBAs. This approach allowed to identify a series of hotspots for pelagic species in the study area, and provided nice examples of stability assessment, which slightly differed in performance between seabird species. They contributed to the Spanish marine IBA inventory, which is in the process of receiving legal protection. Future work should be directed at confirming the stability of the

⁶ This chapter include the original paper published in *Biological Conservation*. The author has written the part of the manuscript related with SDM and has performed all concomitant analyses.

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marine IBAs in the long term, and to address the development of management plans to make effective the protection of these sites

Resum

Les àrees protegides juguen un paper clau en la conservació de la biodiversitat, però la seva implementació en ambients marins, i en especial mar endins, està molt enrederida en comparació amb els ambients terrestres. En aquest treball es descriu la identificació de zones sensibles per l'alimentació d'aus marines pelàgiques en la costà mediterrània de la Península Ibèrica utilitzant les espècies de Procel·lariformes com exemples, i s'avalua la seva estabilitat al llarg del temps. També mostrem com aquestes zones sensibles per l'alimentació han contribuït a la delimitació de Àrees Importants per a les Aus (IBA) en àmbit marí. Aquest procés va consistir en: (1) recollida de dades d'ocells (campanyes oceanogràfiques i telemetria, corresponents al període 1999-2010) i recopilació de descriptors ambientals rellevants de l'ambient marí; (2) modelització de la distribució de les espècies per identificar les àrees amb hàbitats de major qualitat per a les diferents espècies; (3) identificació i delimitació de les principals zones sensibles en base als models de distribució complementats amb les dades de les espècies i supervisats per experts; (4) aplicació dels criteris "BirdLife International IBA" per validar les zones sensibles; (5) combinació de zones sensibles de diferents espècies per delimitar els límits finals de les IBA marines. Aquesta metodologia va permetre identificar un conjunt de zones sensibles per les aus marines pelàgiques en la zona d'estudi, i va proporcionar bons exemples de l'avaluació de la seva estabilitat, observant-se petites diferències entre les espècies analitzades. Les zones sensibles identificades van contribuir a l'inventari espanyol de IBA marines, que es troba en procés de rebre protecció legal. Els treballs futurs haurien servir per confirmar la estabilitat de les IBA marines a llarg termini, així com plantejar el desenvolupament de plans de gestió per fer efectiva la protecció d'aquests espais.

Introduction

Protected areas are recognized as key tools for biodiversity conservation (Lovejoy, 2006). However, the marine environment has received little attention relative to terrestrial areas, and less than 1% of the ocean's surface is included in marine protected areas (MPAs) (Wood et al., 2008). Moreover, most MPAs are small, coastal sites, focusing on benthic habitats (e.g. coral reefs, sea-grass prairies), whereas the dynamic open sea and its related biota have been largely neglected (Game et al., 2009).

In line with this general pattern, seabirds have received protection in many of their breeding colonies, but few sites have been protected at sea for these top predators (Grémillet and Boulinier, 2009). Moreover, the few MPA initiatives regarding seabirds have been primarily directed at protecting the marine areas surrounding seabird colonies (e.g. Airamé et al., 2003; McSorley et al., 2003; Yorio, 2009) and, to a lesser extent, distinct coastal and/or shallow areas hosting non-breeding congregations of highly gregarious species such as sea-duck (McSorley et al., 2005; O'Brien et al., this issue; Skov et al., 2007). Far less attention has been placed on offshore areas, although these include key foraging sites for several seabird species (Hyrenbach et al., 2006; Harris et al., 2007; Louzao et al., 2006; Nur et al., 2011). The dynamic nature of the marine environment, the lack of obvious boundaries and the requirement of large extensions for effective protection of wide ranging megafauna have been among the major concerns regarding the identification of such areas (Alpine and Hobday, 2007; Game et al., 2009; Hyrenbach et al., 2000). In addition, the difficulties to carry out studies at sea have contributed to the scarcity of MPA proposals in offshore areas (Lascelles et al., this issue).

New efforts are directed at addressing this gap, brought about by the increasing awareness of the threats facing the marine environment worldwide, including seabirds (BirdLife International, 2011; Butchart et al., 2004), and also the increasing facilities to study and monitor seabirds at sea (extensive long-term surveys and the upsurge of tracking technologies and analytical tools; e.g. Camphuysen et al., this issue; Le Corre et al., this issue; Louzao et al., 2009, 2011; Montevecchi et al., this issue; Oppel et al., this issue). These efforts are supported by increasing political willingness and commitment, backed by the Convention on Biological Diversity (CBD) target of protecting at least 10% of the World ocean's surface by 2020 (Lascelles et al., this issue). In accordance, BirdLife International has set among its priorities the extension of its Important Bird Area (IBA) Programme to the marine environment, with the aim of guiding the designation of MPAs for seabirds worldwide (BirdLife International, 2004, 2010a).

Within this frame, one of the first comprehensive initiatives to identify marine IBAs at national level was conducted in Spain (Arcos et al., 2009). Based on this initiative, we report here on the most novel contribution of the Spanish marine IBA inventory, the identification of hotspots for pelagic species in the open sea, which primarily represent important foraging grounds. The main aims of this paper are to: (1) depict the process to identify, assess the stability and delimit seabird foraging hotspots for pelagic species; and (2) describe the remaining steps from hotspot identification to IBA delimitation.

Material and methods

Study area

The present study is framed within the initiative of marine IBAs identification in Spain (Arcos et al., 2009). Here we focus on the Iberian Mediterranean shelf and the adjacent pelagic waters, from Almeria in the SW to the Spanish-French border in the NE (Fig. IV.1). Previous work in this region (Abelló et al., 2003; Arcos and Oro, 2002; Louzao et al., 2006) allowed to use longer datasets here than elsewhere in Spain, thus providing the best conditions to exemplify both the identification of seabird foraging hotspots and the assessment of their stability. The continental shelf is very narrow (ca. 3 km) in the south (Vera Gulf) and widens towards the centre of the region, reaching a width of up to 70 km off the Ebro Delta area; in the northernmost area the shelf becomes relatively narrow again, and is indented by submarine canyons (Salat, 1996). Ocean productivity is notoriously heterogeneous in the region, being influenced by marine currents (Atlantic waters flowing northwards in the SW and Mediterranean waters flowing southwards in the NE) and the input of freshwater run-off, which deliver large amounts of nutrients and fertilize the coastal waters (Arnau et al., 2004).

The Iberian Mediterranean marine region is of particular seabird conservation concern, as several sensitive species regularly occur there in high numbers, including Mediterranean endemic taxa: Cory's (Scopoli's) shearwater *Calonectris diomedea diomedea*, Balearic shearwater *Puffinus mauretanicus*, yelkouan shearwater *Puffinus yelkouan*, European (Mediterranean) storm-petrel *Hydrobates pelagicus melitensis*, European (Mediterranean) shag *Phalacrocorax aristotelis desmarestii*, and Audouin's gull *Larus audouinii* (BirdLife International, 2011; Zotier et al., 1999). Here we selected as examples three species of Procellariiforms, as representatives of the seabird "pelagic" community: Cory's and the Balearic shearwaters, and the European storm-petrel. Cory's shearwater and the European storm-petrel are summer visitors

(March–October, breeding May– October), whereas the Balearic shearwater is present most of the year, mainly from October to June (breeding March–June).

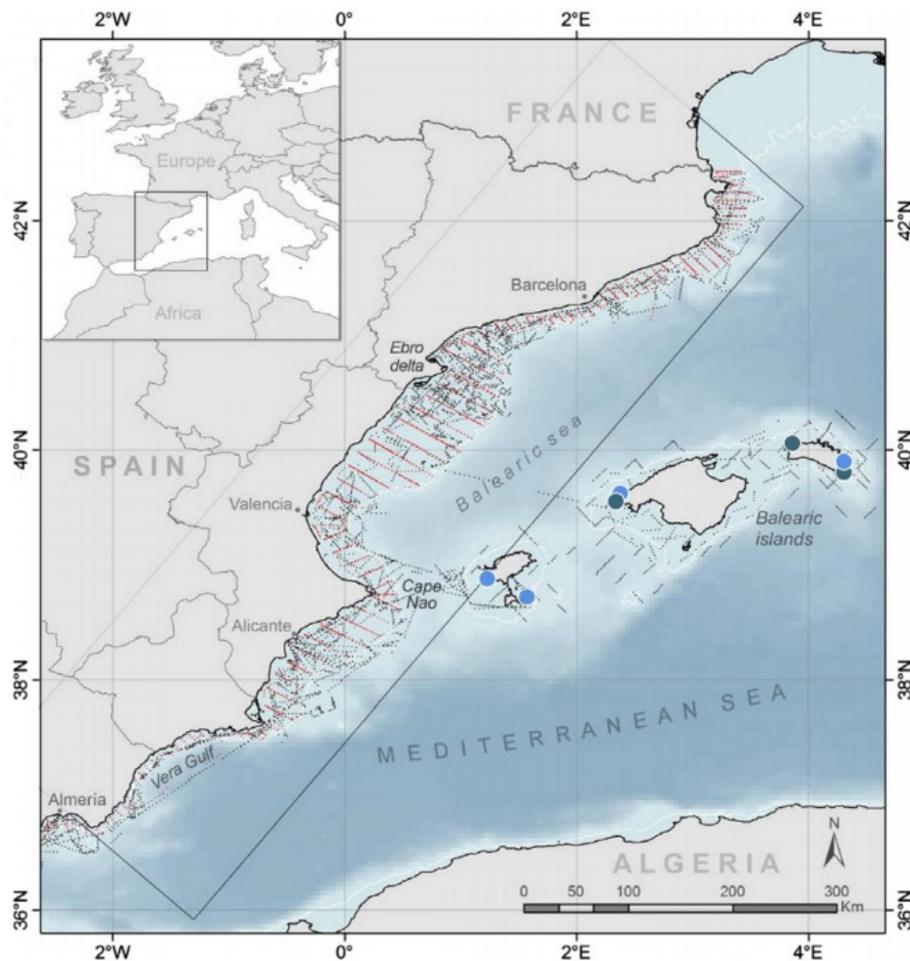


Figure IV.1. Map of the study area (diagonal rectangle) and adjacent waters in the western Mediterranean. Boat-based transect locations (mid-position for the 10-min count units) are represented by small dots (black for the breeding and red for the non-breeding seasons), and the circles correspond to shearwater colonies where tracking was conducted (light for Balearic shearwaters, dark for Cory's shearwaters). Finally, the 200-m isobaths is also shown (white line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Overview of the marine IBA identification process

For the identification of marine IBAs, four types of sites were considered, depending on the ecological reason for seabirds to use them (BirdLife International, 2010a): (1) non-breeding (coastal) concentrations; (2) areas for pelagic species; (3) seaward extensions to breeding colonies; and (4) migration bottlenecks. These sites could be eventually combined into a single IBA (see

Section *Integration of seabird hotspots (inter-species) and final delimitation of marine IBAs*), but followed slightly different approaches to their identification. For the foraging hotspots for pelagic species (type 2), which are the focus of this paper, the process is described in full length in the following Sections 2.3–2.7, and is also outlined in Fig. IV.2.

Data collection

Fieldwork was focused on two main approaches, boat-based seabird counts and remote tracking of tagged individuals. The compilation of remote sensing data was also key to produce habitat species distribution models (SDMs hereafter; see Section *Data analysis*).

BOAT-BASED SURVEYS

Within the study area we relied on information from two annual oceanographic surveys organized by the Spanish Institute of Oceanography (IEO), the MEDITS bottom trawl survey (late Spring, 4 years) and the ECOMED acoustic survey (late Autumn, 5 years), as well as a specific seabird survey around the Ebro Delta in Spring–Summer (3 years), within the period 2000–2007 (Table IV.1). Additional data from another 5 MEDITS cruises within the period 1999–2010 were also compiled and included in the validation of SDMs (Section 2.4), and as supporting information for hotspot delimitation (Section 2.5).

Seabird surveys followed the methodology proposed by Tasker et al. (1984): birds were counted within a 300 m strip transect band, at one or two sides ahead of the vessel depending on census conditions; snap-shot counts were used to count flying birds. Seabird observations were summed up into 10 min survey units, for which species density values were estimated (birds/km²). Birds outside the transect band were also considered for presence/absence information. During the oceanographic surveys, stern counts of seabirds attending the vessel in experimental trawling operations were also recorded following Abelló et al. (2003), to complement transect data.

INDIVIDUAL REMOTE TRACKING

Individual remote tracking relevant to the study area included breeding Cory's shearwaters from three colonies of the Balearic islands, using either Platform Terminal Transmitters (PTTs, 2005–2006) or Global Positioning System loggers (GPS, 2007), attached to the back feathers with TESA tape (Arcos et al., 2009; Louzao et al., 2009). PTT tracking data of Balearic shearwaters were also used, taking advantage of previous work in the region by

SEO/BirdLife (1999–2001; Ruiz and Martí, 2004). These tracking data are summarized in Table IV.2.

ENVIRONMENTAL VARIABLES

Information on habitat features was compiled and used to build SDMs (see Section *Data analysis*). Habitat variables were selected on the basis of data availability and potential biological relevance, after bibliographical revision and preliminary modeling trials. The selected variables included both static and dynamic features (Table IV.3), the latter being behind the variability that characterizes the marine environment.

Static features consisted of a set of measures related both to the topography of the marine environment (depth, slope, distance to coast and distance to shelf-break) and to the location of breeding colonies. These variables were calculated from *ETOPOv2* bathymetric data (NGDC and NOAA, 2006) and GSHHS shoreline (Wessel and Smith, 1996) (Table IV.3).

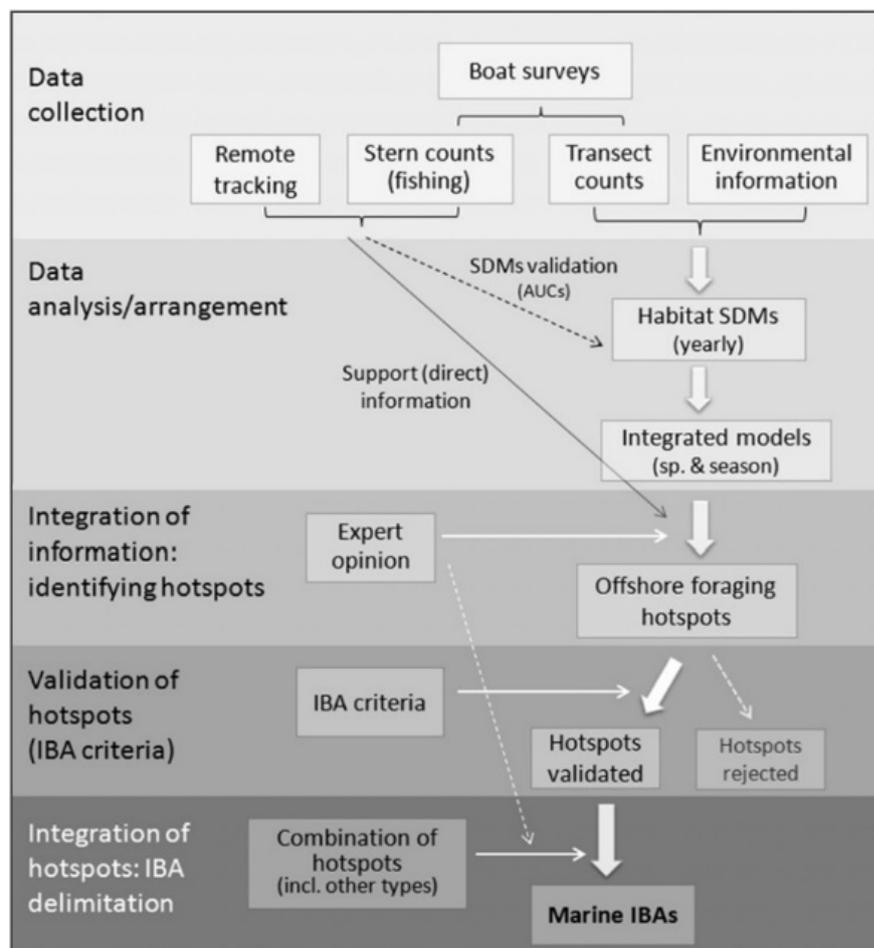


Figure IV.2. Outline of the process of IBA identification, focusing on the foraging hotspots. See text for more details.

Table IV.1. Boat surveys effort for the three cruises conducted within the study area: number of transect units (10-min counts), number of experimental trawling operations for which stern seabird counts were conducted (for IEO cruises), and distance and area surveyed (during transects). For the MEDITS cruise, information from years for which species distribution models (SDMs) were not built (i.e. supporting/validating data) is presented separately.

Cruise	10-min counts	Stern counts	Distance (km)	Area (km ²)	Period	
					Month	Years
ECOMED (IEO)	2256	30	7003.3	2897.8	Nov-Dec	2003-2007
MEDITS (IEO) core years	1792	710	5167.9	2619.2	May-Jun	2000, 2002, 2006, 2007
MEDITS (IEO) support years	1341	278	3772.0	1885.2	May-Jun	1999, 2004, 2005, 2008, 2010
Ebro Delta surveys	708	-	1186.7	629.3	May-Jun	2005-2007
TOTAL	6097	740	17129.9	8031.4		1999-2010

Table IV.2. Remote tracking survey effort for Cory's *Calonectris diomedea* and Balearic shearwaters *Puffinus mauretanicus*. These birds were tagged in their breeding colonies at the Balearic Islands, but foraged extensively within the study area. See Section 2.3.2 for details.

Species	Device	Colonies	Birds tracked (n)	Locations (n)	Period	
					Month	Years
<i>Calonectris diomedea</i>	PTT	2	18	196	Aug-Sep	2005-2006
	GPS	3	29	22422	Aug-Sep	2007
<i>Puffinus mauretanicus</i>	PTT	3	18	573	Jun-Jul	1999-2001
TOTAL			47	22618	Jun-Sep	1999-2007

Dynamic features were derived from time series of remote sensing data, in particular seasonal and monthly Terra MODIS SST (Sea Surface Temperature 11 l daytime) and Aqua MODIS Chl-a (Chlorophyll-a concentration) imagery from Ocean Color Web (Feldman and McClain, 2007) (Table IV.3). We also introduced the distance to oceanic fronts as a surrogate of food availability (Louzao et al., 2006; Valavanis et al., 2005). Oceanic fronts were computed on the basis of monthly Terra MODIS SST imagery using a Sobel edge detection filter (Praca and Gannier, 2008). From the resulting temperature gradients, oceanic fronts were identified as the areas with more pronounced gradients, here defined as areas above the 95 percentile values. Once identified, distance to the fronts was calculated by means of Cost Distance methodology implemented in ESRI Spatial Analyst. The temporal definition of this set of

variables was necessarily linked to the timing of the oceanographic surveys. Thus, we selected (1) eight seasonal variables, related to SST and Chl-a for the four (3-month) seasons previous to the surveys, assuming that the overall productivity of the environment is conditioned by SST and Chl-a values during the previous year; and (2) three monthly variables related to SST, Chl-a and distance to oceanic fronts which coincided with the month with the highest frequency of surveys, assuming that areas where food is concentrated are related to productivity phenomena that determine species' short-term distributions.

Table IV.3. Habitat variables used to produce species distribution models. To build the models, all data sources were adjusted to a resolution of 2.5' (4.5 km) pixels, which was the standard format for most variables.

Variable	Spatial resolution	Temporal resolution	Source
Sea depth	2'	Constant	ETOPO (http://www.ngdc.noaa.gov)
Slope	2'	Constant	Derived from ETOPO
Distance to coast	2,5'	Constant	Derived from GHSS <i>shoreline</i> (http://www.ngdc.noaa.gov)
Distance to shelf-break	2,5'	Constant	Derived from ETOPO
Distance to breeding colonies	2,5'	Constant	Method Cost Distance (GIS)
Sea surface temperature (SST)	2,5'	Monthly & Seasonal	SST Terra MODIS; http://oceancolor.gsfc.nasa.gov
Chlorophyll concentration (Chl-a)	2,5'	Monthly & Seasonal	Chlorophyll Aqua Modis; http://oceancolor.gsfc.nasa.gov
Distance to productivity fronts	2,5'	Monthly	Derived from monthly Terra MODIS SST, using Sobel filter and Cost Distance

Data analysis

This step of the process was focused on the production of SDMs, as they allowed capturing the relationship between seabirds and their habitat and to assess the temporal variability of such habitat. This reduced the biases related to direct seabird data, which represent snap-shots in time and space. However, boat-based and remote tracking data were also arranged to help their visualization and support the identification of seabird foraging hotspots.

MODEL CONSTRUCTION

SDMs were based on transect count data, and were built for each species, for the two most ecologically relevant seasons (breeding and/or non-breeding) on a yearly basis, according to the availability of oceanographic surveys (Table IV.1). The modeled area included the Balearic Islands, though here we report

on the results for the study area as defined in Fig. IV.1. We used a modeling method based on maximum entropy implemented in the software MAXENT (Phillips et al., 2006), because of its flexibility when handling different kind of species data and responses. The basic principle of the statistical approach implemented in MAXENT is the estimation of the probability of a distribution with maximum entropy (that is, the most spread out or the most uniform distribution) given a set of conditions (the environmental characteristics of the site where the species is detected) that shows our incomplete information regarding the distribution of the species (Phillips et al., 2006). This approach based on presence but not absence data seems particularly appropriate in the seascape, where a low encounter probability for many species is to be expected and consequently many false negatives occur (Péron et al., 2010).

The general approach of MAXENT also offers great adaptability and allows incorporating information related to observed seabird numbers to give greater importance to areas where a species is more abundant (Herrando et al., 2011). Preliminary tests showed that abundance improved the predictive strength of the SDMs. Hence, models were developed from quantitative data in which relative abundance categories were used leading to an increasing number of presences. Six abundance categories were defined: 1 for a single individual and for observations from outside the transect band, 2 for 2–5 individuals, 3 for 6–10 individuals, 4 for 11–25 individuals, 5 for 26–100 individuals, and 6 for more than 100 individuals. These intervals were defined considering the existing dataset (with a high proportion of the observations including few birds, and a few counts accounting for large groups), and taking into account expert opinion. SDMs were run on the 100% of training data taking advantage of relative abundance data to provide the best estimates of the species potential distribution. Outputs were projected to the resolution fixed by environmental information, which usually was 2.5 minutes of arc (′), i.e. about 4.5 km pixels (Table IV.3). Default parameterization of MAXENT was used to develop the SDMs, limiting the response to environmental variables to linear and quadratic functions. All available environmental variables (5 static + 11 dynamic) were included, except distance to colonies, which was only considered for the breeding season, when these sites exert their main influence on seabird distribution patterns (Orians and Pearson, 1979). Seasonal and monthly Chl-a and seasonal SST were not available for 2000 and 2002, hence the corresponding breeding season SDMs included only two dynamic variables (i.e. monthly SST and distance to oceanic fronts). For 1999 only static variables were available, and models have not been included here. Finally, MEDITS data for 2004 and 2005 were not modeled as were provided by an external observer

for complementation, and only stern counts were available for MEDITS 2008 and 2010.

MODEL EVALUATION

The predictive reliability of the models was assessed in two ways. First, model performance was estimated with the AUC (Area Under the Curve) generated between the SDMs predictions and presence/absence data from surveys used for model building. The AUC of the ROC curve (Receiver Operating Characteristics) provides a measure of the models predictive capability ranging between 0.5 (no predictive power) and 1 (a perfect model) (Boyce et al., 2002). This metrics was complemented measuring the strength of linear dependence between predictions and relative abundance categories (1–6) based on the Pearson product-moment correlation coefficient (PCC) (Phillips et al., 2009). Second, we used the AUC to test to what extent predictions produced by SDMs matched with data derived from surveys available from other years, as a measure of hotspot stability over time. Thus, seasonal SDMs from a given year were assessed with presence/absence data derived from transect and stern counts (breeding season) conducted on surveys from other years, including years for which models were not available (Table IV.1). Computations were made with *PresenceAbsence* and *Hmisc* libraries implemented in R software.

MODELS INTEGRATION

Hierarchically prioritized maps were created from SDMs to highlight the best seabird areas (for each species, season and year), using two simple and effective approaches with strong ecological components. Firstly, we defined as presence areas (in terms of prevalence of the data used in the model development) those with habitat suitability values above the lowest 10% percentile. Secondly, within the presence areas three scores of habitat suitability were used (1, 2, and 3, from low to high quality), defined by the following thresholds: (1) the average mean of the suitable values within the areas of presence; and (2) the average mean of the values above the previous threshold (Herrando et al., 2011).

For each species and season we combined the models of different years, by averaging the scores defined above. We then defined three categories of habitat quality over time: (1) moderate (averaged score from >1.5 to 2); good (>2–2.5); and (3) optimal (>2.5– 3). This way we combined habitat suitability and stability, as any area above score 2 (which was used as a guiding baseline for the identification of hotspots, see Section *Integration of data sources (intra-specific): identification of hotspots*) would be the result of repeated years of moderate to high annual scores.

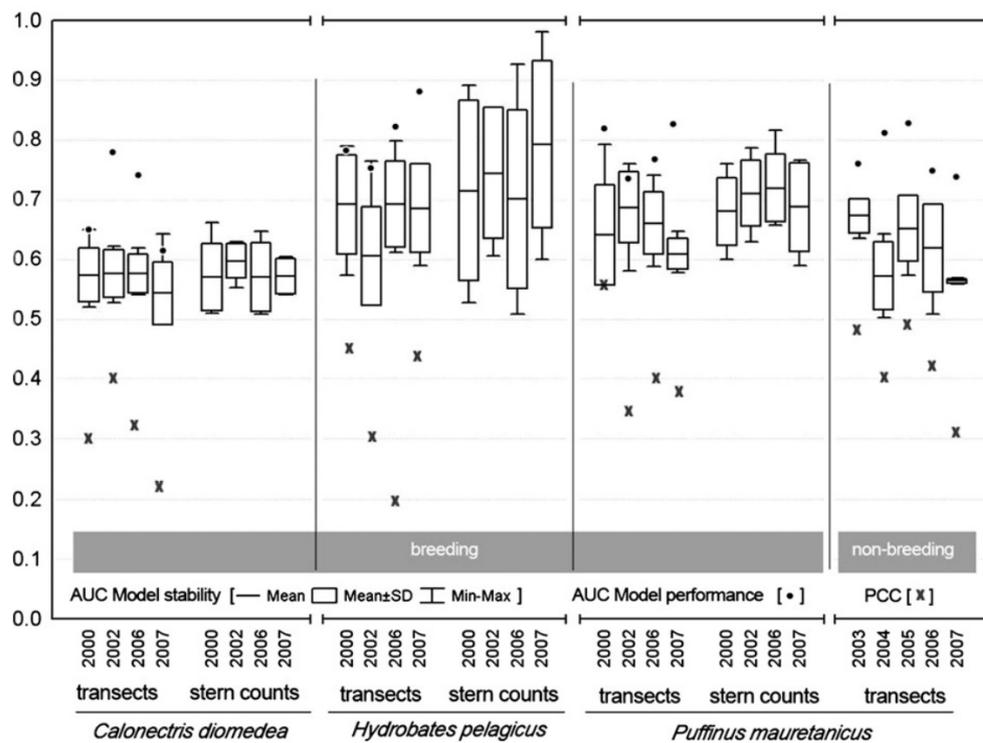


Figure IV.3. Habitat species distribution models (SDMs) validation for Cory's shearwater and the European storm-petrel (breeding period), and the Balearic shearwater (breeding and non-breeding periods), on a year basis. Dots correspond to the AUC values resulting of validating models with the data used to build them (i.e. transect data for the same year), and are used to determine model performance. Box plots correspond to the AUC values obtained when validating models with independent data (transect counts from other years, and stern counts during trawling operations), which provide a measure of model stability across years. Finally, Pearson correlation coefficient (PCC) values indicate the relationship between predictions and relative abundance (range: 1 to 1).

ARRANGEMENT OF DIRECT SEABIRD INFORMATION

Direct information on seabird distribution patterns, as obtained from boat surveys and remote tracking, were arranged in a way that helped their visualization, thus optimizing their contribution to the integration of data sources. BirdLife International (2010a) recommendations were taken into account. Boat-based data were represented selecting the upper 95% percentile of the positive values (i.e. presence data), as well as values above the mean of positive values, to reduce the confusion created by a large number of observations (Table IV.1) when plotted in a map. This way the areas of highest densities were highlighted. For tracking data, 25%, 50% and 75% kernels were used to highlight the most used areas. As the aim was to use this information just for support, the smoothing factor was selected arbitrarily at $h = 0.1$ for

PTTs and $h = 0.05$ for GPSs, taking in consideration the adequacy of the results to the raw data. Kernels were produced independently for every year, colony and species.

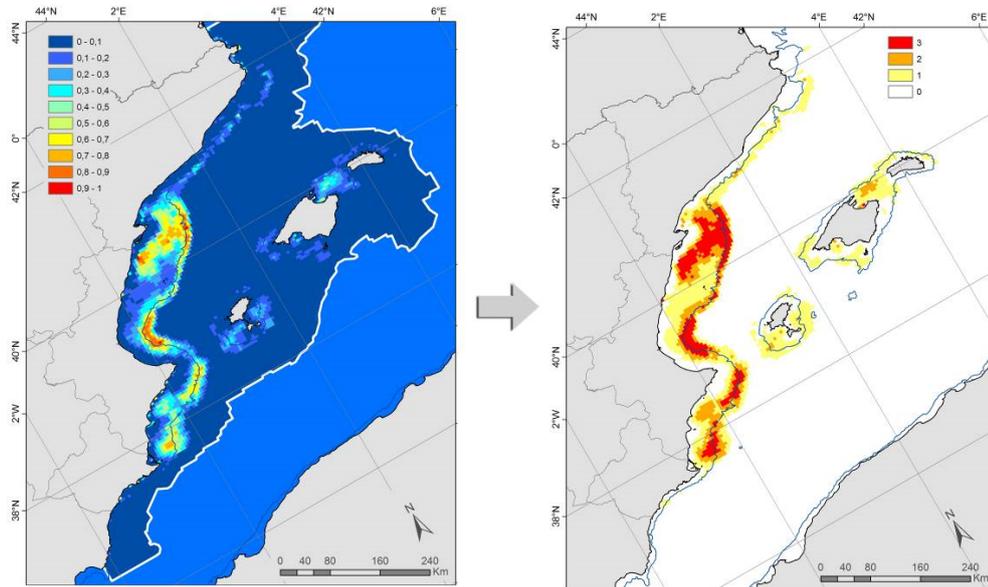


Figure IV.4. Categorization of an annual model, taking as example the European storm-petrel (breeding season, 2007). The left figure shows habitat suitability values on a continuum from 0 (low) to 1 (optimal). On the right figure these values have been converted into in four categories, from 0 (“no presence”) to 3 (highly suitable areas). Only categories 1 (yellow), 2 (orange), and 3 (red) are represented. See Section 2.4.3 for details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Integration of data sources (intra-specific): identification of hotspots

Once all available spatial information had been arranged, hotspots for each seabird species (and relevant season) were identified and delimited. This process was primarily guided by the integrated SDMs, for which optimal areas were almost always selected and good areas most often helped to delimit the hotspots (i.e. averaged scores above 2 were prioritized). However, direct seabird information (i.e. boat-based and tracking data) did also play a role, so that: (1) hotspots revealed by SDMs were only considered if direct data supported their relevance and (2) direct data independent of the SDMs (i.e. not used for modeling) were also used to set the limits, allowing for deviations from the models when obvious hotspots were highlighted and appeared relevant. Moreover, exceptionally a hotspot was identified based on the overlap of two or more independent layers clearly highlighting the site, even if SDMs did not

provide relevant support. Thus the identification and delimitation of hotspots was partly subjective. To maximize the rigor of this process, however, it was guided by expert opinion. This culminated in a small workshop with over 10 people with experience on diverse relevant issues: the local seabird community and marine environment, habitat modeling, IBA criteria, BirdLife International strategy, and similar projects in other parts of the world.

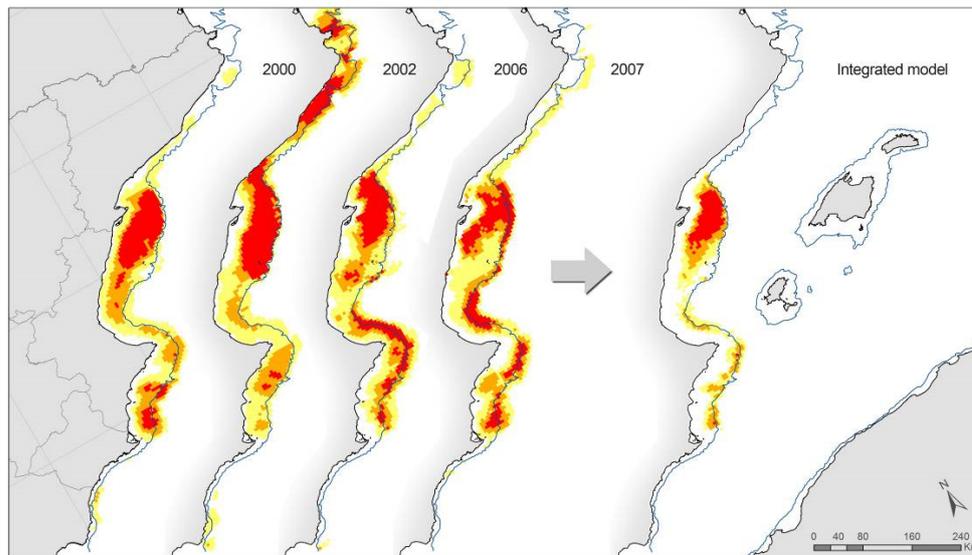


Figure IV.5. Integration of models across different years, taking as example the European storm-petrel (breeding season). Categorized models for different years were averaged, and resulted in an integrated model that showed moderate areas (yellow, averaged score from >1.5 to 2); good (orange, $>2-2.5$); and optimal (red, $>2.5-3$). Note that this is a conservative approach that only enhances those areas that are good or optimal on a regular basis (i.e. stable); for instance, optimal areas in an unusual year such as 2002 are not reflected in the final map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Application of BirdLife International IBA criteria to validate the seabird hotspots

To qualify as an IBA, a given area requires meeting one or more of a series of objective, numerical criteria established by BirdLife International (Heath and Evans, 2000). These criteria allow assessing the ornithological importance of the area in an international context, thus ensuring that sites are comparable throughout the globe. In simple terms, a site meets IBA criteria if it regularly holds over 1% of the global (A), regional (B, Europe) or sub-regional (C, European Union) population of a given species. Species of special conservation concern can also validate IBAs with lower numbers.

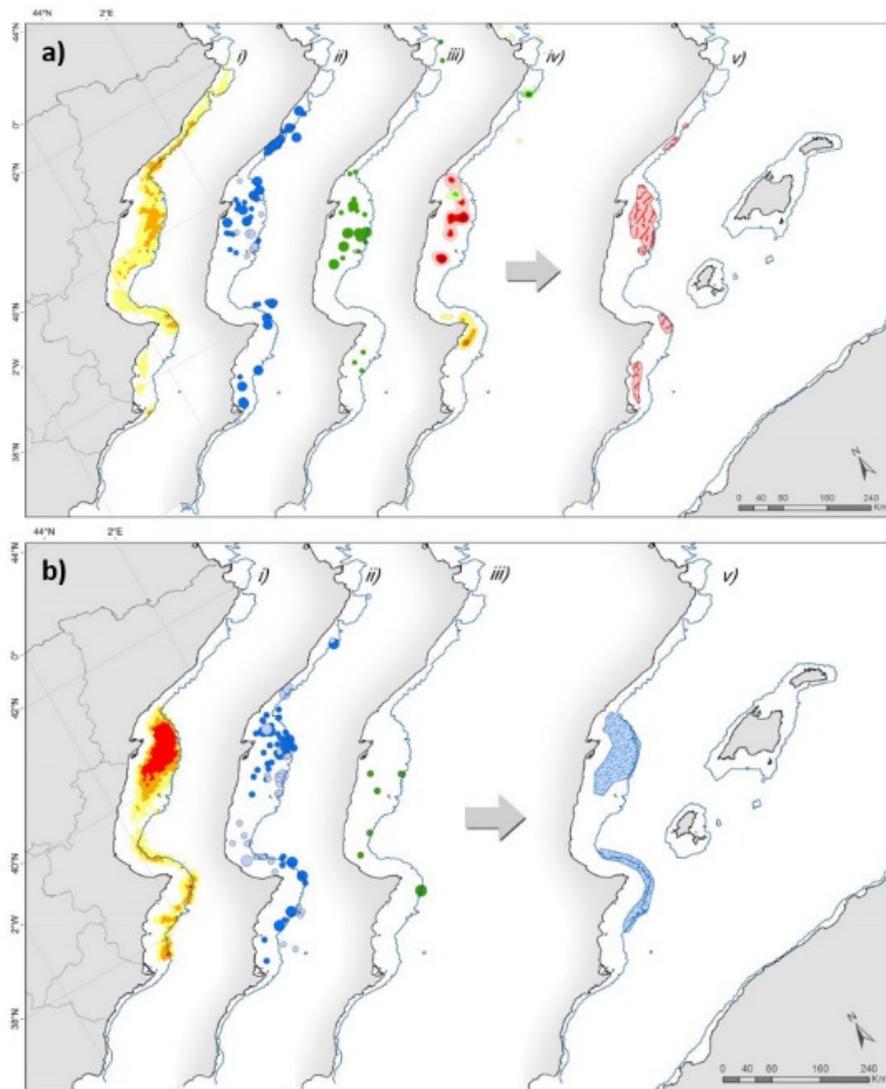
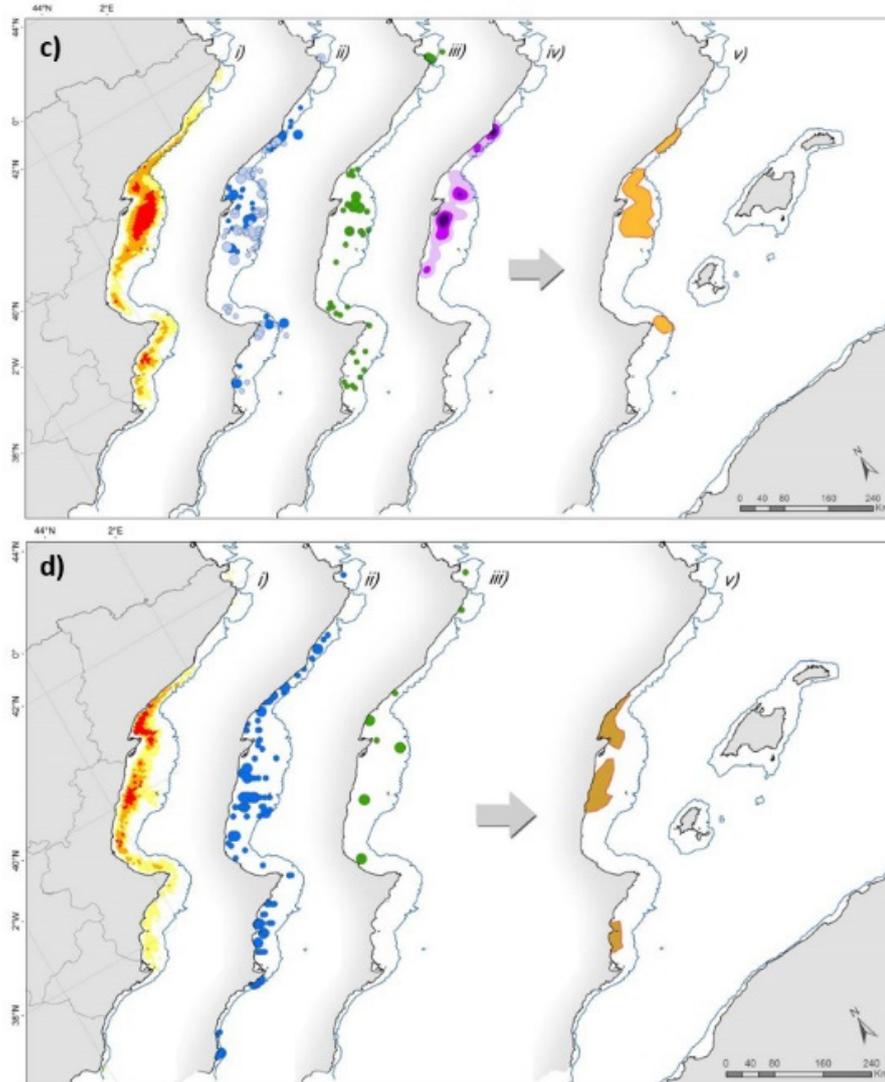


Figure IV.6. Integration of information to identify and delimitate foraging hotspots for the three study species: (a) Cory's shearwater, breeding; (b) European storm-petrel, breeding; (c) Balearic shearwater, breeding; and (d) Balearic shearwater, non-breeding. The process starts with the integrated habitat models ("i"), and incorporates any available direct data to refine the identification and delimitation of the final hotspots ("v"), being mediated by expert opinion. Circles ("ii" and "iii") correspond to boat-based count data, and represent the density/abundance values above the 95% percentile (large circles) and above the mean (small circles) of positive values; "ii" correspond to transect data (dark dots, data used to build the models; light dots, data from years not used for modeling), and "iii" to stern counts during trawling operations. Tracking data is represented by kernels ("iv"; dark colour, 25%; medium, 50%; light 75%). See Section 2.5 for details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Figure IV.6. (continued)



The IBA criteria were used to validate or reject the hotspots identified following the previous steps. If a hotspot regularly held a significant number of individuals of a given seabird species (according to the thresholds set by the corresponding IBA criteria), it was validated as meriting IBA consideration. Otherwise, the hotspot was disregarded.

To assess seabird numbers in a hotspot, density values were averaged from all boat transect-counts within the hotspot (per species and season) and these estimates were projected to the whole hotspot area, provided that these counts were representative in number and coverage. Bootstrap resampling was used to assess confidence intervals (Quinn and Keough, 2002). This provided a figure of total birds using the area ‘simultaneously’. These figures should be regarded as conservative, as turnover rates were not considered.

Integration of seabird hotspots (inter-species) and final delimitation of marine IBAs

Once all foraging hotspots had been identified and validated for each species and season, we set the final boundaries of the marine IBAs. This process incorporated other types of seabird hotspots (e.g. seaward extensions to breeding colonies), and all the species for which relevant sites had been identified and validated. If different seabird hotspots partly overlapped, they were combined to form a single IBA, provided that it made biological sense (i.e. the relevant habitat features were continuous, as well as the overall seabird distribution pattern observed). The final boundaries of marine IBAs consisted of straight lines to facilitate their recognition by marine stakeholders, key to their effective management once protected. When different hotspots were combined to form a larger IBA, seabird numbers occurring there were re-estimated taking into account the new area coverage, and IBA criteria were re-assessed accordingly.

Results

The identification of seabird foraging hotspots within the study area was based on a relatively large dataset of boat-based counts and tracking studies over a period of 11 years, including the data used for validation. In total we used boat data from 6097 transect units (10 min counts) and 740 stern-counts along 17 cruises, counting across 17,130 km and covering over 8000 km² (Table IV.1). Of these, 12 cruises contributed to build the SDMs. Tracking data were obtained for Cory's shearwaters (three colonies, 47 individuals including PTTs and GPSs), and PTT data from another 18 Balearic shearwaters were also used (Table IV.2). Habitat variables were compiled for 2000–2007 (Table IV.3).

For each of the three study species 4 annual SDMs were generated for the breeding season, whereas a further 5 annual SDMs were built for the Balearic shearwater in the non-breeding season (Table IV.1). SMD performance (i.e. evaluation based on data used to build the models) was reasonably good, with all SMDs achieving AUC values above 0.7 (i.e. reasonable discrimination power), with the exception of Cory's shearwater in 2000 and 2007 (Fig. IV.3). As for SMD stability (i.e. evaluation from independent data), AUC values were slightly lower, as expected, but still quite good (Fig. IV.3). In both cases AUCs were consistent between years and sources of validating information, but showed slight differences between species, with Cory's shearwaters displaying the lowest values and European storm-petrels the highest (Fig. IV.3). Regarding the strength of relation between predictions and relative abundance,

for all models there was a moderate linear dependence as measured by the PCC (Fig. IV.3), with a high level of statistical significance in all cases ($p < 0.001$).

The categorization of SDMs and the subsequent integration of different years are shown taking as example the European stormpetrel (Figs. IV.4 and IV.5, respectively). Once integrated, models usually showed consistency with both related data (i.e. transects used to build the models) and independent data (non-related boat counts, tracking locations), allowing to easily identify and delimit the key foraging hotspots (Fig. IV.6). Some sites, however, were not so obvious and expert opinion had a major role on their delimitation (see Section *Integration of data sources (intra-specific): identification of hotspots*; Fig. IV.6).

In total 13 foraging hotspots were identified for the three study species (Table IV.4, Figs. IV.6 and IV.7). These hotspots ranged from strictly coastal areas (for Balearic shearwaters in Autumn–Winter) to outer shelf and continental slope areas (especially for the European storm-petrel). Three hotspots were disregarded following IBA criteria, all of them corresponding to Cory's shearwater (Table IV.4). The remaining 10 sites were combined with seaward extensions for Cory's shearwater and the European storm-petrel, as well as with hotspots of any type (see Section *Overview of the marine IBA identification process*) for other eight seabird species, and altogether contributed to set the limits of four out of eight marine IBAs identified in the study area, representing over 90% of them in terms of surface (Fig. IV.7). Only one of these IBAs, once all the hotspots were integrated, was disconnected from the coastline. The remaining four IBAs were primarily identified as seaward extensions to colonies, except one that included a foraging hotspot for the Yelkouan shearwater.

Discussion

Location and stability of offshore seabird hotspots

The establishment of MPAs for pelagic seabirds faces several difficulties including the wide-ranging nature of these organisms (that makes necessary protecting relatively large areas to be effective), the dynamic nature of the marine environment (which poses a challenge regarding the stability of the protected sites), the lack of obvious boundaries to set MPA limits, and the difficulties to carry out extensive studies in the open sea (Alpine and Hobday, 2007; Game et al., 2009; Hyrenbach et al., 2000; Lascelles et al., this issue). These constraints have often led to suggest that the offshore MPA approach is not appropriate to ensure seabird conservation (Boersma and Parrish, 1999). However, this view has started to change in recent years, due to the increasing

perception of the threats that seabirds face in the open oceans, and also the increasing facilities to address the identification of offshore hotspots, as well as to assess their stability over time (Game et al., 2009; Lascelles et al., this issue). For instance, areas that could merit MPA designation in the Southern Ocean have been proposed using long-term datasets of boat-based seabird counts (Harris et al., 2007), and the compilation of tracking data has helped to identify seabird hotspots in the open seas (BirdLife International, 2004). Boat-count and tracking data are subject to potentially strong biases, as they just represent snap-shots in time and space, but they can be regarded as complementary, and their combined use has been a step forward for the identification of offshore MPAs (e.g. Hyrenbach et al., 2006). A further and significant step has been the development of species distribution modeling techniques incorporating habitat descriptors, which allow capturing the relationship between seabirds and their habitat and to assess the temporal variability of such habitat, thus contributing to reduce data bias and provide more accurate MPA proposals (e.g. Le Corre et al., this issue; Louzao et al., 2006, 2011; Oppel et al., this issue; Nur et al., 2011).

Table IV.4. Hotspots identified for the breeding (all three study specie) and non-breeding seasons (Balearic shearwater). For each hotspot the area and the mean number of birds estimated to be present “simultaneously” are presented, as well as the corresponding 95% Confidence Intervals, within brackets. The necessary thresholds to meet IBA criteria are also shown (both global, A, and regional, B). Finally, last column shows if hotspots were validated or not by IBA criteria, also indicating if their value was global or regional.

Species	Season	Hotspot location	Area (km ²)	Averaged bird numbers	IBA threshold	Validated by IBA criteria
Cory's shearwater	Breeding	Barcelona-N	52.0	111	A: 8700	No
		Barcelona-S	1474.8	1189		Yes (B)
		Ebro Delta	2883.7	1600	B: 1090	Yes (B)
		Cape Nao	456.5	458		No
		Alicante-S	665.4	257		No
European storm-petrel	Breeding	Ebro Delta	4375.8	3783	A: 15,000	Yes (B)
		Cape Nao	643.4	896	B: 300	Yes (B)
Balearic shearwater	Breeding	Barcelona	551.3	2230	A & B: 66	Yes (A)
		Ebro Delta	3872.9	4940		Yes (A)
		Cape Nao	643.4	896		Yes (A)
	Non-breeding	Ebro Delta-N	1865.8	6682	A & B: 66	Yes (A)
		Ebro Delta-S	603.1	5307		Yes (A)
		Alicante-S	1355.7	1926		Yes (A)

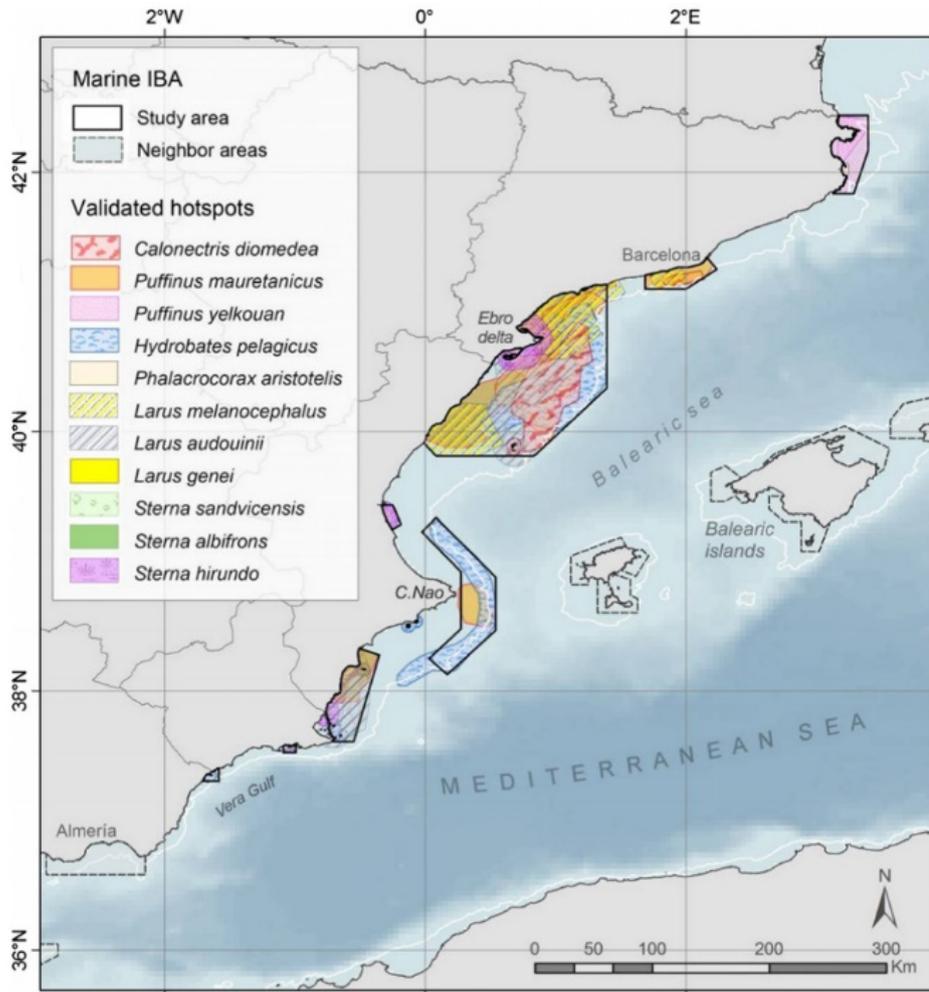


Figure IV.7. Marine IBA delimitation process. Validated foraging hotspots for the three study species were combined with other types of hotspots (seaward extensions to colonies), as well as hotspots identified for other species (both foraging areas and colony extensions). The limits of the marine IBAs were set to encompass the hotspots the best possible way using straight lines to simplify future management. All the hotspots shown in the figure accomplished the required IBA criteria. See Section 2.7 for details.

The present study integrates all these approaches and represents a sound example of hotspot identification for pelagic seabirds. Indeed, the study is based on reasonably large datasets of both boat-based counts and tracking information over a wide area, thus allowing combining complementary data to identify hotspots and, to some degree, assess their stability at relatively large spatial and temporal scales. The process was objectively structured so that objective, reproducible information could be generated through the use of innovative methodologies. SDMs played a fundamental role here, largely contributing to the identification and delimitation of seabird foraging hotspots. The SDMs integration process was a particularly good example of

how models allow assessing hotspot stability, and to disregard areas that are subject to strong inter-year variability, a process supported by the direct seabird information (i.e. boat-count and tracking data). Expert opinion was also a key piece, allowing supervising the process of hotspot delimitation, which necessarily had to incorporate a subjective component when combining several data sources to set limits in a dynamic and roughly continuous habitat. Finally, for hotspots to be considered as meriting IBA consideration, they had to meet BirdLife International IBA criteria, as a last validation step. It is worth to note that this study was integrated into a larger project that ended up with an inventory of marine IBAs for the whole of Spanish waters, now firmly proposed to become MPAs (see Section *Implications for conservation*).

In spite of these achievements, the study had also some limitations worth to be mentioned. Firstly, all the hotspots highlighted here were located over the continental shelf and slope, coinciding with areas of high productivity and high prey availability (Arnau et al., 2004; Bellido et al., 2008; Salat, 1996). These areas are related to features direct or indirectly influenced by topography, such as river plumes and oceanic fronts, which explains their value for seabirds (Ballance, 2007; Louzao et al., 2006; Nur et al., 2011). Therefore, the identification of truly oceanic areas, unrelated to obvious topographical features, still poses a challenge to the identification of seabird foraging hotspots. This is particularly so for the most unpredictable tropical and subtropical areas (Weimerskirch, 2007), which might require flexible approaches to MPAs (Hyrenbach et al., 2000; Game et al., 2009; Lascelles et al., this issue). Secondly, even in the case of sites coinciding with topographical features, we cannot guarantee their stability in the long term under the current scenario of rapid environmental change, though this could also apply to protected sites inland (Hannah et al., 2007). Thirdly, behavioural information from boat observations was collected but not analysed, and tracking devices did not include additional recorders of activity, and therefore there is no sound proof that the hotspots identified were actually foraging areas. However, behavioural information derived from GPS movements (Louzao et al., 2009) and expert opinion input (including experience from the boat observers) were consistent at pointing the identified hotspots as foraging areas. Fourthly, the usefulness of the MPA approach could differ between species, as suggested by the different performance of the models presented here (AUC values), probably linked to the particular ecological requirements of each species (McPherson and Jetz, 2007). Cory's shearwater presented the most ubiquitous distribution, and is also the most widespread of the three study species (BirdLife International, 2011), suggesting that MPA designation for this Procellariiform would not be so

effective as for the Balearic shearwater and the European storm-petrel, which showed higher predictability. Other species for which foraging hotspots were identified within the study area are the Yelkouan shearwater, the Mediterranean gull *Larus melanocephalus* and Audouin's gull. Finally, when considering the whole inventory of Spanish marine IBAs, other areas and/or species counted with more limited datasets, and it was not always possible to count with robust SDMs to guide the process of hotspot identification.

Implications for conservation

The present study was part of a more ambitious project to identify marine IBAs in Spain, which was conducted in parallel to a sister project in Portugal (Ramírez et al., 2008). There was strong feed-back between both projects, which jointly contributed substantially to the “marine IBA toolkit” (BirdLife International, 2010a), a living document that is intended to provide guidance to any new initiative on marine IBA identification worldwide.

The Spanish marine IBA inventory produced a total of 44 marine IBAs, covering altogether over 50,000 km² (i.e. more than 5% of the Spanish waters). These areas have been recently acknowledged and proposed as Special Protection Areas (SPAs) by the Spanish Government, within the Natura 2000 network framework (BirdLife International, 2010b; European Commission, 2007), and once approved will represent the first complete national inventory of SPAs/MPAs for seabirds worldwide. These sites, along with the colonies that already enjoy some degree of protection, will provide a coherent network of protected areas combining the needs of seabirds throughout their life cycle, provided that these are undertaken within Spanish waters. International cooperation will be essential to extend the protection needs of these birds to other countries and international waters, given the large-scale movements of many seabird species (Croxall, 2008).

Along with the designation of MPAs/SPAs, it will be necessary to develop and implement appropriate management plans to gain effective protection for the seabirds and their habitats (Hooker and Gerber, 2004; Norse et al., 2005). This will require a detailed diagnosis of the threats to seabirds on a site by site basis, and the development of management tools that mitigate them. Of the serious threats that seabirds face in the marine environment (Boersma et al., 2002), some will likely be difficult to address on a site-by-site basis, such as diffuse pollution and climate change. But other serious threats can be handled more easily, particularly seabird by-catch (Anderson et al., 2011; Karpouzi et al., 2007). MPAs placed near the coast, as those proposed here, could also

address issues related with pollution (especially point-source events), recreational activities, and industrial development (e.g. wind farms) (Pedersen et al., 2009; Pichegru et al., 2010; Ronconi et al., 2002; Velando and Munilla, 2011). Finally, it is also very important to complement these site-based conservation efforts with other regulations at the wider scale, an issue for which Marine Spatial Planning brings new opportunities (Ehler and Douvere, 2009).

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Chapter V. Integrating species distribution modeling into decision-making to inform conservation actions⁷

Abstract

Species distribution models (SDMs) have been widely tagged as valuable tools in a variety of conservation assessments to address pressing conservation problems. However, these solutions could be hampered by difficulties to overcome the knowledge-action boundary between conservation and modelling practice. These difficulties have been well typified in the ecological modelling sphere, but still lack specific conceptual frameworks on how to bridge this gap. This work reports successful examples of translating SDMs to identify most favourable habitats for implementing conservation management action. Examples drive to a general discussion of the three main topics to enhance information flow between practitioners and modellers: the decision context, the modelling framework and the spatial products. Finally, we stress some practical solutions to improve applications. We emphasize the importance to match modelling goals with decision targets by a close collaboration with decision makers and species experts. Moreover, we highlight model documentation and spatial products to provide relevant and timely feedback for increase understanding and promote utilisation by conservation practitioners, and to inform and involve targeted audiences.

⁷ This chapter includes the original paper submitted to *Biodiversity and Conservation* (1/6/2016). The author has written the manuscript.

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Resum

Els models de distribució d'espècies (SDM) han estat àmpliament assenyalats com eines molt valuoses en gran varietat d'avaluacions relacionades amb problemes urgents de conservació. No obstant, la seva aplicació es pot veure obstaculitzada per les dificultats d'establir ponts entre un àmbit de recerca més acadèmic i la pràctica de la conservació. Aquestes dificultats estan ben tipificades en l'àmbit dels models ecològics, però encara manquen marcs conceptuals que permetin superar-les. Aquest treball documenta exemples exitosos de traducció de SDM per identificar els hàbitat més favorables per implementar accions de conservació. Aquests exemples introdueixen una discussió més general sobre els tres principals elements que permeten reforçar els fluxos de informació entre investigadors i els responsables de les decisions: el context de la decisió, el marc conceptual dels SDM i els productes espacials. Finalment, s'assenyalen algunes solucions pràctiques per millorar les aplicacions, fent èmfasi en la importància de vincular els objectius dels SDM amb els objectius de les decisions a partir d'una estreta col·laboració amb els prenedors de decisions i els experts en les espècies. A més, es recalca la importància de la documentació dels models i dels productes espacials per oferir una resposta adequada, entenedora i útil per a tots els actors clau involucrats en el procés de decisió.

Introduction

Where species occur in space is a key question for biodiversity conservation, since it underlies the context in which conservation actions are to be planned or implemented. Accordingly, the availability of robust and reliable information on species distribution and distribution changes have been one of the cornerstones of biodiversity conservation science (Pullin, 2002). Predictions from spatial models relating species occurrences or abundance to environmental data offer an accountable currency for gathering information on species distributions with strong potential for prioritizing conservation and required management actions (Ferrier et al., 2002; Jetz et al., 2012). Growth and potential of species distribution modelling techniques and approaches has boosted the development of applications in different ecology and biogeography research areas, including biodiversity conservation (Anderson and Martinez-Meyer, 2004; Guisan et al., 2013; Rodriguez et al., 2007). This interest has been recently amplified by the increasing development of species distribution knowledge and GIS tools to handle and analyse spatial information (Jetz et al., 2012).

Models are key tools allowing the exploration of hypotheses and have the potential to appraise solutions in complex systems. Ecological models can therefore become useful tools for practitioners seeking for better decisions in conservation policy and practice, but often the context in which the decisions are to be made is ignored to a large extent (Schmolke et al., 2010), failing to adequately address practical context-dependent issues (e.g. urgent need of action, lack of financial resources, lack of alignment between information needed and research outcomes, bureaucratic restrictions within agencies) so critical to effective implementation. The difficulty for translating research outcomes into conservation action has been tagged as the "implementation crisis" (e.g. Knight et al., 2006; Prendergast et al., 1999; Salafsky et al., 2002), and is contextualized in a broader issue of turning knowledge from applied research into action known as the "knowing-doing gap" (Pfeffer and Sutton, 1999). Conservation practice suffer this gap both planning and management activities. The "assessment-planning gap" concerns to the difficulty to achieve reliable conservation planning strategies by means of over weighted scientific knowledge and without true involvement of relevant agencies and stakeholders in the planning process. Similar obstacles hamper the translation of planning outcomes into conservation management action on the ground, i.e. the "planning-action gap" (Knight et al., 2006). Many authors have pointed out engagement impediments from both researchers and decision makers (i.e. core differences on funding sources, work planning, career aspirations, reward structures, etc.) as the major pitfall to overcome this gaps (Cook et al., 2013;

Guisan et al., 2013). These differences draw a knowledge-action boundary faintly porous to information flow across the research and management machineries, thickened by misconceptions from both academic scientists and conservation practitioners about real conservation management questions (Knight et al., 2008; Laurance et al., 2012), and about the utility (or even the existence) of valuable research insights (Addison et al., 2013; Pullin et al., 2004), respectively. Communication, translation and mediation between scientists and practitioners have been pointed out as necessary functions to better bridge this boundary (Cash et al., 2003; Schmolke et al., 2010). As suggested by Soberón (2004) and Guisan et al. (2013), these functions would be performed by 'translators' between scientists and decision makers, embodied by intermediate organizations, individuals, groups or consortia. These translators would reconcile the research/policy interface by clearly communicating useful scientific contributions and, to ensure that researchers and decision makers are jointly involved to face complex environmental problems (Guisan et al., 2013). But this task is particularly challenging when translating ecological models to non-modeller audiences lacking technical understanding, further when adequate communication skills are not guaranteed. Good modelling practices accompanied by standardized, brief and practical documentation has been acknowledged as a key tool to ensure understanding and acceptance of modelling outcomes in environmental decision support (Addison et al., 2013; Schmolke et al., 2010).

Species distribution models (SDMs) have been widely tagged as valuable tools in a variety of conservation assessments to address pressing conservation problems (Franklin, 2009). Improved knowledge of species actual distributions provide useful ecological insights and strong predictive capabilities to inform species distributions and assess sampling strategies of rare and endangered species (e.g. de Siqueira et al., 2009; Guisan et al., 2006; Marcer et al., 2012; Pearson et al., 2007; Raxworthy et al., 2003; Thomas et al., 2004), to establish conservation priority areas and design nature reserve networks (e.g. Arcos et al., 2012; Fajardo et al., 2014; Hermoso et al., 2015; Pawar et al., 2007; Wintle et al., 2005), or to guide species recovery and ecological restoration efforts (e.g. Angelieri et al., 2016; Clavero and Hermoso, 2015; Fei et al., 2012; Gastón and García-Viñas, 2013). Furthermore, SDMs can be extrapolated to new geographic or temporal scenarios as a component of invasive species risk assessments (e.g. Ficetola et al., 2007; Jiménez-Valverde et al., 2011; Roura-Pascual et al., 2007) and to forecast (or hindcast) potential impacts of climate change (e.g. Ficetola et al., 2010; Runge et al., 2015) or other environmental changes (e.g. Jetz et al., 2007; Martin et al., 2013; Regos et al., 2015; Vallecillo et al., 2009). However, most of these assessments published in peer-reviewed

journals consist of scientific analyses in pursuit of ever-more precise information on, and efficient techniques for, prioritizing elements in a conservation framework, lacking real-world conservation contexts of application (Guisan et al., 2013; Rodriguez et al., 2007). Far less scientific attention has been devoted to practical approaches for developing strategies that make effective use of SDMs through inclusive decision making processes, to improve prospects for implementation and, ultimately, successful conservation efforts (Addison et al., 2013; Guisan et al., 2013; Knight et al., 2006). We currently lack specific conceptual frameworks on how to bridge the gap between methodological developments in SDMs and practical use for effective conservation practice.

This work report selected successful examples of translating SDMs to identify most favourable habitats for implementing conservation management action from species-focused conservation strategies within the framework of a regional conservation project jointly performed by researchers from a boundary organization, as ‘translators’, and the Biodiversity and Animal Protection Agency (hereinafter Wildlife Agency) staff. We discuss the main topics identified to tackle targeted applications, emphasizing the importance to clearly match modelling goals with decision targets based on an early and effective communication with decision makers and other key stakeholders, and highlight model documentation and spatial products to provide relevant and timely feedback for increase understanding and promote utilisation by conservation practitioners, and also to inform and involve targeted audiences.

Moving from theory to application: conservation actions and informing SDMS

Feedback between practitioners and modellers are the main pitfall to boost applied research within conservation practice. Hence, the key issue when designing information flows between conservation and modelling practice is to enhance communication channels, and better if going beyond personal skills of the people involved. Transparent and practical modelling outcomes suited as comprehensive spatial products are potential keystones to span that knowledge-action boundary (Figure V.1). These products should be conceived as a bespoke modelling framework for the decision making process, adjusting SDMs development to the scope of the problem arising from the decision context. Here, the decision context is acknowledged as an early step of the decision process aimed to clarify the decision targets and bounds (i.e. timeline, budget, etc.), and roles of key stakeholders. At the other side, to develop positive contributions to different stages of the decision process, the SDMs

framework needs to fit adequately the challenges arising from the decision context based on a clear definition of the question(s) to be addressed with the models. Products for spatial decision making are focused on tying decision context and SDMs framework by reporting explicitly all these challenges within the modelling framework in order to feed the decision making process with clear and useful modelling outcomes.

Against this background, in 2007 we initiated a project called Mapping priority conservation species in Catalonia (CARTOBIO) promoted by the Wildlife Agency of the Catalan government, to support spatial data analysis from priority species to enhance conservation management actions. The main objective of the project was to increase species habitat mapping to match particular needs of pressing conservation problems, posing a timely opportunity to bridge new developments between decision making and SDMs development. Following information flows in Figure V.1, products for spatial decision making were benefited from a number of CARTOBIO learning experiences materialized in successful examples, according to priorities set by the Wildlife Agency. To illustrate the potential application of these products, three best-practice successful examples with significant impact on decisions related to specific conservation problems are summarized, emphasizing the three main topics of the information flow between practitioners and modellers, i.e. decision context, modelling framework and products for spatial decision-making. As many other CARTOBIO applications, selected examples are typified by short term pressing decisions, and aimed to illustrate different application backgrounds (e.g. species conservation planning, environmental payments and human-wildlife conflict management) and decision outcomes (e.g. special protection plans, funding allocation criteria and legal decrees). Examples are followed by a more general discussion on the main issues to better adjust modelling outcomes to the decision context by refining the products for spatial decision-making.

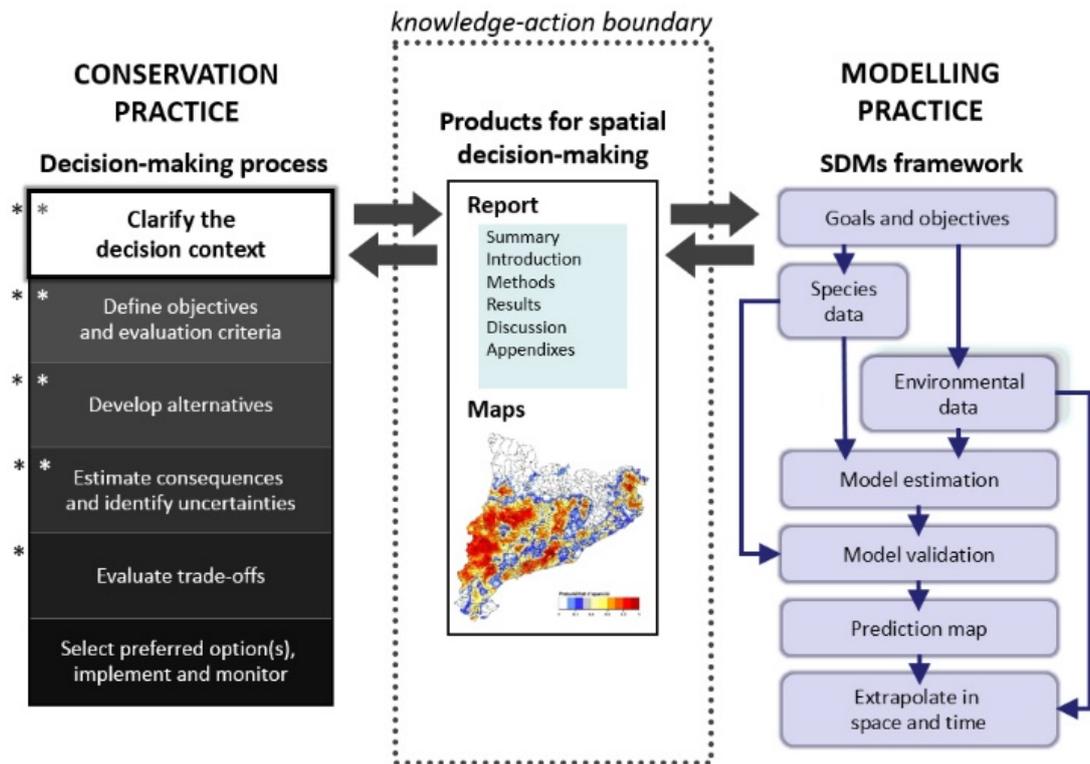


Figure V.1. Information flows between conservation and modelling practices, highlighting the products for spatial decision making as key translation tools to span the knowledge-action boundary. Theoretical decision making process showing potential contributions of SDMs via direct assessments (clear internal asterisk) or uncertainty assessments (dark external asterisk), adapted from Guisan et al. (2013), and SDMs framework adapted from Franklin (2009).

*Example 1: Identification of habitat corridors to ensure Hermann's tortoise (*Testudo hermanni subsp. hermanni*) population connectivity within the Special Protection Plan of the Albera Natural Park*

Decision context: The Albera Massif hosts the last native Hermann's tortoise population in the Iberian Peninsula. The upcoming statement of the Albera Natural Park aims at ensuring Hermann's tortoise conservation, emphasizing the importance connectivity maintenance between nearby meta-populations. Framed in the drafting of the Special Protection Plan, decision makers needed spatial information to formally define Hermann's tortoise core areas within the Natural Park, and corridor areas to guarantee interactions between isolated populations. This process encompassed staff from the Wildlife and Natural Parks agencies, as well as species experts, NGOs (Amics de la Tortuga de l'Albera), local administrations and researchers.

Modelling framework: Model objectives involved the development of actual and potential distribution maps, in order to assess Hermann's tortoise

core areas and corridor areas, respectively. Available species information included standardized census conducted within the Natural Park (Bertolero, 2008). However, preliminary analyses revealed that these censuses omitted significant portions of the species range related with potential suitable corridors outside the protected area. To achieve a more consistent dataset we enriched the 226 records from standardized censuses with 10 pre-processed and complementary telemetry records (see case study 2), covering historical and relevant satellite populations. Species ecological requirements were summarized in 22 predictor variables, including climate (12), relief (2), land cover (5), a single vegetation index (NDVI) and log-distance to valley bottoms and burned areas, bounded in a broad study area at 50x50 m spatial resolution. Additionally, a spatial contagion variable (or auto-covariate, Augustin et al., 1996) was computed by averaging species frequency within a 1 km buffer around each 50x50 cell, in order to examine intrinsic population factors imperative to define species actual core areas. Lacking absence data and environmental gradients incompletely surveyed justified the use of the presence-background approach implemented in Maxent, built-in a hierarchical modelling process. That process aimed first to catch climatic suitability areas intended to constrict the environmental background -and improve predictions- of the subsequent models (Phillips et al., 2009). Next steps produced a potential habitat model and an actual habitat model, both based on non-climatic variables, but the latter emphasizing the real distribution extracted from the spatial contagion variable. All models were trained using Maxent default parameters but only linear and quadratic features, looking for simple models with smooth fitted functions easy to interpret. Models were replicated 5 times in a cross-validation procedure designed to evaluate model performance. This procedure randomly assigned 75% of species records to model calibration while keeping the other 25% records to AUC computations. Statistical validation and expert criteria agreed that both actual (AUC=0.94) and potential (AUC=0.86) averaged models satisfactorily scored species habitat suitability in the Albera Massif.

Products for spatial decision making: Hermann's tortoise core areas were defined by high-suitable areas ranked from actual habitat suitability map (see case study 2 for thresholds calculations). Corridor areas were assessed using cost-distance analyses weighted by main factors affecting species dispersal abilities, i.e. potential habitat suitability, terrain slopes and human activities. Resulting cost-distance maps measured the cumulative cost to move from any point of the study area to the closest species core area, assuming species maximum dispersal distance of 1600 meters/week (Longepierre et al., 2001). Lastly, potential high-suitable areas (ranked from potential suitability

maps) were included in the cost-distance analysis to stress potentially colonized suitable areas.

Delivered maps pictured Hermann's tortoise actual and potential core areas and connectivity between them as continuous swathes of permeable pixels (Figure V.2A). Embedded report stressed the need to broaden species censuses to cover the species' distribution range in the Albera Massif and, hence, upgrade the analytical outlook for the specie. It was also underlined that model refinement would require information from other major environmental pressures (e.g. illegal collection, high-speed railway lines, etc.). But cost-distance analyses were the most harmed by the decision deadlines, reporting the highest levels of uncertainty, from the expert-subjective resistance assessment to the poor validation (based only on expert criteria) of the final connectivity maps. Still, spatial products were very welcome and contributed positively to the drafting of the Special Protection Plan, to the extent that researchers were asked to contribute to the chapter devoted to Hermann's tortoise conservation measures.

*Example 2: Mapping risk for brown bear (*Ursus arctos*) attack on livestock*

Decision context: At the end of the 20th century the brown bear went nearly extinct from the Pyrenees. To prevent extinction, Catalan government, jointly with other national and regional administrations, promoted an ambitious program to strengthen brown bear populations that led the translocation of some individuals from Slovenian bear populations. In order to enhance social acceptance, wildlife managers promoted measures to prevent conflicts between brown bear and livestock by installing electrified fences, encouraging the use of dogs to safeguard herds, supporting farming in high mountain (e.g. grouping together larger herds, building facilities to ease shepherd's life, etc.) and indemnifying livestock farmers for losses caused by brown bear attacks. For the proper implementation of all these measures, decision makers asked for a risk assessment for brown bear attack to livestock, based on precise spatial information of suitable areas for bears. The decision involved Wildlife Agency practitioners, jointly with species experts, farmer clusters, local administrations and researchers.

Modelling framework: Seasonal SDMs were targeted in order to examine brown bear distribution across the year, based on the feeding phenology of the specie. Available species data from translocated brown bears (1996-2010) included individual telemetry data (7 individuals, n=8587) and monitoring and opportunistic recordings (n=1619). Telemetry data enabled to draw seasonal samples (spring, summer and autumn). Individual telemetry positions were

cleaned and bootstrapped following Edrén et al. (2010) to produce 10 replicates per season with equal representation of each individual, harvesting a sample size of 55 in spring, 85 in summer, and 60 in autumn, from 5 individuals (3 females and 2 males; 2 females removed due to insufficient data). Environmental predictors, circumscribed to the Catalan Pyrenees at 50x50 m spatial resolution, included 16 proxies of food availability (% cover of different habitat types) and refuge areas (2 for topography, 5 for human influences and 2 for forest density). Seasonal models were developed using Maxent method due to its robustness when handling presence-only data and small sample sizes (Wisz et al., 2008). Maxent builds habitat suitability based on the comparison of presence records and background environmental conditions, which makes it particularly adequate for telemetry data that provide no indication of where animals do not occur. Replications were averaged to produce seasonal habitat suitability maps. To validate model performance we used threshold-independent (AUC) and threshold-dependent (omission rates and model significance) metrics averaged from seasonal replicates. AUC was computed from seasonal 'untouched' telemetry subsamples (AUC-telemetry) and seasonal independent monitoring/opportunistic recordings (AUC-monitoring), while omission rates and model significance were assessed from binary predictions that defined suitable areas as those with habitat suitability above the average 10 percentile fitted values at the training samples. Both AUCs consistently assessed an excellent performance of seasonal SDMs (AUC-telemetry = 0.962-0.971; AUC-monitoring = 0.902-0.941). In parallel, threshold-dependent measures reaffirmed model accuracy, with mean omission rates lower than 0.1 for all seasons (Spring 0.047 ± 0.018 ; Summer 0.072 ± 0.023 ; Autumn 0.073 ± 0.031), and always highly significant binomial omission tests ($p < 0.001$, one-tailed).

Products for spatial decision-making: Model outcomes included seasonal habitat suitability maps showing brown bear distribution across the year. However, these maps showed serious limitations to be directly used by decision makers because of the difficulties to clarify actual or potential areas of occupancy from continuous habitat suitability scores. To tackle that, first we highlighted the relative importance of different areas by classifying habitat suitability scores in ranked categories. This categorisation was based on two habitat suitability thresholds: suitable areas (used to assess threshold-dependent metrics) and optimal areas (lower limit set as the average habitat suitability values within suitable areas). Second, hierarchically prioritized seasonal maps were integrated in a single annual map, keeping the maximum seasonal ranked suitability, in which expert knowledge was used to distinguish occupied actual areas from the potential ones (J. Pearce et al., 2001). Finally,

two risk categories, low and high attack risk, were defined within the actual occupied areas, based on ranked suitable and optimal areas, respectively.

Final maps enabled decision makers to identify areas according to their likelihood of being occupied by brown bears, and thus potentially conflictive to herds, in different seasons (Figure V.2B). Attached report emphasized incomplete individual and gender equity from the datasets, based on only 3 females and 2 males of the 8-11 individuals present in the Catalan Pyrenees. Additionally, model improvement suggestions stressed the need to expansion of the study area (e.g. based on home ranges from telemetry data) beyond political borders.

*Example 3: Direct payments to beekeepers to compensate the damage produced by bee-eaters (*Merops apiaster*)*

Decision context: Bee-eater is a protected species in Catalonia with a breeding population increasing moderately (+3%) over the last 30 years (see <http://www.sioc.cat/fitxa.php?sp=MERAPI>). But this increase has impacted negatively honey production, due to the intensification of bee predation and the rising stress of hives. To promote activities compatible with conservation of the bee-eater, Catalan government compensates the damage on honey production with environmental payments regulated in a legal Decree. This regulation establishes quid-pro-quo payments to beekeepers based on bee-eater's local abundance as well as land apicultural suitability. Hence, bee-eater abundance maps were a key information to tackle this problem. Here, decision was aimed to rank municipalities based on apicultural suitability maps, provided by beekeeper clusters, and consistent bee-eater's abundance maps based on bird censuses. Decision process was guided by Wildlife Agency practitioners, and involved NGOs (Catalan Ornithological Institute), beekeeper clusters and researchers.

Modelling framework: Aiming to approach a bee-eater consistent abundance map, it was used the best available information at that time, i.e. the bee-eater probability of occurrence map from the Catalan breeding bird atlas (CBBA, Estrada et al., 2004). Based on standard and stratified timed censuses that covered approximately 9% (3077 1x1 km squares) of the total area of Catalonia between 1999 and 2002, the CBBA estimated predicted probability of occurrence of the bee-eater, and other 198 breeding bird species, by means of generalized linear models (GLM) at 1x1 km resolution. Models were trained using species presence-absence reported in standard censuses, and 39 environmental variables, including land use (22), human influence (5), climate (3), relief (2) and geography (3). GLM's included as potential predictors all

linear and quadratic terms, avoiding all those showed correlations higher than 0.9. Interactions between environmental variables were also included only when their ecological interpretation was highly justified. The most parsimonious models were harvested via the Akaike Information Criterion (AIC), computed from an automatic stepwise model-selection procedure starting from a null model containing the intercept only (Chamber and Hastie, 1997). Final models were built adding 3 spatial autocovariables to the best set of environmental variables previously selected (Augustin et al., 1996). This allowed identifying the best environmental model available given the environmental predictors and complementing those with information about the spatial structure of the species data (i.e. spatial autocorrelation). It is important to stress that these atlas GLM models were used as predictive rather than explanatory tools; hence the accuracy of model projections was more important than the significance of a particular ecological term (Legendre and Legendre, 1988). Model performance was evaluated based on expert criteria and AUC outcomes from a cross-validation procedure that randomly assigned 70% of occurrence values for each species to a calibration data set, and the 30% of remaining occurrences to a test data set (Guisan and Zimmermann, 2000), harvesting a very good discrimination capacity for the bee-eater predictions (AUC=0.85). CBBA probability of occurrence maps included an additional step for removing predicted areas outside species known 10×10 km squares distribution range, to ensure that the published occurrence maps corresponded as accurately as possible to real rather than potential distribution maps (J. L. Pearce et al., 2001).

Products for spatial decision making: Based on CBBA bee-eater probability of occurrence map, we ranked bee-eater abundance at municipality level assuming that probability of occurrence is a surrogate for abundance and as such is a reliable estimator of a species' relative abundance in each mapping unit. This assumption was strongly supported within the CBBA by consistent population estimates based on species occurrence maps and data from SOCC (Catalan Common Bird Survey), and other studies (e.g. Brotons et al., 2007; Robertson and Jarvis, 1995). Municipalities were ranked in three abundance categories (medium, high and very high) bounded by (1) the averaged probability of occurrence values within municipalities to set the threshold between medium and high abundances, and (2) averaged probabilities within high abundance municipalities, to define the limit between high and very high species abundance. Delivered spatial products consisted of a short report highlighting the potential to improve (and update) species abundance maps based on monitoring data (SOCC) and dynamic environmental predictors (e.g. remote sensed vegetation indices), coupled with a municipalities digital map

classified in medium, high and very high bee-eater abundance (Figure V.2C). Ultimately, direct payments to beekeepers established in a legal decree (DMAH, 2007) were allocated combining municipalities ranked by bee-eater abundance and the apicultural suitability map.

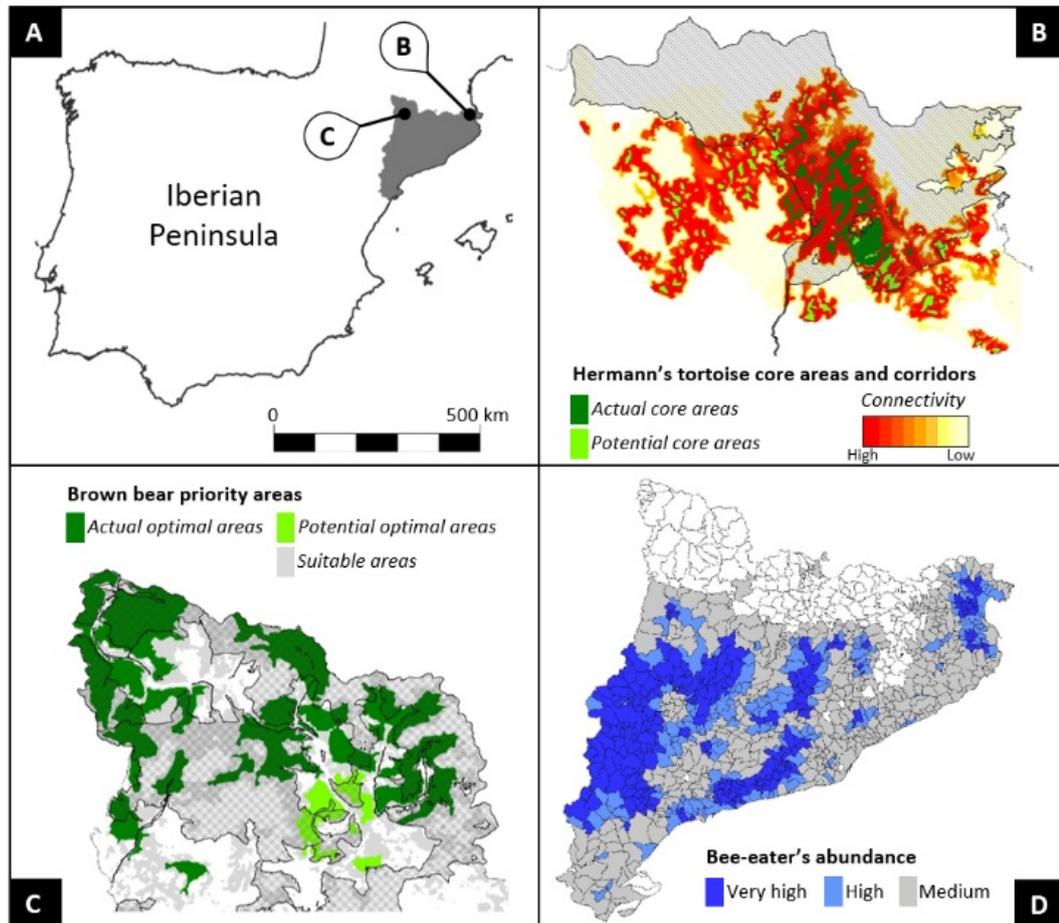


Figure V.2. Examples of digital maps derived from SDMs and appended to products for spatial decision making. (A) Location of Catalonia (shaded area within the Iberian Peninsula) and study areas for B and C examples. (B) Hermann's tortoise (*Testudo hermanni subsp. hermanni*) core areas and corridors to ensure population connectivity within the Special Protection Plan of the Albera Natural Park. (C) Brown bear (*Ursus arctos*) actual and potential priority areas within Natura 2000 (shaded areas). (D) Bee-eaters (*Merops apiaster*) abundance map at municipality level to weigh environmental payments established in a legal decree (DMAH, 2007) to mitigate the decrease in bee hives production due to predation.

Making information accessible to decisions

Generally, decision-making processes are the meeting-point of multisectoral stakeholders (e.g. government agencies practitioners and decision makers,

environmental NGO's, species specialists, researchers, private sectors, etc.), framed within a geographical and cultural background, in which social, economic, scientific and political interests collide (Margules and Pressey, 2000). The involvement of key stakeholders along the process ensures the adoption of "good" analytical and consensus solutions, by taking into account constraints and pit-falls related to competing interests (e.g. negative population trends for endangered forest species vs. social consensus to increase forest productivity) (Carwardine et al., 2008; MacDonald et al., 2007; Theobald et al., 2005). From the researcher perspective, a prerequisite to prevent misconceptions is to clearly play an uninhibitedly (but not unrestrained) role (i.e. provide scientific evidences adjusted to the decision goals). Hence, it is critical to assume that the link between scientific evidences and decision targets is based on the assumption that the question(s) to be addressed is shaped by the policy or management problem, and thus, not necessarily a top priority in the research agenda.

In the following, we discuss the key issues from the decision context, the modelling framework, and the products for spatial decision making (summarized in Table V.1). For the latter, we emphasize certain requirements that should have end-user spatial products to provide relevant and timely information for building trust and promote utilisation by practitioners, and to improve communication to other stakeholders and targeted audiences.

Decision context

The decision process is shaped by the decision context through the definition of explicit objectives and endpoints to address a particular conservation problem, along with budgets, timelines and key stakeholders. The aim of applied model development is to fit the decision problem at hand with targeted and simplified representations of a complex reality. But additionally, we were also responsive to the feasibility of the model in view of the limits drawn by the decision context. An early fluid communication with decision-makers helped to clarify these questions and, moreover, the identification of specific needs of information, while contributing to better recognise of other stakeholder roles within the decision context.

Another key aspect limiting the assembly between decision process and model development were time or budget constraints set by decision-making agenda, often responding to urgent needs of action. To link available human resources with a new schedule set by decision-makers meant that qualified and flexible enough staff was needed. Having a stable yearly budget was a solid incentive to strengthen knowledge transfer in our research group.

Nevertheless, difficulties of training and consolidating scientific and technical staff, and an increasingly demanding scientific career for researchers responsible for adding value to knowledge transfer processes often posed a tough challenge for planning the research group priorities.

Table V.1. Key issues to an effective integration of SDMs in a decision making process.

Decision context
<ul style="list-style-type: none"> ▪ Match particular decision targets with pertinent and precise model objectives. ▪ Ensure the feasibility of the model considering the limitations drawn by the decision context (e.g. time or budget constraints, poor species knowledge, etc.) ▪ Clearly identify specific information needs from the decision making process. ▪ Recognise key roles from other stakeholders, and involve species experts in model development.
Modelling framework
<ul style="list-style-type: none"> ▪ Do not deviate from the model objectives informing the decision process. ▪ Mobilize relevant available species and environmental information, and engage species experts to adequately interpret available species datasets and relevant environmental predictors. ▪ Use contrasted methods with clear and transparent assumptions to increase understanding and confidence from decision makers and other stakeholders. ▪ Strengthen credibility with a multifaceted model validation based on statistical model-performance measures and expert based criteria, bearing in mind the intended application of the model.
Products for spatial decision making
<ul style="list-style-type: none"> ▪ Describe the modelling framework with clear and accessible/plain language using and adapting good practices from standard protocols (e.g. TRACE). ▪ Identify uncertainties from biological data, environmental predictors, modelling methods using both statistical criteria and ecological realism. ▪ Clearly communicate limitations of modelling outcomes, and derive recommendations aimed at the intended use of the spatial products. ▪ Align spatial products to specific needs of information by categorizing model outputs into binary or ranked priority maps (e.g. identification of species core areas) and perform complementary analyses (e.g. corridor analyses). ▪ Deliver comprehensive and informative reports embedded with digital maps in standard file formats.

Poor species knowledge or data often represented an added shortcoming. In fact, models are especially suitable tools to make extrapolations based on incomplete data. Even so, species lacking information became good opportunities for cooperation with species experts' stakeholders, which were especially helpful to complete databases with new biological information, to identify and define relevant environmental predictors, and to validate (by expert opinion) and mainstream (to the extent that experts adopt as their own) model results.

Modelling framework

The first step in any modelling exercise is to clearly formulate the question to be addressed (Franklin, 2009; Schmolke et al., 2010). A broad view of the decision context favoured us to couple information sources and assumptions used for model design, calibration, and validation, and, lastly, to better suit information needs from the decision process.

Species occurrence available data was mobilized and documented, focusing on methodological issues (data types, sample size, life history targets, sampling design, etc.) and fulfilling biodiversity information standards (e.g. Darwin Core: Wiczorek et al., 2012). Information sources were diverse, including specific surveys, monitoring programs, telemetry data and opportunistic observations, and mostly designed to meet particular goals far from SDM development. In fact, many information sources were partially recorded or incomplete (lack of absence data, sampling effort, etc.), and had an inadequate spatio-temporal or environmental coverage (Hirzel and Guisan, 2002; Vaughan and Ormerod, 2003). Hence, the achievement of consistent data to build SDMs often involved to clutch different datasets, seeking the balance between the gain in sample size and the loss in data quality (Chapman, 2005). Data recovery and integration implied extra work for data cleaning and standardization, but fostered to disentangle the potential to meet the challenges posed by the decision context (Hermoso et al., 2013; Rondinini et al., 2006). Experts played an essential role for the correct interpretation of the species databases, but further to identify relevant environmental predictors, or their surrogates, to establish species-environment relationships. The availability of reliable and high-resolution environmental databases (climate, relief, land use, habitats and human activities) greatly simplified this task. Dealing with environmental predictors collinearities and adjusting them to spatio-temporal scale of the decision were the prior steps to the development of the SDM.

Given the myriad of SDM algorithms (Franklin, 2009; Guisan and Zimmermann, 2000), we opted for contrasted methods consistent with available species data and preferably built-in in clear analytical schemes, aimed to make more accessible and straightforward analytical issues, and thus confident, to decision makers and other stakeholders. More understandable model assumptions included minimizing the number of modelling steps and avoiding the combination of different modelling techniques. Correlative approaches were widely used for different applications, although the more demanding general-purpose statistical methods (e.g. GLMs, GAMs) were generally excluded due to a lack of presence-absence or abundance data recorded in systematic surveys. Even, occasionally the lack of presence-only data justified the use of alternative expert based models (e.g. habitat suitability

indices). Nevertheless, presence-only data clearly arised as the best existing data for almost all species, boosting the utilization of techniques based in such data. Among these techniques, Maxent (Phillips et al., 2006, 2004; Phillips and Dudik, 2008) emerged as a feasible solution for a wide number of applications because of its flexibility when handling different types of data and responses and its consistent competitive performance in data poor situations (Elith et al., 2010, 2006). Our model implementations benefited from comprehensive research background on Maxent optimization-use for dealing with sample biases (Anderson and Gonzalez Jr, 2011; Elith et al., 2010; Fourcade et al., 2014; Kramer-Schadt et al., 2013; Phillips et al., 2009; Yackulic et al., 2013), model parameterization (Merow et al., 2013; Warren and Seifert, 2011) and feature types selection (Elith et al., 2010; Phillips and Dudik, 2008; Syfert et al., 2013). Another advantage is that Maxent, similarly to other regression-like methods, correlates species occurrence to selected functionally relevant predictors by fitting response curves using some goodness-of-fit criterion (Phillips et al., 2006; Phillips and Dudik, 2008). Besides, Maxent offers many tuning options for the parameterization of environmental predictors (number of predictors, linearity or non-linearity of the response, additivity or interactions between predictors, etc.), easing to fine-tune predictive or explanatory models to a wider range of applications, and also to furnish spatial predictions with other informative model outputs.

Model validation enhanced the credibility of model outputs by combining statistical and expert based criteria. Among the different kinds of uncertainty arising during model building (Beale and Lennon, 2012), model evaluation was explicitly focused on measuring the accuracy of spatial predictions given the intended application of the model. Statistical criteria included different performance measures frequently used in SDM. In order to get a multifaceted view of the quality of the predictions, models were preferably evaluated by means of threshold-independent and threshold-dependent measures. Debugging treatments of original species data aimed to set aside independent test samples, coming from independent species surveys or from data excluded in model fitting, built with the same optimization guidelines as required to samples meant to build models. When data was not enough, we used common partitioning methods, based on the sample size and the number of predictors, to split the available species data in two-fold (or more) cross-validation subsamples, yielding averaged accuracy estimates among different replicates (Fielding and Bell, 1997; Guisan and Zimmermann, 2000). We used the threshold-independent AUC (Area Under the receiver operating characteristic Curve) (Boyce et al., 2002; Fielding and Bell, 1997) as an all-purpose basic measure of model performance. Despite the limitations of AUC when

comparing performance for different species or study areas and its responsiveness to absences selection when deals with presence-only data (Lobo et al., 2008), it is, however, a reliable and widespread measure of model performance (Anderson and Gonzalez Jr, 2011). If possible, AUC scores were complemented with threshold-dependent metrics, e.g. omission rates, model significance (Anderson and Gonzalez Jr, 2011; Phillips et al., 2006).

As mentioned above, experts were favoured to assess different modelling steps, i.e. understanding species data, defining relevant environmental predictors and verifying the ecological realism of the environmental response functions and the relative importance of different predictors. Furthermore, experts were also asked to visually evaluate the credibility of spatial predictions, based on matching's between predicted spatial patterns, species knowledge and expert intuition. Ultimately, this feedback guaranteed the acceptance of the model and the sufficient degree of belief to justify use for intended application.

Products for spatial decision-making

Modelling outputs were delivered as informative, short executive reports joined to useful digital maps concomitant to decision targets. Species predicted distribution colourful maps can be very appealing and suggestive, and easily can be misinterpreted and misused if model objectives and uncertainties are not clearly explained. To prevent other parties from the limitations of these maps, special attention was devoted to report uncertainties in each modelling step, to highlight the interpretation and limitations of model outputs, and finally to draw some recommendations to stimulate the use of the attached maps. Executive reports explicitly assessed uncertainties inherent to biological data, environmental predictors, modelling methods and predictions, not only based on statistical criteria, but also in ecological realism (i.e. spatio-temporal significance of species occurrence, correct selection of predictors, accurate description of response curves, fitting of ecologically rational relationships, etc.). Reports were inspired by good practices proposed in standard protocols for documenting models (e.g. TRACE: Schmolke et al., 2010), but strongly influenced by scrutiny from end-users to articulate the results in clear schemes and accessible and plain language.

Feedback from key stakeholders and practitioners not only allowed to improve executive reports, but also to align spatial products to specific needs of information (Laurance et al., 2012). Difficulties to clarify what predicted maps meant (habitat suitability, probability of occurrence, species abundance, etc.) and to distinguish actual or potential areas of occupancy from continuous

predictions were explicitly addressed by tuning mapping outputs to better fit decision targets (Guillera-Arroita et al., 2015). For most applications it was necessary to categorize predictions into binary maps (species presence vs. absence or suitable vs. unsuitable habitat) or hierarchically ranked priority maps (ex. suitable, high suitable and optimal areas), to be directly used or to feed further analysis of conservation baselines, corridors, community assemblages, biodiversity indexes, reserve selection, etc. From the number of methods available to transform model continuous predictions into discrete maps (Liu et al., 2005), we followed previous positive experiences on mapping applications in our conservation arena (Arcos et al., 2009; Bota et al., 2008), to separate, first, species suitable and not suitable areas (or presence-absence areas in terms of the prevalence of the data used in the model development) and, secondly, to meaningfully rank different levels of importance for the species based on the average of predicted values within suitable areas (see selected study cases for more details). Additionally, when it was required to discriminate actual vs. potential distributions, we complemented map-tuning with available atlas coarse-scale data and expert knowledge to draw more precise actual species distribution. Once again, consensus with targeted audiences ensured the acceptance of the final spatial products, and last but not least, the use of standard file formats readable by potential end-users to embed reports and digital maps boosted its dissemination and utility.

Concluding remarks

Supporting decisions behind biodiversity management actions with scientific information relies on the premise that decision-makers clearly understand the scope of the information received (Addison et al., 2013). But a prerequisite to ensure the usefulness of scientific information is that it is properly fitted and inspired by the decision context (Guillera-Arroita et al., 2015; Norton, 1998; Schmolke et al., 2010). Broadly, decision context is built around the concept of structured decision making process (Gregory and Long, 2009). That mechanism is fuelled by multi-stakeholder's contribution, all playing different roles and often rowing in different directions, with decision-makers leading from the cockpit (Knight et al., 2006). Among these actors, researchers assume the role of translators of scientific outcomes matching decision goals and constraints (timeline, budget, data, uncertainty, etc.). Therefore, researchers need to be aware of the decision context and consciously be included in the decision-making process to the better fit decision goals. We have identified this step as one of the main bottleneck for effective use of SDMs by practitioners. The availability of data and appropriate methodologies and tools needs to be aligned with the decision context constraints. One possibility is that

researchers acknowledge these constraints and make an effort to adjust these constraints into their routines. The alternative is to develop specific translator teams with a research background that actively bridge the gap between research, method development and applications. In our opinion this option is to be favoured and cost-effective in the medium and long-term perspectives.

Ecological models represent a valuable problem-solving tool for supporting environmental decision making (Schmolke et al., 2010; Starfield, 1997). SDMs ability to express the results in spatially explicit terms, similar to that used in spatial planning, favours its implementation as tools for decision support. But the development of SDMs, as any ecological model, in a decision making schema is a challenging process (Addison et al., 2013; Schmolke et al., 2010). If not carefully checked, decision context may hinder the performance at different stages, from the ambiguous definition of the modelling goals to the incorrect use of the modelling outputs, through various unforeseen or tricky pitfalls along the different modelling steps (Guillera-Arroita et al., 2015). Consequently, model formulation requires a clear conceptualization of the decision targets and requirements and, therefore, the integration of critical constraints into the modelling framework (Schmolke et al., 2010). The challenge here is to bridge the gaps between the decision making process and the modelling practise. This challenge may not entirely depend on the role of scientists in charge of model development, but also on the feedback from other stakeholders. However, our experience is that the early inclusion of the limitations into model development greatly increases the chances of modelling outcomes being used to guide conservation decisions.

The massive development of biodiversity related information systems, including primary biodiversity data repositories and citizen science online portals, in parallel to increasingly profuse environmental data from remote sensing or other initiatives (e.g. Google Street View), is boosting the growth of SDMs methods and applications (Arts et al., 2015; Brotons, 2014; Jetz et al., 2012; Rousset et al., 2013; Shanmughavel, 2007). In this virtuous circle, critical limitations hampering effective implementation of SDMs are likely to shrink while expanding the widespread use of that models to support environmental decisions (Guisan et al., 2013; Hermoso et al., 2015). Assuming that biodiversity data, even for well-known taxa, are grossly incomplete and often biased taxonomically, temporally and geographically (Reddy and Dávalos, 2003), many authors have pointed out the efficacy of presence-only data (Elith and Leathwick, 2007; Pearce and Boyce, 2006; Phillips et al., 2009), or even other modelling alternatives with scarce data (Elith and Leathwick, 2009), to avoid delaying conservation actions for improved knowledge (Grantham et al., 2009). But if real world decisions are to be based on model outcomes, the

critical issue is to thoroughly assess model suitability and uncertainties in the context of conservation planning and action (Beale and Lennon, 2012). Model's evaluation not only means to report objective criteria to assess data sources, assumptions and performance requirements inherent to the modelling framework, but also to meet subjective criteria that determines the acceptability of the model framed within a political and social background (Barry and Elith, 2006; Ludwig et al., 2001; Rykiel, 1996).

Reporting models following good practices is a good starting point for more comprehensive and transparent spatial products. But despite there is a general consensus on which elements need to be addressed in good modelling practices (Margules and Pressey, 2000; Schmolke et al., 2010), they are widely ignored due to the lack of involvement of key stakeholders, lack of incentives for modellers to follow good practices, and the use of inconsistent terminologies regarding the elements and issues of the modelling process (Addison et al., 2013; Schmolke et al., 2010; Soberon, 2004). In addition, clear documentation is not enough for mainstreaming modelling results if not accompanied by user-useful and user-friendly spatial products (Driver and Maze, 2003; Reyers et al., 2007). The development of valuable products for spatial decision-making requires an effective communication with decision makers and other stakeholders, especially at early stages of a project (Laurance et al., 2012). Frequent personal contacts (face-to-face meetings, telephone calls, emails) are the best investment to build trust and to better understand particular information needs from end-users, in order to accurately fine-tune the modelling outcomes to the challenges posed by the decision context (Addison et al., 2013). Thus, products for spatial decision making can operate as the roller chain to ensure feedback between the decision-making process and the modelling framework, and to enhance communication channels for gaining complicity with practitioners and other targeted audiences (e.g. land-owners, tourism promotion boards, NGO's, etc.) (Addison et al., 2013; Guisan et al., 2013).

In a rapidly changing and uncertain world, the costs of facing urgent and complex environmental problems with impromptu solutions may imply social and/or environmental irreparable impacts (Cook et al., 2010; McDonald-Madden et al., 2008). Ultimately, a simple, rapidly completed plan is better than no plan, but to avoid costly conservation mistakes conservation policies should reinforce linkages between science and both conservation planning and action for more efficient and transparent decision-making (Knight et al., 2006). This means building capacities by promoting innovative research to impact environmental decisions, which are the substratum for relevant applications in the knowledge-action boundary (Cash et al., 2003; Cook et al.,

2013). There are some promising initiatives devoted to reconcile science and policy agendas, both from the perspective of science (e.g. Biodiversity Observation Networks: Scholes et al., 2008; Wetzell et al., 2015) and policy (e.g. Australian National Environmental Research Program: Campbell et al., 2015). Nevertheless, experience-based non-informed decisions still widely predominant in the real-world conservation practice (Cook et al., 2010; Sutherland et al., 2004), exacerbating the importance for scientists to take advantage from every opportunity to contribute positively and determinedly in multifaceted decision-making processes (Laurance et al., 2012). In the ecological modelling sphere, this means promoting “positive” modelling experiences by properly adjust the modelling goals to constraints posed by the environmental problem at hand, but also by systematically fuel communication channels to engage participants for broadcasting modelling outcomes in clear, accessible and useful information products, to aid more rigorous, transparent and reliable environmental decisions.

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Chapter VI. Mapping from heterogeneous biodiversity monitoring data sources⁸

Abstract

Field monitoring can vary from simple volunteer opportunistic observations to professional standardised monitoring surveys, leading to a trade-off between data quality and data collection costs. Such variability in data quality may result in biased predictions obtained from species distribution models (SDMs). We aimed to identify the limitations of different monitoring data sources for developing species distribution maps and to evaluate their potential for spatial data integration in a conservation context. Using Maxent, SDMs were generated from three different bird data sources in Catalonia, which differ in the degree of standardisation and available sample size. In addition, an alternative approach for modelling species distributions was applied, which combined the three data sources at a large spatial scale, but then downscaling to the required resolution. Finally, SDM predictions were used to identify species richness and high quality areas (hotspots) from different treatments. Models were evaluated by using high quality Atlas information. We show that both sample size and survey methodology used to collect the data are important in delivering robust information on species distributions. Models based on standardized monitoring provided higher accuracy with a lower sample size, especially when modelling common species. Accuracy of models from opportunistic observations substantially increased when modelling uncommon species, giving similar accuracy to a more standardized survey. Although downscaling data through a SDM approach appears to be a useful tool in cases of data shortage or low data quality and heterogeneity, it will tend to overestimate species distributions. In order to identify distributions of species,

⁸ This chapter include the original paper published in *Biodiversity and Conservation*. The author has written the part of the manuscript related with SDM and has performed all concomitant analysis.

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data with different quality may be appropriate. However, to identify biodiversity hotspots high quality information is needed.

Resum

El monitoratge de les espècies es pot basar en diverses metodologies que van des d'esquemes senzills basats en voluntaris que recullen dades oportunistes, fins a esquemes estandarditzats i professionals de seguiment, cercant sempre un compromís entre els costos de recollida de dades i la seva qualitat. Aquesta variabilitat en la qualitat de dades es tradueix en biaixos importants en les prediccions obtingudes amb models de distribució d'espècies (SDM). Aquest treball té com a objectiu identificar les limitacions de diferents fonts d'informació per desenvolupar SDM i avaluar la seva capacitat d'integrar informació espacial en un context de conservació. Es van desenvolupar SDM en base a tres fonts d'informació d'aus que diferien entre elles pel grau d'estandardització i la mida de mostra. A més, es va aplicar un mètode alternatiu per modelitzar la distribució de les espècies basat en la combinació de les tres fonts d'informació en una mostra de resolució geogràfica més grollera, però projectant els models resultants a la resolució dels altres models. Finalment, les prediccions obtingudes en els diferents tractaments es van utilitzar per mesurar la riquesa d'espècies i definir zones sensibles d'elevada qualitat d'hàbitat. Els SDM es van avaluar utilitzant informació d'elevada qualitat. Els resultats mostren que tant la mida de mostra com la metodologia de mostreig són importants per obtenir informació robusta sobre la distribució de les espècies. Els models basats en dades estandarditzades de seguiment van proporcionar prediccions més precises amb mides de mostra menors, especialment per a les espècies comuns. La precisió dels models desenvolupats amb dades oportunistes va augmentar substancialment per a les espècies poc comunes, assolint valors semblants als obtinguts amb metodologies estandarditzades. Davant d'una manca important de dades, l'alternativa de projectar models basats en dades grolleres a resolucions més detallades va sobreestimar la distribució de les espècies. Així, l'anàlisi de la distribució de les espècies es pot fer en base a una àmplia varietat de dades procedents de diferents metodologies de monitoratge. No obstant, per identificar zones sensibles de biodiversitat es necessari utilitzar informació de bona qualitat.

Introduction

The availability of representative spatial biodiversity data is essential for efficient species conservation, planning and management (Stem et al. 2005). However, biodiversity data are often fragmented, posing problems on how to make best use of the available information for biodiversity management and planning strategies (Soberon and Peterson 2004; Boakes et al. 2010). Species distribution models (SDMs) have been widely used to bridge the gap between fragmentary species observations and the need for continuous information at large spatial scales. SDMs rely on determining species—environmental relationships and representing these in space. However, while much has been done on technical developments of such methods (Elith et al. 2006; Araújo and New 2007; Guisan et al. 2007; Phillips and Dudik 2008), less work has focused on the effects of limitations regarding data availability, quality and spatial scale, specifically regarding the origin of the biodiversity data used for modelling (Vaughan and Ormerod 2003; Boakes et al. 2010; Feeley and Silman 2011).

Data sources of differing quality and characteristics may be available for different species in a given region, which could be used in species distribution modelling (Boakes et al. 2010). However, whilst it is assumed that models based on opportunistic observations perform less well than those based on systematic and well designed sampling (Schreuder et al. 2001), repeated standardised sampling of large areas over time is generally outside the scope of most conservation programs (Danielsen et al. 2005; Brotons et al. 2007). An alternative approach is to make use of museum specimens, and lately opportunistic records collected by volunteers through web-based tools (Roberts et al. 2007; Schmeller et al. 2009; Munson et al. 2010; Conrad and Hilchey 2011). However, this kind of opportunistic information may have considerable shortcomings, limiting its application in a spatial modelling context. For instance, observations may be biased towards areas where there are more visits, and the quality of the data is often heterogeneous (Snall et al. 2011). Little work has looked at the consequences of the method used for gathering information for species distribution modelling, but it appears important to make optimal use of resources invested in future biodiversity data collection effort. This is especially relevant in a context in which multiple data sources coexist in time and space.

Thus, due to financial constraints and lack of human resources, there is usually a trade-off between the quality of sampling, sample size and survey area covered (Danielsen et al. 2005; Snall et al. 2011). Consequently, for biodiversity conservation it is crucial to know where the investment of resources should be

prioritised, into systematic and more accurate local sampling, or into monitoring strategies based on opportunistic records. In this context, quantifying the limitations of different data characteristics and how these may be overcome is critical to guide monitoring strategies in areas where resources are limited (Braunisch and Suchant 2010). One of the issues arising when combining locally collected data across larger spatial and temporal scales relates to the need to make the best possible use of data obtained from different monitoring schemes and alternative data sources, and as a consequence, contribute to the evaluation of the efficiency of existing monitoring schemes (Brotons et al. 2007; Schmeller et al. 2009).

Here, we aim to identify the power of different data sources for mapping species distributions and the potential for map integration or compatibility of information derived from such diversity of raw information. Thus, it is important to understand the power of different types of data to produce maps from SDMs. If different data qualities and sample sizes are available for model development from different areas, one strategy may be to make the best possible use of available data in each region and integrate the maps obtained. In particular, we investigate the predictive value of models built with these different data sets of differing quality, and second we quantify the degree in spatial matching of suitable habitat maps derived from these models with high quality independent reference data already available for these species.

Our study focuses on farmland birds. This group is threatened in Europe and considerable attention is being directed towards the identification of areas where conservation effort should be invested (Green et al. 2005; Gregory et al. 2005). Getting reliable spatial information of farmland bird distributions from different data sources is important to detect farmland bird hotspots, a need for biodiversity conservation under an efficient agricultural landscape management and planning. By using a set of farmland bird species as study models, we test the impact of data quality and quantity on common and uncommon species in order to derive general guidelines relating the power of different biodiversity data sources to model species distributions. Finally, we also test the impact of data quality and quantity in identifying species richness and habitat quality hotspots, which play an important role in management and conservation programs.

Methods

Study area and species selection

We used bird data from Catalonia in north-east Spain. Catalonia is environmentally heterogeneous with a long tradition in ornithological monitoring that has allowed the gathering of several independent bird data sets of different quality. A total of 30 farmland bird species were selected. These species were chosen to include those in the European Farmland Bird Indicator developed by Gregory et al. (2005) that breed in Catalonia. We also included some additional farmland species in Catalonia, which are more specific to the Mediterranean farmland areas (Brotons et al. 2004a; Burfield 2004; Estrada et al. 2004). These species were classified into two groups, common and uncommon species. In order to establish a general criterion to define these two groups (common and uncommon) we used a criterion based on the frequency with which a species is found in standardized samples (Estrada et al. 2004), as a measure of their overall presence in the environment. Thus, the 50 % of the species with the lower number of occurrences were classified as uncommon, while the rest were classified as common.

All data used in our study originated from large scale volunteer based monitoring programs with different characteristics with respect to standardisation in data collection. We only included data from the breeding period, from 15 April to 30 June for 2009 and 2010, when all the monitoring programs were fully operational.

Available data sets

OCCASIONAL OBSERVATIONAL DATA (OBS)

These data were collected by volunteers through the web-based monitoring tool Ornitho (Kery et al. 2010) which started to be used as a tool for volunteer data collection in 2006 in Catalonia (www.ornitho.cat). These data only include opportunistic bird records, with no information on the time spent in the field or information on other species recorded on the same visit to a given site. Thus, this kind of opportunistic data is very easy to collect and increasingly gathered by ornithological societies around the world (Roberts et al. 2005; Roberts et al. 2007). However, opportunistic information is characterised by a lack of information on the area sampled and strong spatial biases. Furthermore, our expectation is that this kind of survey is more likely to sample uncommon species compared to more standardised surveys due to particular interest in these species for bird observers.

TIMED BIRD LISTS DATA (LIST)

This kind of information was also derived from web-based monitoring tool Ornitho. In this monitoring programme, volunteers report timed species lists of variable duration in which species seen or heard at the same site during a single timed visit are recorded. Recording time in these lists ranged from 5 to 982 min, however only those lists included within 95 % confidence interval were included (5–135 min). There were occasions where the same observer sampled the same locality more than once, in these cases we selected the total number of species detected in this locality and summed the minutes expended.

Timed species lists are relatively easy to collect, and although the area sampled is not recorded, the observer provides information on species not seen (those not included in the list) and some information on time effort. Lists are expected to sample both common and uncommon species relatively well.

BREEDING BIRD SURVEY DATA (BBS)

Bird contacts were recorded along 3-km line transects divided into three 1-km sections in which bird numbers were surveyed twice every year (see Herrando et al. 2008 for detailed information). Thus, in this study we used 1-km sections as sampling units to provide information on bird presence at a 1-km resolution (Brotons et al. 2007). Data from the central 1-km section were not used to reduce spatial autocorrelation in the bird data used. Recording time for the 1-km sections ranged from 11 to 78 min. One of the main strengths of BBS is that the same observer visits the same locality over years. Thus, in each locality we selected the total number of species detected in this locality and summed the minutes expended.

BBS transects are distributed according to two different criteria: transects located in a randomly chosen 10-km square within each of five biogeographically determined strata or transects located in a 10-km square freely chosen by the observer. These two possibilities aim at attracting volunteers to the main areas of interest without losing any possible contributor because of distant or undesired census locations.

These data contained high quality information on sampling area and effort. Common species are expected to be very well sampled since breeding bird surveys are commonly designed to track common species abundances through time. While uncommon species are also recorded, effort to count common species may lead to the under recording of uncommon species.

COARSE GRAINED HETEROGENEOUS BIRD DATA (COARSE)

An alternative approach is to downscale coarse gridded data to the required resolution (Witte et al. 2008). Presence–absence data of species was gathered

at 10-km UTM sampling squares, considering all available evidence of breeding. This represents a very comprehensive cover of the region but at the sacrifice of spatial resolution and detail. Thus, the coarse scale dataset used to train models synthesized the results of all sampling surveys (OBS, LIST and BBS) at 10-km UTM grid squares, covering 95 % of the total area (309 squares). A sub-sampling method was applied for downscaling (see McPherson et al. 2006), randomly selecting 25 % of the 1-km UTM squares as occurrences within each 10-km UTM. Only 1-km UTM squares with at least 5 % of agricultural surface were selected (information obtained from SIGPAC: Spanish Geographic Information System of Agricultural Plots). Different sub-sampling sizes (5, 20, 25 and 50 %) were previously tested, finally selecting the sample size that better performed in the final model (i.e.: 25 %).

FINE GRAINED ATLAS DATA (ATLAS)

Reference, high quality information on species distribution was gathered through the Catalan Breeding Bird Atlas (Estrada et al. 2004; Brotons et al. 2007). In the atlas survey, 1-km UTM sampling squares were visited twice for an hour in a given year during the period 1999–2002 within the breeding period. These represent a high quality, highly standardised independent data set, with a homogenous spatial cover and large sample of 3,077 1-km squares (approximately 9 % of the total area). Sampled squares were stratified over the main habitat types within each 10-km UTM squares (Hirzel and Guisan 2002).

Atlas data was used as an independent standard reference to be compared with results obtained from the other data sets. However, atlas data can be affected by the non-detection of species that are actually present (see e.g., Kery et al. 2010; McCarthy et al. 2012). Furthermore, the atlas data were collected in 1999–2002, while volunteer data were collected in 2009–2010. Although non-detection of presences during atlas sampling and species distribution changes over one decade may occur, we always compared monitoring data from the same period of the year with the best available and most standardized method (ATLAS). Possible non-detected presences and/or changes occurred in the last decade would be the same for all comparisons.

Data treatments

QUALITY TREATMENT

Here we used data sets of increasing quality, quantified according to the amount of standardisation required for data collection. Standardisation in data collection is translated according to information on sampled area and sampling effort therefore allowing modelling to account for spatial and temporal variability in bird data. In our case this gradient ranges from low quality

opportunistic observational data (OBS, LISTS) and coarse scale data (COARSE) to data from standardised monitoring (BBS). Our final treatments were: species opportunistic observations (OBS, presence-only data, 1-km), opportunistic collection of species lists (LISTS, presence-absence data, low standardisation, 1-km), breeding bird survey (BBS, presence-absence data, high standardisation, 1-km), coarse combined information at 10-km (COARSE, presence data, low standardisation).

In the different monitoring methods used, information was not collected uniformly within each 1-km square. In the case of LIST and BBS the accumulated time expended in each 1-km square was used as an estimate of sampling effort. Sampling effort was therefore included as an independent variable in final models. The resulting models were projected to the whole study area using common values of 43 min for all pixels (average time expended in BBS sections). In OBS there was no information available on the sampling time and therefore this variable was not used in the model calibration.

In spite of the difficulties in comparing sampling effort between the different methods, the similar number of total records for the total number of species analysed suggest that treatments containing all available data were comparable (Table VI.1).

Table VI.1. Information regarding data included in species distribution modelling and percentage of uncommon species detected according to each monitoring scheme.

	OBS	LIST	BBS	ATLAS
Total data	5472	7223	5621	18520
Total sample units	5472	1337	576	2731
% uncommon species	21.9	13.9	11.3	12.5

QUANTITY TREATMENT

We used subsets of the overall data sets for each monitoring program to simulate limited data availability and therefore assess the impact of data shortage in mapping species distributions. In the case of BBS, sample size was selected according to the percentage of sections (5, 10, 25, 50 and 100 % of the total 1-km sections sampled). With regard to web collected bird data (OBS and LIST), the thresholds (5, 10, 25, 50 and 100 %) were randomly applied across the whole data-base including all the species. With this treatment, we expect that uncommon species would be less represented or even missing when using a small percentage of the data set.

Environmental predictors

Environmental predictors for model training included a set of 27 explanatory variables circumscribed to Catalonia including climate (6), topography (5) and land-cover (17). All variables were re-sampled from their original spatial resolution to 1-km UTM grid cells. Climate predictors included mean annual temperature, mean minimum temperature for the coldest month (January), mean maximum temperature for the hottest month (July), annual precipitation, summer precipitation and annual solar radiation, from the Digital Climatic Atlas of Catalonia (180 m resolution) (Pons 1996; Ninyerola et al. 2005) from a climatic standardized series of 48 years (1951–1999). Topographic predictors included mean altitude, mean slope, standard deviation of slope and proportion of sunny surface, derived from a digital elevation model (10 m resolution) generated by the Cartographic Institute of Catalonia from topographic 1:50,000 maps. Land-cover predictors were derived from the Cartographic Institute of Catalonia classification of 2002 Landsat-TM remote sensing imagery (Viñas and Baulies 1995) (30 m resolution) (available from the web of the Department of the Environment and Housing of Catalonia). From the 22 original classes, we defined 17 variables as the percentage of each land-cover class within each individual 1-km UTM grid cell. Our classification comprised: coniferous, deciduous and sclerophyllous forests, shrub lands, alpine grasslands, sandy areas, bare ground, wetlands, continental and marine waters, snowdrifts, dry and irrigated herbaceous and woody crops, vineyards and built-up areas (urban areas, industrial areas and infrastructures). Regarding the definition of land-cover classes, we adopted the categories given from the Land-cover map, grouping the three categories of artificial surfaces into one single category (built-up areas).

Species distribution modelling

We used Maxent to develop SDMs. Maxent is a general-purpose method for making predictions from incomplete information based on the maximum entropy principle. This approach assumes that the best approximation to an unknown probability distribution is to ensure that it satisfies any constraints that we are aware of (Phillips and Dudik 2004; Phillips et al. 2006). Generally applied to presence-only species distribution modelling, the idea is to estimate the distribution of a species as a probability distribution across a study region, subject to the constraints that each expected predictor variable has to match its empirical average over the presence sites. Of all the probability distributions that meet these constraints, Maxent chooses the most unconstrained one, i.e. the one of maximum entropy (Phillips and Dudik 2008).

Following Elith et al. (2010), we applied the method to both presence-only (OBS, COARSE) and presence–absence data (LIST, BBS and ATLAS) by using different protocols for the Maxent algorithm. In the case of presence-only data, we applied the standard Maxent protocol in which the whole study area (i.e. Catalonia) is used to sample for absences, so that the background model includes all sites with no information. On the other hand, in the case of presence–absence data, we restricted model calibration to sampled areas where there is information on presences and absences, so that the background model includes areas with absences or species not detected. Importantly ‘absences’ are more likely to represent true absences in the ATLAS, where there was greater survey effort and imperfect detection less likely. Imperfect detection is most likely to be an issue for LIST with short sampling sessions. To avoid bias in predictions as a result of low quality samples, when modelling from BBS and LIST, we trained models with the environmental background area restricted to 1-km UTM squares surveyed (Phillips and Dudik 2008; Phillips et al. 2009). This forces the algorithm to select background information only from sampled areas (either leading to species presence or not). In these cases, Maxent approach is roughly comparable to the one employed in logistic regression (Elith et al. 2010).

In some cases, with reduced sample sizes, some species showed less than five occurrences. In those cases models were not run. Even when modelling some species distributions with larger sample sizes, some model predictions were equivalent to random predictions (Table VI.2). In the case of uncommon species, a higher number of models could be run from data from low standardization programs than from more standardized programmes. When modelling uncommon species from BBS some models with 5 % of the total sample size could not be run or their distributions did not overlap with the atlas distribution. In these cases results did not show omission or commission errors.

Table VI.2. Number of species distribution models that could not be run due to small sample size or which predictions were equal or worse than a random prediction. Values are shown for quantity treatment (sample size), quality treatment (OBS, LIST, BBS) and for common (C) and uncommon (U) species.

Sample size	OBS		LIST		BBS	
	C	U	C	U	C	U
5	2	9	1	9	2	13
10	0	2	0	7	0	9
25	0	0	0	2	0	4

50	0	0	0	0	0	2
100	0	0	0	0	0	0

Evaluation of SDMs

We used 10 fold-cross validation strategy AUC statistics (Pearce and Ferrier 2000) on independent fine grained Atlas data as a measure to identify the predictive power of all different treatments. After testing for normality, paired sample t tests were applied to compare AUC results obtained for each species between treatments.

We used a second evaluation procedure to check SDMs performance in which we assessed the degree to which species distribution obtained with the developed models matched those obtained in our independent species distribution model references (ATLAS). Here we assessed the overlap of resulting species maps between treatments (OBS, LIST, BBS and COARSE) and reference models (ATLAS). Different methods can be applied to select thresholds of occurrence in the prediction of species distributions (Liu et al. 2005). In this case we applied a zoning protocol (Herrando et al. 2011) aimed at categorising species distribution in areas of increasing environmental quality based on predefined thresholds. First, we searched for an environmental quality threshold that defined the distribution of the species (hereafter species distribution), below which the absence areas for species defined corresponds to the average tenth percentile of the data used for developing the models (i.e. 10 % of the data with the lowest suitability). A second threshold was applied to identify areas above the mean environment quality of the species within its distribution (Pearson et al. 2007). This protocol allowed us to derive ecologically sound and simple representations of species models as the area within the species distribution where environment suitability was above average (hereafter high quality areas).

We then calculated the overlap between species high quality areas for each species, obtained from each monitoring method and the corresponding reference model from the ATLAS to assess the degree to which a given model differed from our reference. Thus, it allowed us to calculate the percent omission and commission errors (Feeley and Silman 2011; Sardà-Palomera and Vieites 2011).

Beyond the overall predictive statistics obtained in the first evaluation exercises, overlap measures allow a more focused and direct evaluation of how far from our best available reference, the identification of suitable sites for the species derived from our different treatment models fell.

Species richness

Using the species distribution and high quality areas identified we calculated, for each pixel of our study area, the number of species for which species distribution and high quality area could be found. The number of species present in each square for each quality and quantity treatment was determined, thus, identifying and mapping farmland bird hotspots in Catalonia. We applied Spearman correlations to calculate the correlation between richness for each quality and quantity treatment with the actual richness, observed in the 3,077 1 km squares where the ATLAS data have been collected.

Results

Total amount of data collected by each of the three monitoring methods used in our study was roughly comparable. However, a first look at the type of data sources offers light on the type of info contained. OBS seem to have a disproportionate focus on uncommon species compared to the other data sources (Table VI.1). LIST and BBS data have similar ratios therefore suggesting that these methods sample species proportionally to their abundance in the area.

General patterns in model accuracy across types of data

Model performance varied across the different data treatments for model training: quality and quantity. AUC generally increased with sample size for all monitoring methods (Fig. VI.1). BBS tended to result in higher AUC when modelling with the complete data set. This is especially relevant when comparing results obtained when including common species only. Models with highest AUC were obtained from BBS, while data from web based monitoring in general gave similar results in the case of both opportunistic or lists data types. COARSE always showed a lower AUC mean than BBS with the complete data set (Fig. VI.1). Apart from ATLAS based models, the maximum AUC values were obtained from BBS when modelling uncommon species with the complete data set. However for common species, LIST using all available data (mean AUC = 0.70) performed better than OBS (mean AUC = 0.67) (t test for paired samples: $t_{14} = -3.26$, $p = 0.005$). When modelling common species models obtained from COARSE (mean AUC = 0.74) were more accurate than from LIST from the complete data set (t test for paired samples: $t_{14} = -3.26$, $p = 0.002$). When modelling uncommon species, all quality treatments showed similar results. Models for uncommon species tended to show higher AUC standard errors (Fig. VI.1).

The percentage of overlap with atlas was highest with high quality areas from COARSE in all cases (Fig. VI.2). In general, models from different monitoring programs showed similar overlapping ranges. However, BBS showed higher predictive model accuracy for common species modelling, followed by LIST, while for uncommon species OBS with the whole sample size showed the highest overlap. Models from uncommon species showed higher standard errors in all cases (Fig. VI.2).

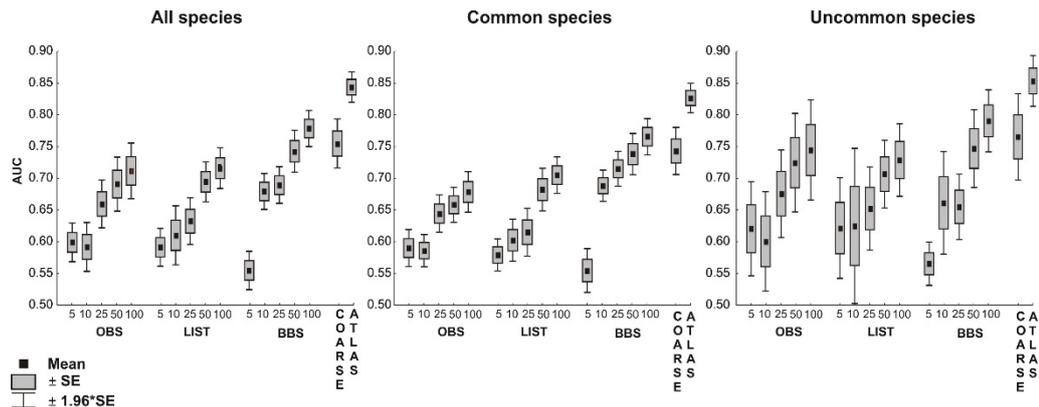


Figure VI.1. Species distribution models mean AUC, boxplot, mean, standard error and confidence interval. Results are shown across different sample size percentage for each quality treatment (OBS, LIST, BBS) and for all the species, for common and uncommon species.

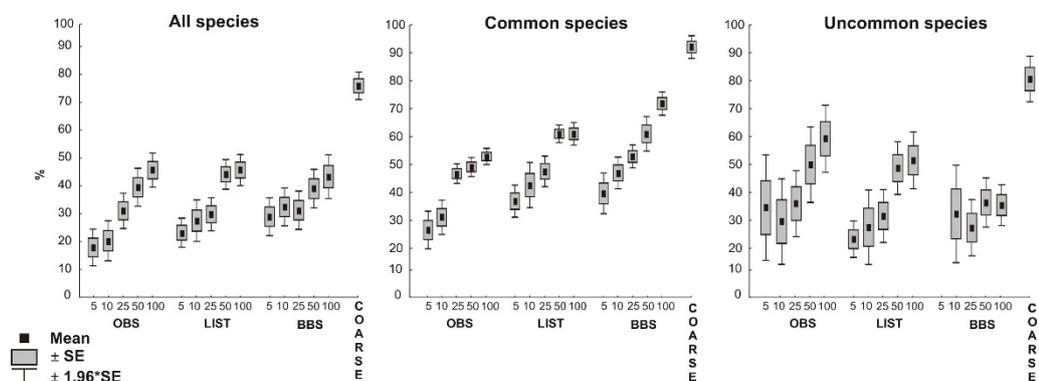


Figure VI.2 Species high quality areas mean percent overlap, standard error and confidence interval. Results are shown across different sample size percentage for each quality treatment (OBS, LIST, BBS) for all the species, for common and uncommon species.

An inverse pattern was shown in the percentage of omission (Fig. VI.3), which decreased with sample size. Models from COARSE always showed less omission errors. With regard to the different monitoring programs, when analysing all species together, there were not significant differences (t test for paired samples $p[0.05]$). In the case of common species, however, models from

BBS using the complete data set showed less omission errors, on contrary models from OBS showed higher omission. However omission for uncommon species showed a different pattern, as OBS and LIST showed less omission than BBS when modelling from higher sample sizes (50 and 100 %). When modelling uncommon species from BBS, data omission did not decrease when increasing sample size (Fig. VI.3).

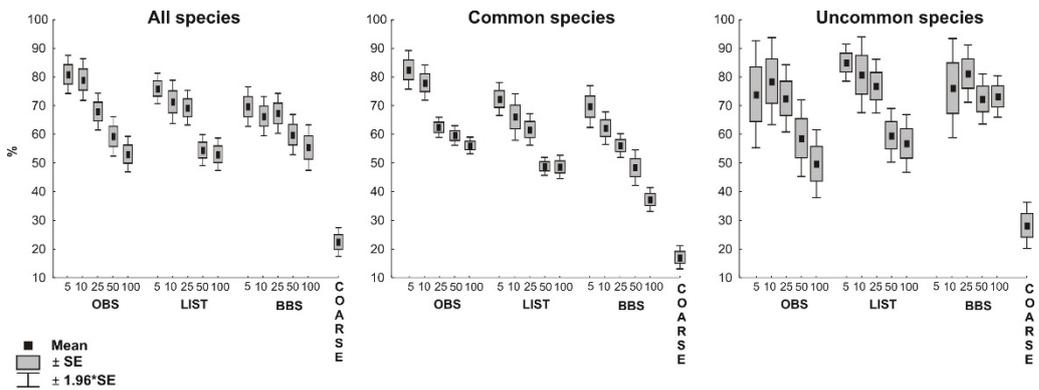


Figure VI.3. Species high quality areas mean percent omission, standard error and confidence interval. Results are shown across different sample size percentage for each quality treatment (OBS, LIST, BBS) for all the species, for common and uncommon species.

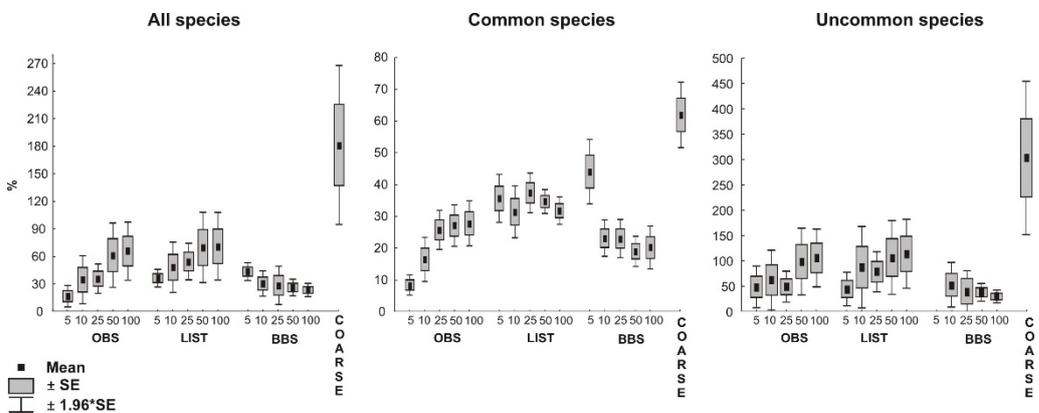


Figure VI.4. Species high quality areas mean percent commission, standard error and confidence interval. Results are shown across different sample size percentage for each quality treatment (OBS, LIST, BBS) for all the species, for common and uncommon species.

In the case of commission errors, COARSE showed the highest values when comparing with the other treatments, and especially when modelling uncommon species (Fig. VI.4). They also showed the highest standard errors and confidence intervals, thus they were less predictable. When taking into account all the species, models from BBS data showed lower commission when modelling from bigger sample sizes, both for common and uncommon species.

Models from OBS with small sample size showed the lower commission for common species (Fig. VI.4). In general, models showed higher commission when modelling common than uncommon species.

Species richness

Most of the species richness maps derived from different quality and quantity treatments were significantly correlated with species richness predictions from ATLAS data (Table VI.3). From a sample size of 10 % presences, predictions from BBS showed the highest agreements, showing the highest correlation when the complete data set was used. On the other hand, when modelling from five presences, models derived from opportunistic observations showed the highest correlation with ATLAS data (Table VI.3). In most of the cases, richness obtained from species distributions showed higher agreement with ATLAS data than richness obtained from high quality areas.

When predicting richness from species distributions all quality treatments over predicted the number of species detected during ATLAS data collection. BBS was the monitoring method that showed a richness prediction closer to ATLAS richness, while predictions from OBS and LIST showed a similar pattern but with a higher over prediction than BBS (Figs. VI.5, VI.6). When predicting from high quality areas, predictions from BBS were very close to ATLAS richness with a slight overestimation in areas with few species but with a very high concordance in richest areas. OBS and LIST also followed a very similar pattern, tending to increase underestimation in richer areas. Finally, model predictions from downscaled data showed the highest overestimation when predicting species richness both from species distribution and from high quality areas (Figs. VI.5, VI.6).

Table VI.3. R values for Spearman correlation when comparing species richness predictions from models obtained from different quality treatments (OBS, LIST, BBS and COARSE) with species richness obtained from atlas data. Results are shown for different sample size models (quantity treatment) and for species distribution (SD) and high quality (HQ) areas. NS non-significant at $p < 0.05$.

	Quantity treatment									
	5		10		25		50		100	
	SD	HQ	SD	HQ	SD	HQ	SD	HQ	SD	HQ
OBS	0.37	0.38	0.27	0.32	0.49	0.44	0.51	0.42	0.53	0.41
LIST	0.27	0.16	0.40	0.38	0.47	0.24	0.53	0.53	0.61	0.57
BBS	0.04	NS	0.56	0.40	0.65	0.56	0.66	0.62	0.67	0.66
COARSE	-	-	-	-	-	-	-	-	0.66	0.63

Accuracy patterns across species abundance

Model predictive accuracy throughout the species abundance in the region was also analysed. Only AUC values from OBS based models were negatively correlated with the number of presences per species (Spearman's $R = -0.39$, $p < 0.05$). Thus, the difference between ATLAS and OBS based models accuracy significantly increased along the uncommon to common species gradient (Spearman's $R = 0.47$, $p < 0.01$) (Fig. VI.7). The five most uncommon species showed the highest predictive power independent of data quality treatment used (Fig. VI.7).

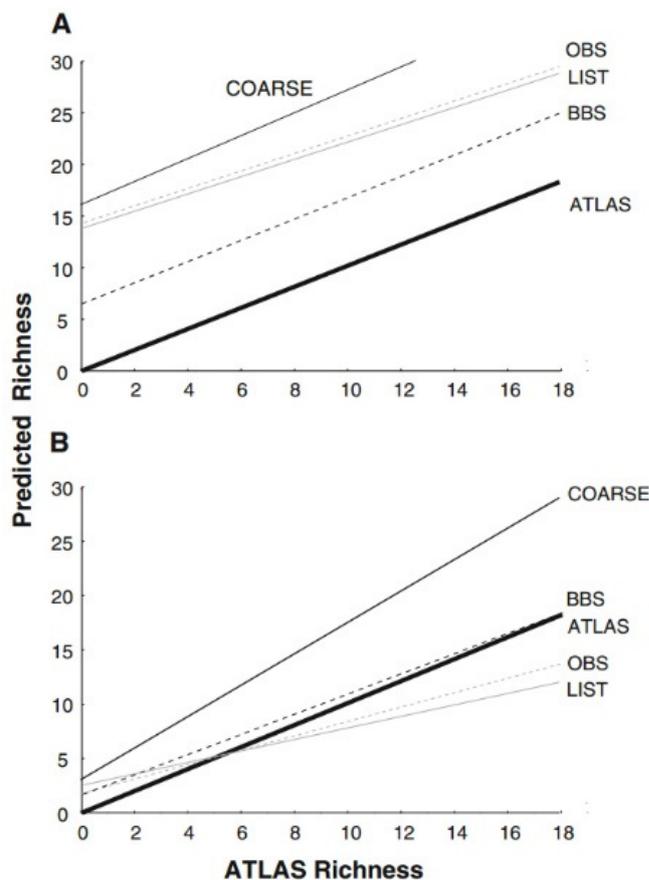


Figure VI.5. Quantitative estimates of richness from each monitoring method correlated with richness from atlas data ($N = 3077$). Results are shown for ATLAS (thick black solid line), COARSE (thin black solid line), LIST (thin grey solid line), OBS (grey broken line) and BBS (black broken line), and for (A) species distribution area, and (B) high quality areas. Results are shown only for full sample size models.

Discussion

Data standardisation and quality

Models from monitoring breeding bird surveys showed the best results for modelling common species. This supports the results obtained by Brotons et al. (2007), which show that long term monitoring programs have the potential for being a source of good quality data for species distribution modelling. However, we have further increased our assessment of the potential of emergent monitoring programs based on the collection of opportunistic observations to derive useful distribution information. This information has the potential to deliver relevant insights into the distribution of species especially when no other information is available (Braunisch and Suchant 2010; Snall et al. 2011). They can be especially good for modelling uncommon species. In that case these two data sources may be relevant.

It has been previously noted that ecological characteristics of modelled species may affect model accuracy (Stockwell and Peterson 2002; Segurado and Araújo 2004) and that specialists in terms of both geographic and environmental space are easier to model than species with widespread distributions. In this study we have also shown that rarer, specialist species, may not require complex monitoring methods to obtain reliable models, providing that the sampling covers the environmental conditions used by the species. Keeping in mind that a highest predictive power (estimated through AUC) of rare species is probably related to how the AUC is calculated for presence-only models (Phillips et al. 2006), in our case, models for those species obtained highest accuracies independent of the monitoring and validation method.

How much quality data is enough?

Our results show that the standardized breeding bird survey was the most accurate method for monitoring common species and, in general, an increase in sample size will result in the best performing models (Feeley and Silman 2011). This can vary depending on species specificity (Hernández et al. 2006), as in some cases models for uncommon species can reach high accuracy even with a small sample size (Stockwell and Peterson 2002). In the case of commission and omission, an increase in sample size does not necessarily decrease the error, obtaining similar results from a priori less quality monitoring data. We also note that in the case of commission, an increase in sample size did not decrease the over prediction, which in some cases can even increase (Sardà-Palomera and Vieites 2011).

The fact that an asymptote was not reached for any monitoring method suggests that maximal concordance was not achieved and will likely continue to increase with sample size until a certain point. This point may depend on the species ecological characteristics (Stockwell and Peterson 2002) or when sample size reaches the optimum for an adequate weighting of predictor variables (Feeley and Silman 2011; Sardà-Palomera and Vieites 2011). All in all, when modelling from small sample size, the predictions should be used with caution, as no algorithm will predict consistently well (Wisz et al. 2008).

More standardized methods provide the best quality data, but this comes at a cost in terms of money and man power and will normally result in a smaller sample size (Braunisch and Suchant 2010). Less standardized methods provide lower quality data but are easier to obtain, thus allowing ‘a posteriori’ corrections. In consequence, it will also depend on the abundance of particular species. Because uncommon species are less abundant and show smaller sample sizes, when modelling uncommon species from more standardised bird surveys, in some cases, there is not enough data to run or obtain reliable models.

Data integration across scales

Understanding environmental limitations of species distributions modelling across scales is essential to develop useful applications of SDMs that can provide reliable predictions of species distributions (Witte et al. 2008). Modelling species distributions across scales could become important in complementing information from different programs, in particular for uncommon species, so that the best use of available information is made. In this context, we have evaluated the usefulness of aggregated information at a coarse scale to subsequently downscale SDMs. While the statistics and models appeared generally good, these models tended to over predict species distribution (Araújo et al. 2005). Presence-only models show higher over prediction compared with presence-absence models (Brotons et al. 2004b). This is probably the reason that model predictions based on opportunistic observations show broader distributions than those based on lists and breeding bird survey data.

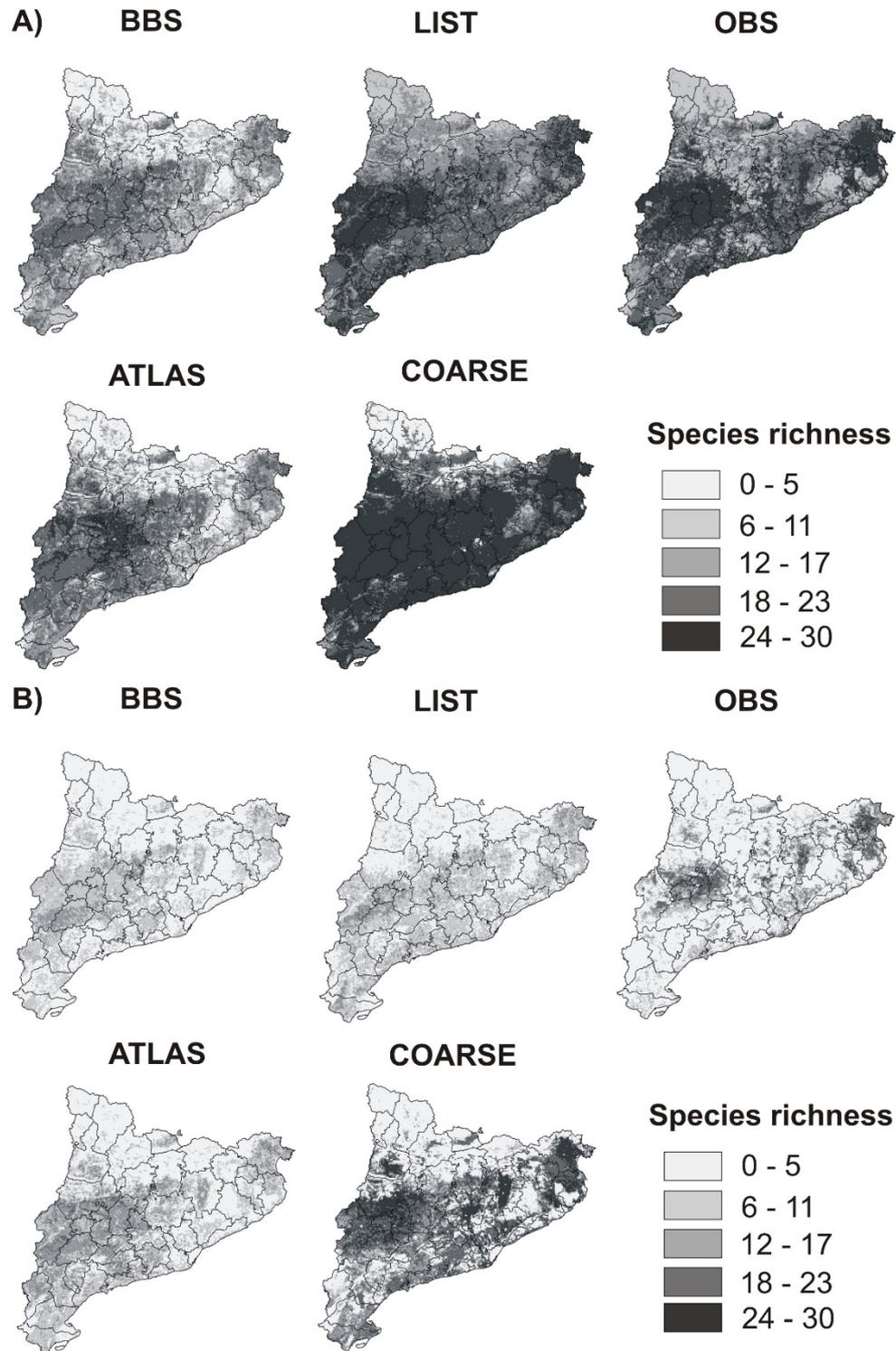


Figure VI.6. Predictions of farmland bird species richness in Catalonia obtained from different quality treatments (ATLAS, BBS, LIST, OBS and COARSE) with the whole sample size. Maps are show for (A) species distribution area, and (B) high quality areas.

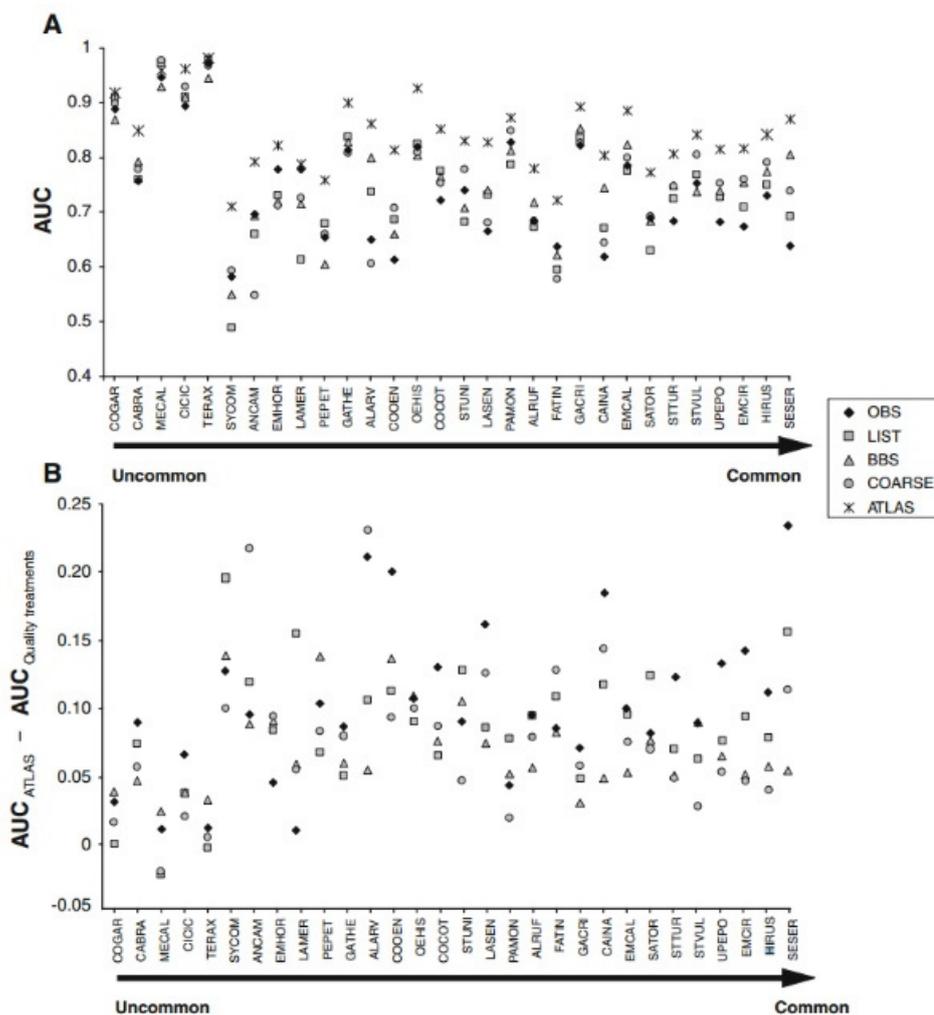


Figure VI.7. (A) Species distribution models mean AUC values for each species and quality treatment and (B) mean AUC difference between quality treatments and ATLAS. Values are shown for models built with a sample size of 100% occurrences. Farmland species are sorted according to the total number of occurrences in ATLAS (from uncommon to common).

Applications for species conservation

Different treatments have different implications for predicting hotspots and detecting areas of conservation priority. Richness predictions from BBS were closer to richness predicted from the atlas data, while predictions from OBS, LIST and COARSE were less accurate. However, in all cases predictions of high quality habitat areas were less accurate than predictions of species distributions, suggesting that high quality data is needed to accurately identify hotspots.

In general, models with higher accuracy (i.e.: AUC values) are desirable. However, as estimates through AUC can be related to how the AUC is calculated (Phillips et al. 2006; Lobo et al. 2008) in some cases omission and commission errors can give more information about the suitability of a certain model than AUC values. For example, when designing nature protection areas, misclassifications of commission must be regarded as a more serious drawback than the opposite, while low omission is desirable when searching for new species or populations (see Peterson 2006). Models from data aggregated at a coarse scale resulted in maps with the highest over prediction.

In a conservation framework, over prediction can be interpreted in the light that models derived from this source of information, while adequate in some cases, may be too conservative in identifying too many good areas for species. When the aim is to protect uncommon or endangered species, overestimating areas of potentially elevated biodiversity might be preferable than underestimating their existence (Zaniewski et al. 2002). On the other hand, over prediction of the range of species can lead to erroneously conclude that there are larger and more suitable areas for that species, and therefore no need for conservation action. Thus, downscaling of species distribution through modelling may be a useful approach for areas with scarce or heterogeneous information, and also when integrating different quality data from different regions or countries across scales. However, special attention should be paid to correct the over prediction generated from these models, and downscaled occupancies should be interpreted cautiously (Witte et al. 2008).

We must stress that any monitoring scheme involves some losses and gains of information and only a professional standardized (in terms of effort and spatial cover) project, could obtain optimal results (Engel and Voshell 2002). However, the cost of this kind of project is not always affordable whereas the acquisition of big amounts of data from simple volunteer, opportunistic monitoring schemes is relatively easy and inexpensive.

Conclusions

In general, an increase in sample size will give more accurate distribution models regardless of the monitoring source, indicating that data availability will likely constrain the predictive accuracy of species distribution modelling applications. However, in some cases models based on more standardized methods can provide the same accuracy with smaller sample size than models based on opportunistic data with bigger data sets. This leads to a trade-off between data quality and data collection costs, suggesting that in cases in which good quality data is available the use of this information for developing SDMs

should be prioritised, since for comparable sample sizes information derived from carefully designed surveys appear to be more suitable for deriving species distribution maps than information derived from opportunistic data sources. We have also shown that opportunistic data sources may offer relatively good approximations especially in the case of predicting the distribution of uncommon species. In that case, opportunistic data gives similar accuracy and even a higher overlap with the real distribution than a more standardized survey. Also in that case, opportunistic data gives fewer omission errors but with higher commission. When modelling uncommon species or with very narrow ecological niches all monitoring methods show high accuracy.

Aggregation of heterogeneous data at a coarse scale and downscaling to a targeted spatial scale generated maps which tended to over predict species distributions. Thus, although downscaling of data through a SDM approach appears useful in cases of data shortage or when data availability strongly differs in quality characteristics, it must be used with caution because will tend to overestimate species suitable habitats.

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Discussion⁹

Mathematical models are paramount tools to analyse complex systems, test hypotheses and evaluate alternatives. This fact is clear by its affiliation to disciplines as diverse as economics, medicine and climatology, among many other disciplines including ecology. In ecology there is a huge and growing variety of models to face an increasing number of questions from various research fields (energy flow, population dynamics, species interactions, etc.). In this context, SDM are designed to analyse species-environment relationships, a core issue in autoecology. But beyond the relevance of SDM as a research tool, there is a broad consensus on SDM potential application in a wide variety of conservation topics. Undeniably, *where conservation should be done?* is a key question to design effective strategies for sustainable management of populations, species and ecosystems. SDM allow to answer that question, even when lacking important species information, but also express modeling outcomes in spatially explicit terms, closest to those used in conservation planning and management, favouring its implementation as a decision support tool. Indeed, progress towards more structured decision-making processes represent a strong incentive for the spread of SDM to inform conservation practice (Addison et al., 2013). Structured decision-making framework, based on the definition of clear objectives agreed on participatory processes, promotes the use of a wide range of analytical tools to provide rigorous, transparent and logical solutions. In this context, SDM are able to inform and enrich different steps of the decision-making processes (Figure 3).

⁹ This chapter translate the original discussion written in catalan (**see Appendix**).

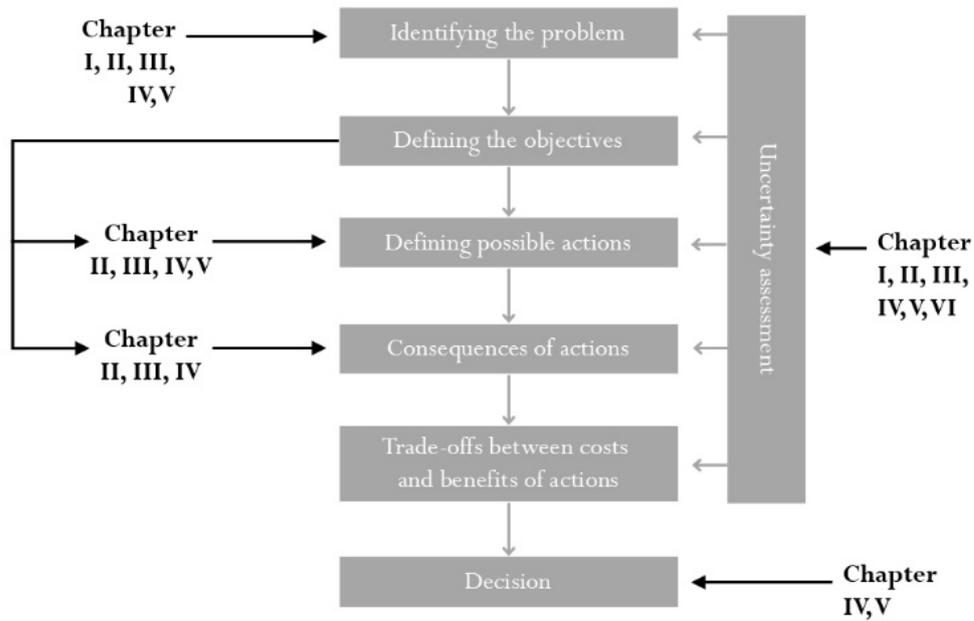


Figure 3. A structured decision-making process (Gregory et al. 2012) with indication of main SDM contributions from that Thesis. Adapted from Guisan et al. (2013).

Identifying conservation problems

Comprehensive knowledge of species current distribution offers a first diagnosis of main conservation problems. The improvement of this knowledge has been a central issue in environmental policies and biodiversity atlases have become key conservation tools. In addition to synthesizing knowledge about relevant biological issues (e.g. ecology, population estimates, threats, trends, etc.), atlases have traditionally focused to inform species distribution in uniform and standardized maps, but with too coarse resolution (10x10 km) in relation to conservation decision-making scales. This shortcoming has been overcome in the 2nd generation atlases, which have taken advantage from SDM and geostatistics to produce species distribution or abundance maps with higher resolution (1x1 km or lower), based on surveys specifically designed at local spatial scales. Bird atlases are pioneers in the use of these techniques (e.g. UK: Gibbons et al., 1993; Switzerland: Schmid et al., 1998; Catalonia: Estrada et al., 2004) and provide good examples of potential applications in conservation (e.g. in Catalonia Brotons et al., 2004; Gil-Tena et al., 2010; Herrando et al., 2009; Vallecillo et al., 2008) (Chap. V). However, this leap forward points out one of the weaknesses of 2nd generation atlases, i.e. the difficulty to fund specific surveys in a context of scarce economic resources. Cost savings in data collection implies using alternative sources of information, e.g. volunteers, specific studies or monitoring programs. These savings,

however, can have a significant impact on data quality and SDM reliability (Chap. VI). Among these alternatives, monitoring programs, relying on regularly repeated surveys where relative abundances of different species are registered, are those that best fit minimum data quality requirements. Again, birds are the most advantaged group, with established monitoring programs around the world with a demonstrated potential to provide large amounts of spatial data to improve SDM in an atlas framework, but also to develop SDM showing changes in distribution and abundance of species (Brotons et al., 2007; Jiguet et al., 2005) (Chap. I, IV & VI). In that case, gradual convergence of objectives between the atlas and monitoring programs will soon provide substantial improvements in terms of spatial but also temporal resolution (current distributions of species in shorter time intervals) of SDM, thereby favouring the knowledge improvement of short and mid-term distribution trends, as well as migratory patterns, so far partially considered in conservation strategies (EBP-partnership and EBCC, 2015; Price et al., 1995) .

Beyond improving knowledge of the current species distribution (Chap. I), SDM ability to examine species response to new past (Chap. II) and future (Chap. III) environmental conditions opens new horizons in analysis and diagnosis of species conservation problems. The increasing amounts of available information about past and future environmental features enables to build predictions about hypothetical distribution of species in places and times where there is no original data, and provides a powerful tool to examine scenarios and test ecological hypotheses. Furthermore, when these scenarios are based on key environmental factors related to species persistence, SDM become well suited tools to analyse specific conservation problems. Thus, SDM have been widely used to assess conservation implications of future changes in species distributions due to global warming (Araujo et al., 2004; Richardson et al., 2010) (Chap. III), landscape changes (Brotons et al., 2011; Gil-Tena et al., 2016; Regos et al., 2015), and impacts of invasive species (Roura-Pascual et al., 2004; Thuillier et al., 2005) (Chap. III), among others. The lack of examples of extrapolations to past environmental conditions does not mean that they are less interesting. In addition to assess impacts of historical trajectories of landscape and climate on species (Améztegui et al., 2010; Kharouba et al., 2009; Vallecillo et al., 2009) (Chap. II), retrospective extrapolations are valuable tools to establish baseline conditions of historical species distribution (*where we come from?*) and, therefore, inform more consistent assessments of the actual extent of conservation problems (Clavero and Delibes, 2013; Clavero and Villero, 2014; Lotze and Worm, 2009) (Chap. II).

Assigning objectives, defining alternative actions and predicting consequences

The definition of conservation objectives is the result of a consensus of key stakeholders of the decision-making process (Chap. IV & V). In this process, SDM can be used to ensure that decision goals are realistic, taking into account the factors that determine species current, historical or future distributions. For example, SDM can be used to establish conservation priorities based on the relative importance of the distribution within and outside protected areas (Chap. IV & V), or anticipate impacts in different management scenarios (e.g. historical trajectories landscape, Chap. II; future impacts of invasive species, Chap. III; or securing habitat corridors connecting isolated populations, Chap. V). Ideally, these scenarios may be reviewed and, if necessary, redefined based on updated information within an adaptive management framework (Runge, 2011).

SDM can also contribute to define alternative conservation actions, examining a variety of alternatives aimed to conciliate conservation targets with economic (budget), logistic (e.g. staff available, accessibility, etc.) and social (conflicts of interest between the parties concerned, e.g. access to public aid) issues, determining the viability of proposed actions. Some good examples are the delimitation of candidate sites to be included in protected areas (Chap. IV) or the allocation of environmental payments (Chap. V).

Finally, SDM extrapolation to scenarios of changing climate or landscape allows to anticipate consequences of different conservation actions in terms of distribution (Chap. II) or habitat suitability (Chap. III) changes. One of the most prolific fields of application of SDM in conservation is the evaluation of the efficiency of protected areas facing the challenges posed by climate warming (Araujo et al., 2004; Hannah et al., 2007; Maiorano et al., 2013) (Chap. II, III & IV). In these applications, SDM aid trade-off analyses of alternative conservation actions, such as prioritize environmental management actions to conserve protected forest bird species (Chap. II), or optimize the control of invasive species in both geographic and temporal dimension (Chap. III).

Assessing uncertainties

All steps of the decision-making processes have implicit degrees of uncertainty: from the correct identification of the conservation problem, through the definition of realistic objectives and feasible actions, the proper assessment of the consequences and the accurate trade-off analysis, until the degree of success of the final decision (Burgman et al., 2005). A part of this

uncertainty stems from the complexity of the decision-making processes (e.g. uncertainty about whether an approved budget planned to carry out planned actions) and, although it is important to document, its control is too often out of reach of decision-makers. Moreover, there are other uncertainty sources related to practical issues within the decision context (e.g. calendar, human resources, available information, etc.), which can be evaluated in order to identify critical points to reduce uncertainty and to improve the decision outcomes (Ludwig et al., 2001).

Uncertainty measurement is a key aspect in any model development and SDM contributions at different decision-making key steps can be complemented with explicit uncertainty assessments (Barry and Elith, 2006; Pearson et al. 2006), e.g. in terms of predictions accuracy (Chap. I, II, III, IV & V) and their temporal short and long-term stability (Chap. I, II, III, IV & V). The estimation of the uncertainty in SDM has implications at different modelling steps (i.e. quality of biological and environmental information, suitability of modeling methods and evaluation of model outcomes) and can be measured on the basis of objective criteria, such model accuracy calculations based on threshold-dependent (commission and omission errors, prevalence, kappa, etc.) or threshold-independent (AUC, correlations, etc.) measures, but also using subjective criteria, based on the credibility of predictions (e.g. model acceptance) or expertise (e.g. consistency of specie/predictors response curves) (Rykiel, 1996).

Many scientific publications have stated the contrasted predictive ability and robustness of SDM based on different mathematical algorithms, as well as the high accuracy of the predictions derived (e.g. Elith et al., 2006; Franklin , 2009). A common characteristic of the best techniques identified in these studies is that they are based on high quality biological information, which can only be obtained in the framework of surveys specifically designed to record species presence-absence or abundance across stratified environmental and geographic ranges. However, the excellent analytical capabilities of these methods become also the main obstacle when they are applied to solve real conservation problems, in which biological information available is often incomplete and offers serious taxonomic, temporal and geographic biases, even for the most well-known vertebrate groups (Reddy and Dávalos 2003) (Chap. V & VI). Hence, in a context of increasing availability of environmental information, SDM conservation applications have benefited from modelling techniques based on presence-only data, which usually offer a better balance between the quality and quantity of biological data required and the strength of its predictive ability (Elith and Leathwick, 2007; Pearce and Boyce, 2006) (Chap. I, II, IV, VI & VI). In the academic ecological research, the widespread

use of some of these techniques (e.g. Maxent and GARP) has stimulated a debate that has contributed positively to broadening the knowledge to optimize their use and adapt it to the limitations of the available biological information, e.g. lack of information, heterogeneous information sources, and spatial and environmental biases (Anderson and Gonzalez Jr., 2011; Fourcade et al., 2014; Kramer-Schadt et al., 2013; Merow et al., 2013; Phillips et al., 2009; Syfert et al., 2013; Warren and Seifert, 2011; Wisz et al., 2008; Yackulic et al., 2013) (Chap. V & VI).

Species information sources are a decisive factor of uncertainty in SDM conservation applications. Many studies indicate that the increase in the sample size results in greater accuracy of predictions (Pearce and Ferrier, 2000; Wisz et al., 2008) (Chap. VI). However, SDM based on large volumes of opportunistic low-quality data offer similar degrees of accuracy than predictions based on standardized surveys with lower sample sizes (Chap. VI). Moreover, opportunistic data also provide good predictions when dealing with rare species, poorly represented in standardized surveys (Chap. VI). Thus, even in favourable contexts with different information sources available, criteria for selecting the most suitable species data to develop SDM should consider species ecology, sample sizes and surveying methods (Chap. I).

The importance of species information sources goes beyond its role as response variables in the SDM calibration process, also playing a key role in measuring model accuracy to assess whether it meets minimum requirements for proper application (Rykiel, 1996). Although ideally the assessment of SDM accuracy should be based on independent datasets from that used in the SDM development (Guisan and Zimmermann, 2000), there are several strategies to evaluate predictions based on data subsets excluded from the calibration process (e.g. subsampling, cross-validation and bootstrapping). Systematic and repeated use of these strategies allows for robust measures of SDM accuracy and estimates of uncertainty based on the results compiled in different replicates. Depending on the volume and type of biological information available, these designs can be adapted to respond to specific objectives set out in the decision-making process, going from a basic definition of different subsets of data to validate the accuracy of SDM outcomes (Chap. I, II & V) to more complex schemes that integrate heterogeneous information sources (e.g. assessing pelagic seabirds predictions with data from different years and periods to evaluate the temporal stability of protected areas, Chap. IV), or different modeling techniques (e.g. assessment of climatic suitability predictions of amphibians to examine the impact of the global warming, Chap. III).

Effective implementation in decision-making processes

Successful integration of SDM in decision-making processes necessarily entails adjusting the modelling goals to questions posed in the context of a particular conservation problem (Chap. IV & V). Decision-making processes are the confluence of different stakeholders with competing interests, and researchers have a specific role of translating SDM matching decision goals and constraints (timeline, budget, species information, uncertainty, etc.). But this adjustment is only possible to the extent that researchers are aware of the complexity of the conservation problem and actively involved in the decision-making process to the better fit decision goals (Chap. IV). At this point there is one of the main obstacles to more effective implementation of SDM in solving conservation problems, based on the difficulties of reconciling research activities and conservation practice (Chap. V). For researchers, the adaptation to constraints of decision-making processes often represent an additional cost in terms of mobilization of personnel and resources, and changes in roles and routines of research groups, exacerbated by the absence of impact on the performance of research indicators. An alternative to strengthen these shortcomings is to promote research groups aimed at developing specific methods and applications to fill the gaps between research and conservation practice. This option seems the most profitable in the medium and long-term, in a context of increasingly less room to address urgent and complex conservation problems (Chap. V)

However, to promote the use of SDM outcomes it is also necessary that key stakeholders involved in decision-making processes clearly understand SDM contributions (Chap. V). Reporting models following good practices is a good starting point for more comprehensive and transparent spatial products. But despite there is a general consensus on which elements need to be addressed in good modelling practices, they are widely ignored due to the lack of incentives for modellers to follow good practices, and the use of inconsistent terminologies regarding the elements and issues of the modelling process (Schmolke et al., 2010; Soberon, 2004).

The follow best practices in SDM documentation is a good starting point for the most complete and transparent spatial products. But although there is a broad consensus on the elements that should be documented to achieve the minimum requirements of information, they are systematically ignored due to lack of incentives for researchers to follow best practices or by the use of inconsistent terminology and too cumbersome to describe the elements included in the modeling process (Schmolke et al., 2010; Soberon, 2004). In addition, clear documentation is not enough for mainstreaming modelling

results if not accompanied by user-useful and user-friendly spatial products (Chap. V). The development of valuable products should be based on information needs expressed in the decision context, and therefore requires an active and direct communication with decision-makers from the early stages of the decision-making process. Thus, products for spatial decision making can operate as the roller chain to ensure feedback between the decision-making process and the modelling framework, and to enhance communication channels for gaining complicity with practitioners and other targeted audiences (Chap. V).

Conclusions¹⁰

- SDM are key tools to find better solutions for a variety of conservation problems, with strong implications at various steps of decision-making process, encompassing:
 - » To identify conservation problems based on accurate knowledge of species current distribution, and also to predict both historical and future distributions in relation to climate and landscape changes.
 - » To ensure the validity of conservation objectives, taking into account environmental factors affecting species distribution.
 - » To define conservation actions and provide alternatives that allow them to reconcile conservation objectives and constraints of the decision context.
 - » To anticipate consequences of conservation actions on the basis of landscape and climate change scenarios, and also species management scenarios.
 - » To quantify uncertainty related to SDM applications and to explicitly incorporate it in decision-making processes to improve the cost/benefit analyses of alternative conservation actions.

- Effective SDM implementation in decision-making processes have to meet two necessary conditions:
 - » Adjust SDM objectives to questions posed from particular conservation problems.
 - » Promote utilisation of SDM outcomes through active communication and clear, valuable and useful information products matching specific needs of information arising from the decision context.

¹⁰ This chapter translate the original conclusions written in catalan (**see Appendix**).

Conclusions

- » These two conditions are also sufficient for an effective knowledge-transfer from other scientific developments to inform and improve conservation practice.

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Appendix

Introducció, Objectius, Discussió i Conclusions

Introducció

On cal actuar en Biologia de la conservació?

La biologia de la conservació és una disciplina orientada a la resolució de problemes urgents partint d'un coneixement parcial i esbiaixat de les espècies i dels processos ecològics afectats (Pullin, 2002). Igual que en altres disciplines de "crisi", com la medicina d'emergències o l'extinció d'incendis, els professionals implicats han de fer ús de la seva intuïció per prendre decisions i oferir solucions amb elevats graus d'incertesa (Pullin et al., 2004; Soulé, 1985). A més, la repercussió d'aquestes decisions més enllà de la conservació -per exemple, en la definició d'àrees protegides en el context de les polítiques de desenvolupament territorial, o en el control d'espècies invasores per evitar impactes en el sector primari- provoca que sovint els processos de decisió estiguin governats per fortes pressions externes relacionades amb l'agenda administrativa i política (Whittaker et al., 2005). Tanmateix, el canvi global i la pèrdua de biodiversitat plantegen reptes molt seriosos per la biologia de la conservació en el S.XXI (Brook et al., 2016; Sodhi et al., 2008; Vitousek et al., 1997), que només es poden afrontar amb suficients garanties a partir de la millora en l'acció de la conservació basada en una ciència més pràctica i més aplicada (Conveni sobre la Diversitat Biològica, 1992).

El *on*, el *quan* i el *com* actuar són qüestions fonamentals i complementàries que cal afrontar en conservació (Redford et al., 2003). *On i quan actuar?* aborden la definició de prioritats espacials i temporals, mentre que *Com actuar?* posa l'accent en desenvolupar i implementar estratègies per assolir dels objectius de conservació, ja siguin espècies, hàbitats o processos ecològics. La resposta a aquestes qüestions requereix importants inversions econòmiques, que es multipliquen quan s'amplia el focus de conservació a grups taxonòmics amb dèficits importants de coneixement. Però lluny de ser suficients, els recursos econòmics destinats a conservació no sembla que puguin arribar a créixer per cobrir totes les necessitats d'inversió (James et al., 1999). Ben al contrari, les crisis socials, econòmiques i culturals presents i futures no ofereixen unes perspectives gaire afalagadores per la biologia de la conservació. Davant l'exigüitat de recursos econòmics, els corrents crítics amb el *statu quo* de la conservació cada cop tenen més arguments per defensar la necessitat de millorar la implementació d'estratègies efectives de conservació (*Com actuar?*) enfront l'acumulació d'informació per recolzar-les (*On i quan actuar?*). La seva crítica es basa en l'evidència que l'èxit de les estratègies de conservació està més condicionada per factors socials, econòmics i polítics relacionats amb la seva

implementació, més que no pas per l'acumulació de coneixement sobre la biologia de les espècies (Knight et al., 2010). Aquest debat posa de manifest la tensió existent entre diferents enfocaments per com fer front als greus i creixents problemes de conservació que s'albiren en les properes dècades. Davant d'aquests reptes, la implementació de noves eines analítiques dins dels processos de decisió, desenvolupades en l'àmbit de la recerca ecològica, obre noves possibilitats tant per optimitzar l'ús de la informació disponible, com també per millorar l'eficiència de les accions de conservació (Sutherland et al., 2004).

La qüestió *On actuar?* ofereix bons exemples de l'impacte de noves eines en la implementació d'accions de conservació. La selecció d'àrees protegides ha estat fins no fa gaire un bon reflex de les subjectivitats en la presa de decisions (Pressey et al., 1994). Aquesta visió, però, ha començat a canviar amb el progressiu desenvolupament d'eines de planificació sistemàtica de la conservació (Bedward, M. et al., 1992; Groves et al., 2002; Jennings, 2000; Margules and Pressey, 2000), aplicades per donar suport en la definició, la localització i l'extensió de les àrees protegides, dins de processos de decisió estructurats i dinàmics basats en evidències científiques (Margules and Pressey, 2000; Wilson et al., 2007). Aquestes eines permeten optimitzar el temps i els recursos necessaris per desenvolupar estratègies de conservació més efectives, partint d'un ús més eficient de la informació sobre la distribució i la dinàmica de les espècies (Ferrier et al., 2002; Margules et al., 1994), però també d'informació sobre l'impacte i la severitat de les pressions ambientals (Pressey and Bottrill, 2008), els aspectes socials, econòmics, polítics i culturals que configuren el context dels problemes de conservació (Knight et al., 2006), i també els costos i els beneficis de diferents accions alternatives, així com les oportunitats i les limitacions per implementar-les (Cowling et al., 2008; Knight et al., 2008, 2006; Naidoo and Ricketts, 2006).

Entre aquestes noves eines, els models de distribució d'espècies han estat assenyalats pel seu gran potencial d'aplicació en conservació. Aquests mètodes, desenvolupats en el marc de la teoria del nínxol ecològic, permeten aprofundir en els factors ambientals que determinen la distribució de les espècies, i contrastar hipòtesis ecològiques i evolutives amb l'extrapolació de les prediccions en l'espai i el temps (Araújo et al., 2005; Thuiller et al., 2005). Dins l'àmbit de la conservació, les seves aplicacions no es limiten a millorar el coneixement de la distribució actual de les espècies, sinó que permeten examinar el rerefons dels processos de contracció, expansió i fragmentació dels rangs de distribució de les espècies en àmplies escales espacials i temporals (Garcia et al., 2014; Whittaker et al., 2005; Willis et al., 2007), però també a

escales reduïdes més properes a la gestió de les espècies (Richardson et al., 2010; Sebastián-González et al., 2011; Starfield, 1997).

Base teòrica dels models de distribució d'espècies

El terme *nínxol ecològic* referit al conjunt de condicions abiòtiques (temperatura, pluja, etc.) i biòtiques (competència, depredació, etc.) en què les espècies poden sobreviure i reproduir-se, va aparèixer per primer cop en la literatura científica en els treballs de Joseph Grinnell publicats a principis del S.XX (Grinnell, 1924, 1917). En paral·lel, Charles Elton (1927) va afegir un matís a aquesta definició, assenyalant que el nínxol es referia al rol de les espècies dins les comunitats ecològiques, fent èmfasi en les condicions biòtiques i en l'impacte de les espècies en la configuració de les comunitats ecològiques, i rebaixant la importància de les condicions abiòtiques. Però no va ser fins uns anys més tard que George Evelyn Hutchinson (1957) va formalitzar la teoria del nínxol ecològic, obrint les portes de l'ecologia moderna (Leibold, 1995; Vandermeer, 1972). En la seva teoria, Hutchinson diferenciava el nínxol fonamental (*fundamental niche*) -conjunt de condicions ambientals en que les espècies poden sobreviure i reproduir-se en absència d'interaccions amb altres espècies- del nínxol realitzat (*realized niche*) -conjunt de condicions en que viuen actualment les espècies, incloent les interaccions amb altres espècies (Figure 1).

Més recentment, la irrupció de la teoria unificada neutra (Hubbell, 2001) ha posat en qüestió el paper del nínxol ecològic per explicar els patrons espacials actuals de les espècies. Aquesta teoria defensa que els esdeveniments poblacionals estocàstics (i.e. natalitat, mortalitat, immigració i emigració), i no les diferències en el nínxol de les espècies, són el que determinen la composició de les comunitats a escales locals, partint de les assumpcions que totes les espècies són equivalents davant d'aquests esdeveniments poblacionals, i que totes elles tenen una capacitat de dispersió limitada (Figura 1). Aquest debat ha estat un dels focus d'atenció de la recerca ecològica des de principis del S.XXI, essent el substrat on progressivament s'ha anat consolidant una visió més holística en que ambdues teories representen els extrems oposats d'un gradient continu al llarg del que es situen les comunitats ecològiques (Gaston et al., 2008; Kelly et al., 2008; Leibold and McPeck, 2006).

En aquest marc teòric, el desenvolupament dels models de distribució d'espècies ha tingut un paper clau per analitzar els patrons de distribució i abundància de les espècies davant les hipòtesis plantejades per la teoria neutra (Gaston and Chown, 2005; Hubbell, 2005; Kelly et al., 2008). Aquests anàlisis

s'han beneficiat també de la integració d'alguns aspectes de la teoria neutra en els models de distribució d'espècies, com les limitacions en dispersió (Brotons et al., 2011; Smith and Green, 2006; Snyder and Chesson, 2003) o els processos demogràfics estocàstics (Carnicer et al., 2007; Sebastián-González et al., 2011; Tilman, 2004). Més enllà, els models de distribució d'espècies han permès aprofundir en altres aspectes de la teoria del nínxol, per exemple els patrons de co-ocurrència i exclusió competitiva en comunitats ecològiques (Helmus et al., 2007; Kraft et al., 2007; Webb, 2000).

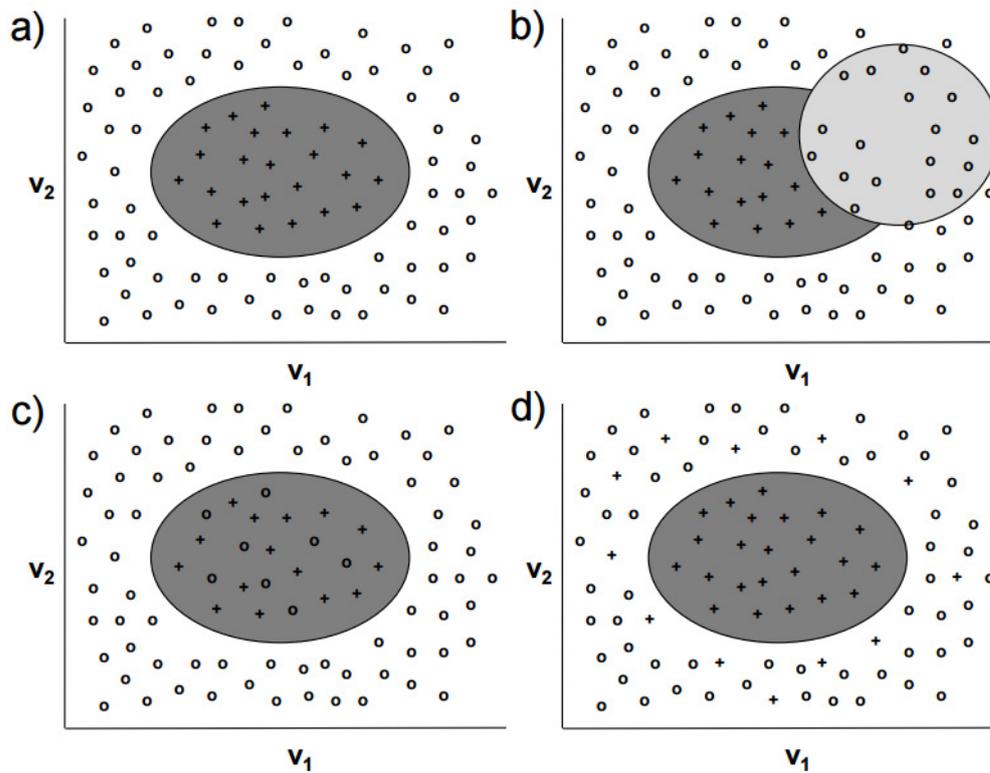


Figura 1. Relacions teòriques entre el nínxol fonamental (gris fosc), i la presència (+) o absència (-) d'una espècie hipotètica. Per simplificar, es defineix el nínxol en funció de dos variables ambientals, v_1 i v_2 : (a) l'espècie ocupa totes les àrees ambientalment adequades dins el seu nínxol fonamental; (b) l'espècie queda exclosa d'una part del seu nínxol fonamental per la presència d'un competidor (gris clar); (c) l'espècie no pot ocupar totes les àrees ambientalment adequades degut a una capacitat de dispersió limitada; (d) l'espècie persisteix fora del seu nínxol fonamental per la migració sostinguda d'individus des d'àrees ambientalment adequades. Font: Pulliam, 2000.

Els models de distribució d'espècies (en endavant SDM, de l'anglès *Species Distribution Models*) fan referència a un conjunt força heterogeni de mètodes numèrics que relacionen informació biològica sobre la distribució de les espècies i informació ambiental per obtenir prediccions espacialment explícites

de la distribució de les espècies dins un àmbit geogràfic d'interès (Guisan and Zimmermann, 2000). L'ús d'aquests mètodes, basats inicialment en regressions lineals múltiples i en anàlisis discriminants (Franklin, 1995), ha estat impulsat per l'aparició de nous algorismes de modelització (Guisan and Thuiller, 2005; Wintle et al., 2005), simultani a la ràpida emergència dels sistemes d'informació geogràfica i de grans bases de dades ambientals (Gillespie et al., 2008; Shanmughavel, 2007), tot emmarcat en el procés d'acceleració tecnològica experimentat les dues darreres dècades (Figure 2). La disponibilitat d'informació robusta i detallada sobre el clima, la topografia i els hàbitats per tots els ambients terrestres i marins ha generalitzat la seva aplicació a l'estudi de tota classe d'organismes (Hawkes et al., 2007; Kaschner et al., 2006; Wiley et al., 2003). Els avenços en aquests mètodes ha quedat reflectit en nombrosos articles, assajos i llibres que estableixen un marc general per a la modelització de la distribució d'espècies (Elith and Leathwick, 2009; Franklin, 1995; Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Mackey and Lindenmayer, 2001; Wintle et al., 2005), els lligams amb la teoria ecològica (Austin, 2007, 2002; Hirzel and Le Lay, 2008), els mètodes de modelització (Guisan et al., 2002; Pearce and Boyce, 2006), la informació biològica i l'escala dels models (Graham et al., 2004a; Rushton et al., 2004), la modelització de comunitats ecològiques (Ferrier and Guisan, 2006), i les seves aplicacions en conservació (Burgman et al., 2005; Ferrier et al., 2002; Franklin, 2010; Rodriguez et al., 2007), entre moltes altres qüestions.

Una consideració prèvia fonamental en els SDM es definir quin component del nínxol és objecte d'anàlisi (Pulliam, 2000). Alguns mètodes parteixen d'un enfoc correlatiu per establir relacions estadístiques entre un conjunt de variables abiòtiques i la distribució actual observada de les espècies. Donat que la distribució actual de les espècies no està condicionada únicament per factors abiòtics, sinó que també hi intervé la interacció amb altres espècies i/o les limitacions en la dispersió, els mètodes correlatius s'acosten més a la predicció del nínxol realitzat de les espècies (Araújo and Guisan, 2006; Guisan and Zimmermann, 2000; Soberón and Townsend Peterson, 2005). Altres mètodes parteixen d'un enfoc mecanicista per cercar prediccions del nínxol fonamental de les espècies, basant-se en mesures directes de la resposta fisiològica de les espècies a les condicions ambientals. Addicionalment, aquests mètodes també poden incorporar interaccions biòtiques per desplaçar les prediccions cap al nínxol realitzat de les espècies (Austin, 2002; Pearson and Dawson, 2003).

Aquestes consideracions constitueixen els fonaments de les aplicacions dels SDM, en especial quan s'utilitzen per predir la distribució de les espècies més enllà de les condicions ambientals utilitzades per al seu desenvolupament; els mètodes que capturen el nínxol fonamental haurien d'oferir millors

extrapolacions que capturen el nínxol realitzat per a un conjunt particular de condicions ambientals (Pearson and Dawson, 2003). No obstant això, l'aplicació de mètodes mecanicistes comporta algunes limitacions conceptuals, relacionades amb estimacions parcials del nínxol fonamental, i.e. la resposta fisiològica a les condicions ambientals per a una espècie pot variar a nivell poblacional (plasticitat fenotípica) i evolutiu (*niche shift*), i amb que les seves prediccions no reflecteixen bé la distribució de les espècies, i.e. els rangs de distribució actuals representen només una part de les àrees dins el nínxol fonamental de les espècies (concretament les àrees dins el nínxol realitzat on les espècies han pogut accedir per dispersió). A aquestes limitacions conceptuals també s'afegeix la gran complexitat i l'elevat cost en la seva parametrització i validació, fet que ha condicionat fortament l'aplicació generalitzada dels mètodes mecanicistes (Webber et al., 2011).

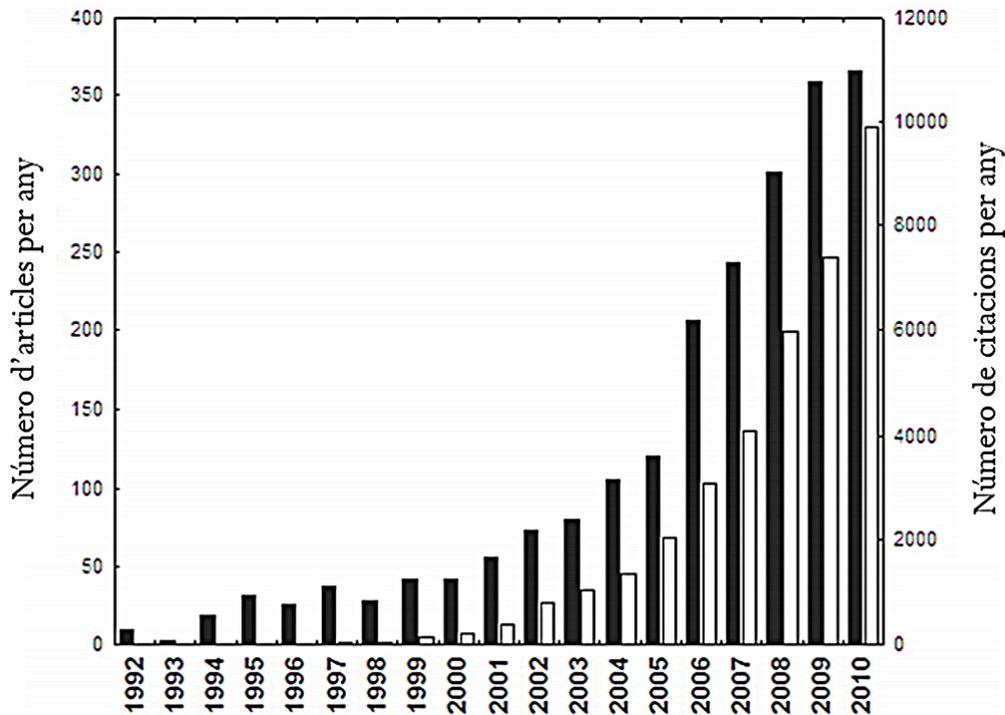


Figura 2. Número d'articles científics publicats relacionats amb SDM en publicacions sobre Ecologia (barres negres) i nombre de citacions que han rebut aquests articles (barres blanques) en el període 1992–2010. Font: Brotons, 2014

Pel que fa als mètodes correlatius, una de les crítiques més esteses incideix en que permeten obtenir prediccions aparentment precises que no capturen necessàriament les relacions causals entre les espècies i el medi, obviant així tot fonament teòric (Hirzel and Le Lay, 2008). Aquesta característica està

íntimament relacionada amb l'ús dels SDM per respondre dues preguntes clau diferents. Per una banda, en ecologia quantitativa i biologia evolutiva s'utilitzen per *explicar* els factors causals que condicionen la distribució de les espècies (Graham et al., 2004b; Leathwick and Austin, 2001; Mac Nally, 2000). Per altra banda, l'augment en la demanda d'aplicacions relacionades amb la planificació del territori i la conservació de la biodiversitat ha impulsat el seu ús per *predir* la distribució de les espècies (Ferrier and Wintle, 2009; Franklin, 2009; Guisan et al., 2013) en base a les relacions espècies/medi definides amb criteri estadístic però amb un fort component ecològic, especialment en la selecció de les variables predictores i en la interpretació dels models.

En conservació, l'ús de models correlatius per predir la distribució de les espècies permet millorar el coneixement de la distribució actual de les espècies, o la corresponent a l'àmbit temporal de les dades disponibles de l'espècie i dels predictors ambientals utilitzats per desenvolupar el model. Aquestes aplicacions son efectives en la mesura que les prediccions siguin el resultat de SDM basats en dades biològiques fiables correlacionades amb variables ambientals adequades, d'acord amb l'ecologia de l'espècie (Guisan and Zimmermann, 2000; Tulloch et al., 2016). Més enllà, els models també permeten predir la distribució en nous àmbits geogràfics o temporals, històrics o futurs. Aquí, les noves condicions ambientals han de ser adequadament analitzades, especialment quan representen rangs ambientals ampliat en relació als rangs presents en el desenvolupament dels models. Més enllà dels riscos inherents a la projecció o extrapolació dels models a noves condicions ambientals, relacionats amb la manca de dades per validar les prediccions obtingudes, la seva aplicació posa en qüestió l'assumpció que les espècies es troben en equilibri amb als seu medi, que és una de les principals assumpcions dels SDM. Malgrat això, els models correlatius son encara un dels pocs mètodes que permeten analitzar els impactes dels canvis ambientals en la distribució de les espècies, fet que justifica que estiguin entre els mètodes capdavaners en recerca ecològica (Brotons, 2014; Elith and Leathwick, 2009).

Aplicació de models de distribució d'espècies en conservació

Les prediccions espacialment explícites obtingudes amb SDM ofereixen un valor afegit indiscutible respecte a les simples dades de distribució utilitzades fins ara per informar sobre la distribució de les espècies, amb un fort potencial per prioritzar accions de conservació de la biodiversitat (Ferrier et al., 2002; Franklin, 2009; Jetz et al., 2012). La millora del coneixement de la distribució de les espècies permet aprofundir en els factors ecològics que la determinen i, en base a una sòlida capacitat predictiva, obtenir prediccions de la seva

distribució per diferents aplicacions en conservació (Tulloch et al., 2016). Alguns exemples són la millora de les estratègies de mostreig d'espècies rares o amenaçades (p.ex. de Siqueira et al., 2009; Guisan et al., 2006; Marcer et al., 2012; Pearson et al., 2007; Raxworthy et al., 2003; Thomas et al., 2004), la identificació d'àrees prioritàries de conservació i el disseny de xarxes d'espais protegits (p.ex. Arcos et al., 2012; Fajardo et al., 2014; Hermoso et al., 2015; Pawar et al., 2007; Wintle et al., 2005), o l'orientació de programes de recuperació o reintroducció d'espècies i restauració ecològica (p.ex. Angelieri et al., 2016; Clavero and Hermoso, 2015; Fei et al., 2012; Gastón and García-Viñas, 2013). Així mateix, els SDM es poden projectar cap a nous escenaris geogràfics o temporals per avaluar el risc d'espècies invasores (p.ex. Ficetola et al., 2007; Jiménez-Valverde et al., 2011; Roura-Pascual et al., 2007) o bé per pronosticar -o explicar de forma retrospectiva- els impactes potencials derivats de canvis en el clima (p.ex. Ficetola et al., 2010; Runge et al., 2015) o els usos del sòl (p.ex. Jetz et al., 2007; Martin et al., 2013; Regos et al., 2015; Vallecillo et al., 2009). No obstant això, la major part d'aquestes aplicacions han estat desenvolupades dins l'àmbit de la recerca amb l'objectiu de contrastar mètodes relacionats amb diferents tipologies de dades, així com la seva integració per prioritzar espècies en contextos hipotètics de conservació, i obviant enfoc més pràctics per al desenvolupament efectiu de SDM per millorar les seves perspectives d'aplicació dins de processos de decisió en conservació (Addison et al., 2013; Guisan et al., 2013; Knight et al., 2006; Rodriguez et al., 2007).

La manca d'aplicacions de SDM en la resolució de problemes reals de conservació s'emmarca dins un context més general de crisi d'implementació de desenvolupaments científics que va més enllà de la conservació de la biodiversitat, i que va estar tipificada per primer cop en l'àmbit de les ciències econòmiques i la psicologia social (Pfeffer and Sutton, 1999). En biologia de la conservació, la dificultat de traduir els resultats de la recerca té repercussions a diferents nivells, des de la planificació estratègica (p.ex. plans poc efectius basats únicament en coneixement científic i sense la participació d'entitats clau en el procés de planificació) fins al desenvolupament d'accions de conservació sobre el terreny (p.ex. proposta d'accions de conservació efectives però social o econòmicament inviables) (Knight et al., 2006; Prendergast et al., 1999; Salafsky et al., 2002).

Molts autors assenyalen que aquestes dificultats estan arrelades en les diferències entre els científics i els professionals que es dediquen a la conservació, des del vessant tècnic o polític, fent referència a la divergència en fonts de finançament, agendes i activitats, i carreres i millores professionals (Cook et al., 2013; Guisan et al., 2013). Aquestes diferències condicionen punts de partida distants davant d'un mateix problema de conservació, que sovint

s'allunyen encara més a causa de concepcions errònies de la conservació per part dels científics (Knight et al., 2008; Laurance et al., 2012), però també pel desconeixement per part de tècnics o polítics de l'existència d'aplicacions útils desenvolupades en el marc de la recerca (Addison et al., 2013; Pullin et al., 2004). Per revertir aquesta tendència, aquests autors plantegen la necessitat de promoure “traductors” que facilitin els fluxos d'informació entre els investigadors i els organismes responsables de les decisions en conservació, i que podrien estar personificats per grups de recerca, consorcis, universitats, etc. (Cash et al., 2003; Guisan et al., 2013; Schmolke et al., 2010; Soberon, 2004). A més, també proposen el marc estructurat de presa de decisions (Gregory et al., 2012) com a fonament conceptual per apropar els desenvolupaments en recerca a les aplicacions pràctiques per la millora de les activitats de conservació (Addison et al., 2013; Guisan et al., 2013; Knight et al., 2006).

Els marcs estructurats de decisió promouen la participació de tots els actors clau implicats dins d'un procés seqüencial que inclou des de la definició dels objectius a assolir fins a la implementació de la decisió (Addison et al., 2013; Gregory and Long, 2009; Gregory et al., 2001; Reed, 2008) (Taula 1). Aquests processos estimulen l'ús d'un ampli conjunt d'eines analítiques per dotar de rigor, transparència i lògica a les solucions finals adoptades. A més, ofereixen un bon context per als “traductors”, doncs potencien els aspectes socials de les decisions, generalment obviats en la formació científica convencional (Addison et al., 2013), per maximitzar l'eficiència de decisions a partir de la millora de la comunicació entre els participants i, per tant, de la confiança en els resultats finals.

Taula 1. Passos clau del procés estructurat de presa de decisions (Gregory and Long, 2009).

Aclarir el context de la decisió	Definir el problema i l'abast de la decisió, juntament amb el pressupost i els terminis.
Definir els objectius i els criteris d'avaluació	Especificar els objectius i els resultats esperats al final del procés.
Desenvolupar alternatives	Proposar un ventall ampli d'opcions que mostrin el major nombre d'alternatives possibles.
Avaluar conseqüències i incerteses	Anticipar les conseqüències de les alternatives proposades en base a evidències científiques juntament amb les aportacions dels actors implicats. Incloure estimes de la incertesa.
Estimar beneficis	Mesurar el grau d'ajust de les opcions avaluades amb els objectius plantejats.
Seleccionar una opció, implementar i monitoritzar	Documentar el procés de decisió, posar en pràctica l'opció o opcions seleccionades, i fer el seguiment per avaluar l'assoliment dels objectius inicials.

Objectius

Aquesta tesi es situa en la cruïlla on conflueixen els problemes de conservació, derivats de la pèrdua de biodiversitat i la crisi ambiental, amb els problemes d'implementació de solucions efectives, relacionats amb les dificultats d'aplicar els resultats de la recerca en la pràctica de la conservació, tot plegat emmarcat dins un context més general de crisi econòmica i social que es tradueix en una reducció progressiva dels recursos destinats a la conservació de la biodiversitat. L'objectiu general de la tesi es aprofundir en la utilització de SDM (models de distribució d'espècies) per millorar els processos de decisió en conservació de la biodiversitat. Amb l'ambició de bastir ponts entre la recerca ecològica i la conservació sobre el terreny, la tesi es planteja anar una mica més enllà dels exercicis teòrics i apropar-se a contextos reals de presa de decisions per fer contribucions més efectives a la conservació de les espècies. Pel que fa als aspectes metodològics, la tesi posa l'accent en la importància de les fonts d'informació sobre distribució d'espècies, atès que es un aspecte clau de la qualitat dels resultats dels SDM, i alhora un dels apartats més controvertits en els pressupostos públics destinats a la conservació. Els objectius específics que plantejats inclouen:

- Avaluar el paper dels SDM en diversos contextos d'aplicació relacionats amb problemes de conservació.
- Explorar els lligams entre el marc conceptual dels SDM i els processos de decisió reals per potenciar la utilització efectiva dels resultats obtinguts en la pràctica de la conservació de la biodiversitat.
- Examinar la utilització de diferents tipus d'informació biològica per desenvolupar SDM i les seves implicacions en la qualitat dels resultats obtinguts, així com en les perspectives d'aplicació.

La tesi està estructurada en tres blocs coherents amb cadascun dels objectius plantejats, malgrat que alguns capítols aborden de forma explícita més d'un dels objectius, i, per tant, han quedat inclosos en els dos primers blocs. En el primer bloc es desenvolupen exemples d'aplicació de SDM en diferents contextos de conservació (Capítols I, II, III, IV i V). De forma complementària, el segon bloc explora com potenciar els resultats derivats dels SDM per informar la pràctica real de la conservació (Capítol IV i V). Finalment, el tercer bloc examina el potencial de diferents tipologies de dades sobre distribució d'espècies per desenvolupar SDM, tenint en comte diferents àmbits d'aplicació (Capítol VI).

Discussió

Els models matemàtics són eines idònies per analitzar sistemes complexos, contrastar hipòtesis i avaluar diferents solucions. Aquesta fet queda palès en la seva afiliació a disciplines tant diverses com l'economia, la medicina i la climatologia, entre moltes altres entre les quals l'ecologia ocupa un lloc destacat. En ecologia hi ha una immensa i creixent varietat de models que permeten afrontar de forma cada cop més consistent les preguntes plantejades des de diversos camps de recerca (fluxos d'energia, dinàmica de poblacions, interaccions entre espècies, etc.). En aquest context, els SDM permeten abordar l'anàlisi de les relacions entre les espècies i el seu medi, una qüestió central en autoecologia. Però més enllà de la rellevància dels SDM com a eina de recerca, existeix un ampli consens sobre el seu potencial d'aplicació en una extensa varietat de problemes de conservació. Efectivament, el “*on actuar?*” es una de les qüestions clau en el disseny d'estratègies efectives per la gestió sostenible de poblacions, espècies i ecosistemes. Els SDM permeten respondre aquesta qüestió, fins i tot amb mancances importants d'informació biològica, però també per que permeten expressar els resultats en un llenguatge espacialment explícit proper a l'utilitzat en la gestió i planificació de la biodiversitat, fet que afavoreix la seva implementació com a eines de suport a les decisions en conservació. Precisament el progrés de les decisions cap a un marc més estructurat de presa de decisions suposa un estímul important per la generalització dels SDM per guiar la pràctica de la conservació (Addison et al., 2013). Aquests marcs estructurats de decisió, basats en la definició d'objectius clars i consensuats en processos participatius, promouen la utilització d'un ampli conjunt d'eines analítiques per dotar de rigor, transparència i lògica les solucions adoptades. En aquest context, doncs, els SDM permeten informar i enriquir els diversos punt clau dels processos de decisió (Figura 3).

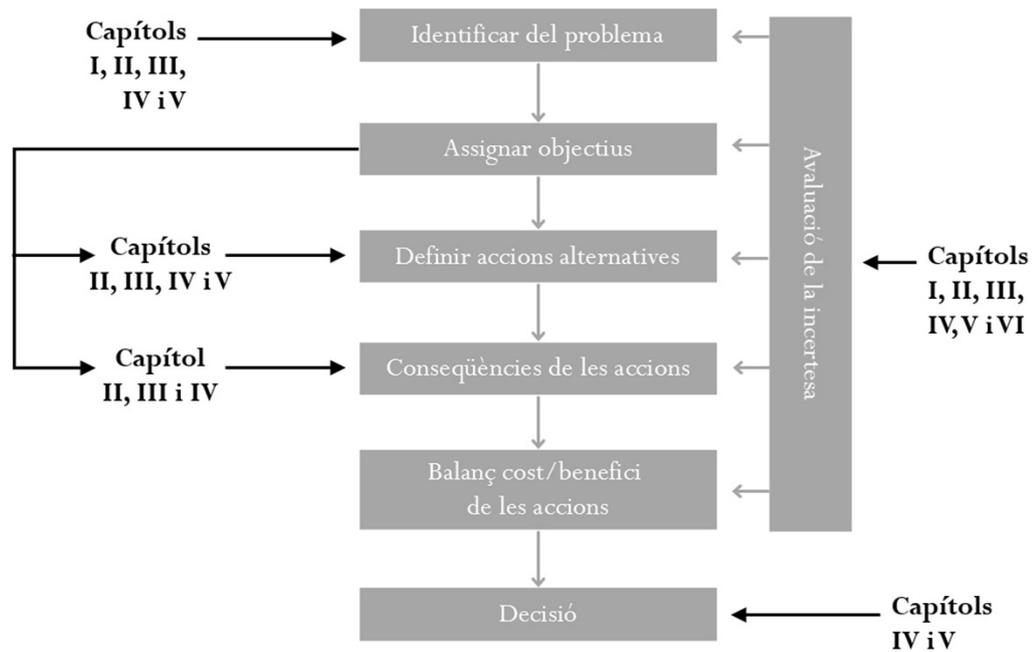


Figura 3. Marc estructurat de presa de decisions (Gregory et al., 2012) indicant els principals aspectes discutits i les contribucions realitzades en la present memòria. Adaptat a partir de Guisan et al. (2013). Per més detalls, veure el capítol introductori.

Identificació de problemes de conservació

El coneixement acurat de la distribució actual de les espècies ofereix un primer diagnòstic dels principals problemes de conservació que les afecten. La millora d'aquest coneixement ha estat una qüestió central en les polítiques ambientals, fent que els atles de distribució d'espècies esdevinguin eines clau de conservació. A més de sintetitzar el coneixement sobre altres aspectes biològics rellevants (p.ex. ecologia, estimes poblacionals, amenaces, tendències, etc.) per grups d'espècies d'arrel taxonòmica comuna, tradicionalment els atles s'han focalitzat en documentar la distribució geogràfica de forma homogènia i estandarditzada en àmplies àrees geogràfiques però amb una resolució massa grollera (10x10 km) en relació als dominis geogràfics en que es desenvolupa la presa de decisions en conservació. Aquesta mancança ha quedat superada en els atles de segona generació, que s'han beneficiat del desenvolupament dels SDM i la geoestadística per produir mapes de distribució i/o abundància de major resolució (1x1 km o inferior), a partir de mostrejos específicament dissenyats a escales espacials locals. Els atles d'ocells han estat pioners en la utilització d'aquestes tècniques (p.ex. Regne Unit: Gibbons et al., 1993; Suïssa: Schmid et al., 1998; Catalunya: Estrada et al., 2004) i ofereixen bons exemples del seu potencial d'aplicació en conservació (p.ex. a Catalunya: Brotons et al., 2004; Gil-Tena et al., 2010; Herrando et al., 2009; Vallecillo et al., 2008) (cap.

V). No obstant això, aquest salt qualitatiu posa de manifest una de les principals febleses dels atlas, que és la dificultat d'obtenir un major finançament en un context d'escassetat de recursos econòmics. L'estalvi de costos en la recollida de dades passa per la utilització de fonts d'informació alternatives procedents, per exemple, d'observadors voluntaris, d'estudis específics o bé de programes de seguiment. Aquest estalvi, però, pot tenir importants repercussions en la qualitat de les dades i en la fiabilitat dels SDM que se'n deriven (cap. VI). Entre aquestes alternatives, els programes de seguiment són els que s'ajusten millor a uns requisits mínims de qualitat doncs es basen en xarxes d'estacions on s'enregistra l'abundància relativa de diverses espècies de forma periòdica (en diferents èpoques de l'any) i repetida al llarg dels anys. Novament els ocells són el grup més avantatjat, amb programes de seguiment consolidats arreu del món amb un potencial contrastat de proporcionar grans quantitats de dades espacials per millorar els SDM en els marcs dels atlas, però també per desenvolupar SDM que mostrin els canvis en la distribució i abundància d'espècies (Brotons et al., 2007; Jiguet et al., 2005) (Cap. I, IV i VI). En el cas dels ocells, la convergència progressiva d'objectius entre els atlas i els programes de seguiment aviat proporcionarà millores substancials en termes de resolució espacial però també temporal (actualització de la distribució d'espècies en intervals de temps més curts) dels SDM, fet que afavorirà la incorporació de tendències a curt i mig termini de les espècies, així com també patrons migratoris, fins ara parcialment considerats en les estratègies de conservació de la biodiversitat (EBP-partnership and EBCC, 2015; Price et al., 1995).

Més enllà de millorar el coneixement de la distribució actual de les espècies (cap. I), la capacitat dels SDM de ser projectats a noves condicions ambientals del passat (cap. II) o del futur (cap. III) obre nous horitzons en l'anàlisi i la diagnosi dels problemes de conservació de les espècies. La creixent quantitat d'informació disponible sobre les característiques ambientals passades i futures facilita la obtenció de prediccions sobre la distribució hipotètica de les espècies en llocs i moments on no es disposa de dades originals, i ofereix una eina molt potent per generar escenaris i contrastar hipòtesis ecològiques. A més, quan aquests escenaris estan basats en factors ambientals clau per la persistència de les espècies, esdevenen eines molt adients per l'anàlisi dels problemes de conservació de les espècies. Així, els SDM han estat extensament utilitzats per avaluar les implicacions en conservació dels canvis futurs en els patrons espacials de la distribució de les espècies en base a l'escalfament global (Araujo et al., 2004; Richardson et al., 2010) (cap. III), als canvis en el paisatge (Brotons et al., 2011; Gil-Tena et al., 2016; Regos et al., 2015), i/o als impactes de les espècies invasores (Roura-Pascual et al., 2004; Thuiller et al., 2005) (cap.

III), entre d'altres. La manca d'exemples de projeccions cap al passat no vol dir que siguin menys interessants. A més d'avaluar l'impacte de les trajectòries històriques del paisatge i el clima sobre les espècies (Améztegui et al., 2010; Kharouba et al., 2009; Vallecillo et al., 2009) (cap. II), les projeccions retrospectives permeten establir condicions de referència sobre la distribució de les espècies en el passat (*d'on venim?*), i, per tant, fer una avaluació més consistent de l'abast real dels problemes de conservació (Clavero and Delibes, 2013; Clavero and Villero, 2014; Lotze and Worm, 2009) (cap. II).

Assignació d'objectius, definició d'accions alternatives i predicció de les seves conseqüències

L'assignació d'objectius de conservació és el resultat d'un consens dels actors clau involucrats en el procés de decisió (cap. IV i V). En aquest procés, els SDM poden utilitzar-se per garantir que aquests objectius son realistes, tenint en compte els factors que condicionen la distribució actual, històrica o futura de les espècies. Per exemple, els SDM es poden utilitzar com a marc de referència per establir prioritats de conservació en base a la importància relativa de la distribució dins i fora de les àrees protegides (cap. IV i V), o als impactes previstos en diferents escenaris de gestió (p.ex. trajectòries històriques del paisatge, cap. II; impactes futurs d'una espècie invasora, cap. III; corredors d'hàbitat per garantir la connexió de poblacions aïllades, cap. V), que més endavant poden ser revisades i redefinides a partir d'informació actualitzada, per exemple dins d'un marc de gestió adaptativa (Runge, 2011).

Els SDM també poden contribuir a la definició de possibles accions de conservació, obrint un ventall d'alternatives que permetin conciliar els objectius de conservació amb qüestions econòmiques (pressupost), logístiques (p.ex. personal disponible, accessibilitat, etc.) i socials (conflictes d'interessos entre les parts afectades, p.ex. accés a ajuts públics), que condicionen, en darrera instància, la viabilitat de les accions plantejades. En són bons exemples la delimitació de llocs candidats per ser inclosos en àrees protegides (cap. IV) o de llocs on destinar els pagaments ambientals (cap. V).

Finalment, la projecció de SDM a escenaris de canvi de paisatge o clima permet anticipar el resultat d'accions de conservació alternatives, en termes de canvis en la distribució de les espècies (cap. II) o en la qualitat del seu hàbitat (cap. III). L'avaluació de l'eficiència dels espais protegits davant dels reptes que planteja el canvi global és un dels camps d'aplicació més prolífics dels SDM en biologia de la conservació (Araujo et al., 2004; Hannah et al., 2007; Maiorano et al., 2013) (cap. II, III i IV). Aquí, els SDM faciliten l'anàlisi cost-benefici de

diverses accions alternatives, com ara la prioritització d'accions de gestió del medi per conservar espècies protegides d'ocells forestals (cap. II), o bé en la optimització d'accions de control d'espècies invasores en l'espai i el temps (cap. III).

Avaluació de la incertesa

Totes les etapes dels processos de decisió tenen implícit diferents graus d'incertesa; des de la correcta identificació del problema de conservació, passant per la definició d'objectius realistes, la identificació d'accions viables, l'avaluació adequada de les conseqüències i el correcte balanç dels costos/beneficis, fins al grau d'encert de la decisió (Burgman et al., 2005). Una part d'aquesta incertesa emana de la complexitat dels processos de decisió (p.ex. incertesa sobre si s'aprovarà una partida pressupostària prevista per dur a terme les accions previstes) i, tot i que es important documentar-la, el seu control queda massa sovint fora de l'abast dels actors implicats en la decisió. Per altra banda, hi ha la incertesa relacionada amb qüestions més pràctiques dins el context de la decisió, (p.ex. calendari, recursos humans, informació disponible, etc.), que pot ser avaluada amb l'objectiu d'identificar els punts crítics on seria factible reduir-la per millorar els resultats finals de les decisions (Ludwig et al., 2001).

La quantificació de la incertesa es un aspecte clau en el desenvolupament de SDM i, per tant, les seves contribucions en diferents etapes dels processos de decisió es poden complementar amb avaluacions explícites de la incertesa (Barry and Elith, 2006; Pearson et al., 2006), p.ex. en termes de precisió de les prediccions (cap. I, II, III, IV, V) i de la seva estabilitat temporal a curt i llarg termini (cap. I, II, III, IV i V). L'estimació de la incertesa en SDM té implicacions en les diverses etapes del procés de modelització (i.e. qualitat de la informació biològica i ambiental, adequació dels mètodes de modelització i avaluació de les prediccions obtingudes) i es pot mesurar en base a criteris objectius, com ara càlculs del poder predictiu lliardar-dependents (errors de comissió i omissió, prevalença, kappa, etc.) o lliardar-independents (AUC, correlacions, etc.), però també emprant criteris subjectius, basats en la credibilitat de les prediccions (p.ex. acceptació per part dels usuaris) o el coneixement expert (p.ex. congruència de les corbes de resposta espècies/hàbitat) (Rykiel, 1996).

La excel·lent capacitat predictiva i robustesa dels SDM basats en diferents algoritmes matemàtics, així com la gran precisió de les prediccions que se'n deriven, han quedat constatats en nombroses publicacions científiques (p.ex. Elith et al., 2006; Franklin, 2009). Una característica comuna de les millors

tècniques assenyalades en aquests estudis es que es basen en informació biològica de gran qualitat, que només pot ser obtinguda en el marc de mostrejos específicament dissenyats per documentar la presència/absència o l'abundància d'una o diverses espècies en un rang geogràfic i ambiental adequadament estratificat. No obstant això, el potencial analític que fa excel·lir aquestes tècniques esdevé alhora el principal entrebanc quan es volen aplicar en l'àmbit de la conservació en què la informació biològica disponible és sovint incompleta i presenta greus biaixos taxonòmics, temporals i geogràfics, fins i tot per als grups de vertebrats més ben coneguts (Reddy and Dávalos, 2003) (cap. V, VI). Així doncs, en un context d'abundància d'informació ambiental amb qualitat temàtica i resolució geogràfica creixents, les aplicacions de SDM en conservació s'han beneficiat profusament de les tècniques basades en dades de només-presència, que en general ofereixen un millor balanç entre la qualitat i quantitat de dades biològiques requerides i la solidesa de la seva capacitat predictiva (Elith and Leathwick, 2007; Pearce and Boyce, 2006) (cap. I, II, IV, V i VI). En l'àmbit acadèmic, l'ús estès d'algunes d'aquestes tècniques (p.ex. Maxent o GARP) ha estimulat un debat que ha contribuït positivament a eixamplar la base de coneixement per optimitzar el seu ús i adaptar-lo a les limitacions de la informació biològica disponible, p.ex. mancances d'informació, heterogeneïtat de fonts d'informació, biaixos espacials i ambientals de les dades (Anderson and Gonzalez Jr, 2011; Fourcade et al., 2014; Kramer-Schadt et al., 2013; Merow et al., 2013; Phillips et al., 2009; Syfert et al., 2013; Warren and Seifert, 2011; Wisz et al., 2008; Yackulic et al., 2013) (cap. V i VI).

La disponibilitat de dades biològiques és, doncs, un factor determinant de la incertesa de les aplicacions de SDM en conservació. Molts estudis indiquen que l'augment en la mida de la mostra es tradueix en una major precisió dels SDM (Pearce and Ferrier, 2000; Wisz et al., 2008) (cap. VI). Tanmateix, els SDM basats en grans volums de dades oportunistes procedents d'observadors voluntaris ofereixen un grau de precisió semblant a les prediccions obtingudes a partir de dades recollides en mostrejos estandarditzats, i, per tant, amb mides de mostra inferiors (cap. VI). D'altra banda, les dades oportunistes també ofereixen bones prediccions, especialment quan s'analitzen espècies poc comunes i, per tant, mal representades en les mostrejos estandarditzats (cap. VI). Així doncs, fins i tot en contextos favorables amb diverses fonts d'informació disponibles, els criteris per seleccionar les dades per desenvolupar els SDM han de considerar l'ecologia de les espècies, a més de la mida de mostra i els mètodes de recollida de dades (cap. I).

La importància de les dades biològiques va més enllà del seu rol com a variables de resposta en el procés de calibratge dels SDM, i també juguen un

paper clau per mesurar el seu poder predictiu per avaluar si compleix uns requisits mínims per a la seva correcta aplicació (Rykiel, 1996). Malgrat que idealment l'avaluació de la precisió dels SDM s'hauria de basar en conjunts de dades independents als utilitzats en el desenvolupament dels models (Guisan and Zimmermann, 2000), existeixen diverses estratègies destinades a avaluar els SDM en base a subconjunts de dades exclosos del procés de calibratge (p.ex. submostratge, validació creuada o *bootstrapping*). La utilització sistematitzada i repetida d'aquestes estratègies permet obtenir mesures robustes de la precisió de les prediccions i estimes de la seva incertesa en base als resultats compilats en diferents rèpliques. Segons el volum i la tipologia d'informació biològica disponible, aquests dissenys permeten gran flexibilitat per donar resposta als objectius plantejats en els processos de decisió, anant des d'una definició bàsica de diferents subconjunts de dades per validar la precisió de les prediccions (cap. I, II i V), fins a esquemes més elaborats que integrin fonts d'informació heterogènies (p.ex. l'avaluació de models d'aus marines amb dades d'anys i èpoques diferents a les utilitzades per desenvolupar els SDM amb l'objectiu d'analitzar l'estabilitat temporal d'àrees candidates a ser protegides, cap. IV), o tècniques de modelització diferents (p.ex. avaluació de models d'idoneïtat climàtica d'amfibis per examinar els impactes de l'escalfament global, cap. V).

Aplicació efectiva en processos de decisió

L'èxit de la integració de SDM en la presa de decisions passa necessàriament per ajustar els objectius dels models a les preguntes plantejades en el context particular del problema de conservació (cap. IV i V). Dins la complexitat dels processos de decisió, on conflueixen diversos actors amb interessos contraposats, els investigadors tenen reservat el rol específic de traduir i ajustar els resultats dels SDM als objectius del context de la decisió, però també a les seves limitacions (p.ex. calendari, pressupost, informació biològica disponible, etc.). Però aquest ajust només és possible en la mesura que els investigadors prenen consciència de la complexitat del problema de conservació i s'involucren activament en els processos de decisió (cap. IV). Aquí rau un dels principals obstacles per una aplicació més eficaç dels SDM en la resolució de problemes de conservació, fonamentat en les dificultats de conciliació entre l'activitat acadèmica i la pràctica de la conservació (cap. V). Per als investigadors, l'adaptació a les restriccions del context de decisió suposa un sobrecost en termes de mobilització de personal i recursos, i de canvis de rols i rutines en els grups de recerca, agreujat per la manca d'impacte en la millora del indicadors de rendiment de les activitats de recerca. L'alternativa per reforçar aquestes mancances és promoure grups de recerca específics orientats a desenvolupar

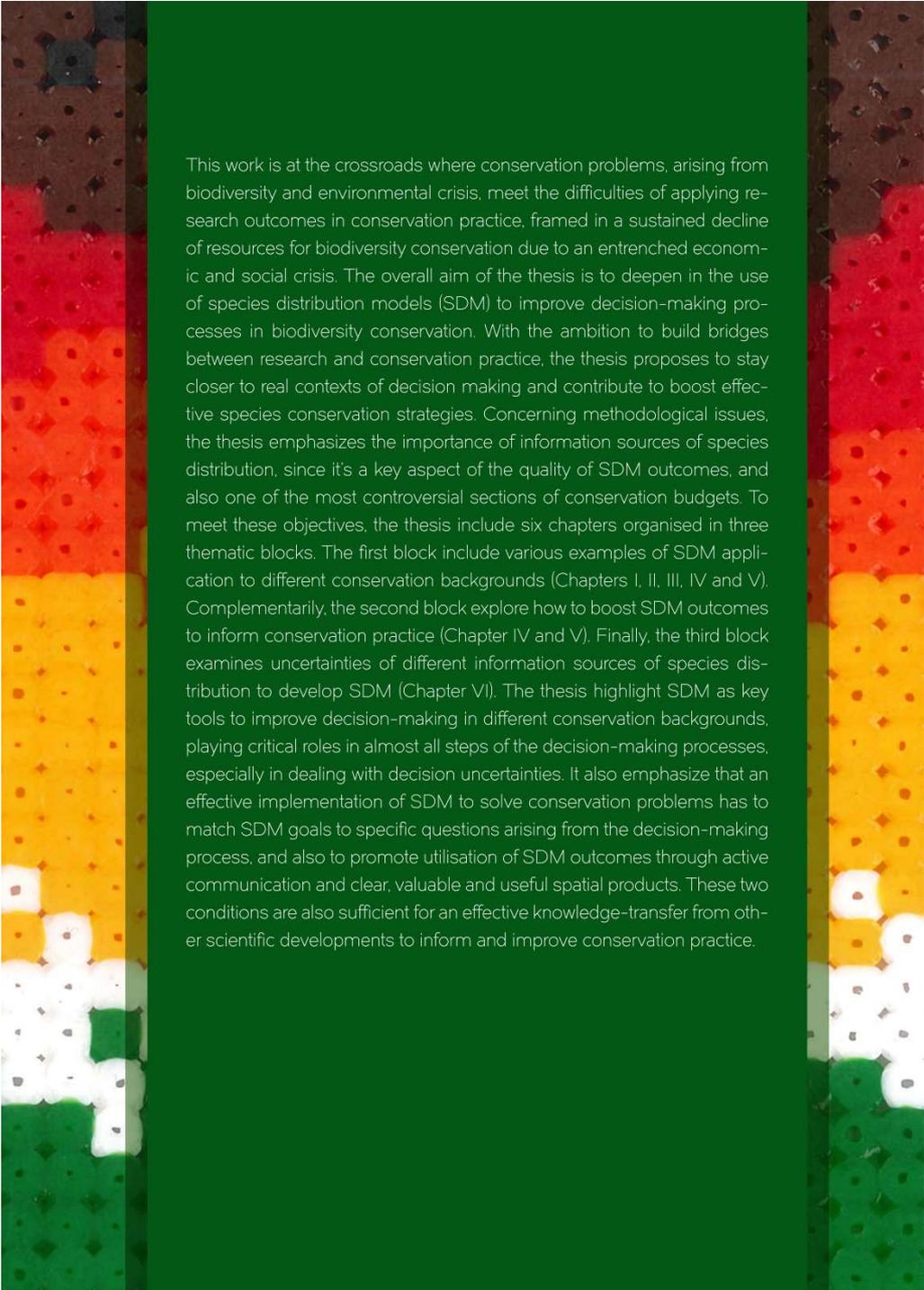
mètodes i aplicacions per construir ponts entre la recerca i la pràctica de la conservació. Aquesta segona opció s'albira com la més rendible a mig i llarg termini, en un context amb cada cop menys marge per afrontar problemes de conservació urgents i complexos (cap. V)

Tanmateix, per promoure la utilització dels resultats obtinguts amb SDM cal també que els actors clau implicats compreguin clarament les seves aportacions dins el procés de decisió (cap. V). La documentació de SDM seguint bones pràctiques es un bon punt de partida per obtenir productes espacials més complerts i transparents. Però malgrat que existeix un ampli consens sobre els elements que cal documentar per assolir un requisits mínims d'informació, aquests son sistemàticament ignorats degut a la manca d'incentius per seguir bones pràctiques en els investigadors, o bé per l'ús de terminologies inconsistentes i massa feixugues per descriure els elements inclosos en els processos de modelització (Schmolke et al., 2010; Soberon, 2004). A més, una documentació clara no es suficient per divulgar els resultats dels SDM si no va acompanyada de productes espacials útils i accessibles (cap. V). El desenvolupament d'aquests productes s'ha de basar en les necessitats d'informació expressades en el context de la decisió, i requereix, per tant, una comunicació directa i activa amb els responsables de les decisions des de les primeres etapes del procés de decisió (cap. V). Aquesta comunicació, a més de reforçar els vincles de confiança, permet identificar els requeriments d'informació i, en conseqüència, adaptar els resultats dels SDM a necessitats particulars d'informació relacionades amb diferents etapes del procés de decisió. Així doncs, en la mesura que aquests productes espacials derivats de SDM encaixen de forma explícita i transparent en el procés de decisió, esdevenen també una peça de l'engranatge per millorar els fluxos d'informació entre els investigadors i el procés de decisió, i reforçar la complicitat amb els diversos actors involucrats en el procés de decisió (cap. V).

Conclusions

- Els SDM son eines clau per trobar millors solucions per una gran varietat de problemes de conservació, amb implicacions en diverses etapes dels processos de decisió, permetent:
 - » Identificar problemes de conservació a partir d'un coneixement acurat de la distribució actual de les espècies, i alhora predir la seva distribució tant històrica i com futura en relació a canvis en el paisatge o el clima.
 - » Garantir la validesa dels objectius de conservació, tenint en compte els factors ambientals que condicionen la distribució de les espècies.
 - » Definir accions de conservació i oferir alternatives que permetin conciliar els objectius de conservació i les limitacions del context de la decisió.
 - » Anticipar els resultats de les accions de conservació en base a escenaris de canvi de paisatge o clima, així com escenaris de gestió de les espècies.
 - » Quantificar la incertesa relacionada amb els punts abans esmentats i incorporar-la de forma explícita dins el procés de decisió per millorar l'anàlisi cost/benefici d'accions alternatives.

- L'aplicació efectiva de SDM en processos de decisió passa per complir dues condicions necessàries:
 - » Ajustar els objectius dels SDM a les preguntes plantejades en el context particular del problema de conservació.
 - » Promoure la utilització dels resultats obtinguts amb SDM a través d'una comunicació activa acompanyada de productes espacials clars, útils, accessibles i ben ajustats a les necessitats particulars d'informació expressades en el context de la decisió.
 - » Aquestes dues condicions son igualment vàlides per la transferència efectiva d'altres desenvolupaments científics per la millora de la pràctica de la conservació.



This work is at the crossroads where conservation problems, arising from biodiversity and environmental crisis, meet the difficulties of applying research outcomes in conservation practice, framed in a sustained decline of resources for biodiversity conservation due to an entrenched economic and social crisis. The overall aim of the thesis is to deepen in the use of species distribution models (SDM) to improve decision-making processes in biodiversity conservation. With the ambition to build bridges between research and conservation practice, the thesis proposes to stay closer to real contexts of decision making and contribute to boost effective species conservation strategies. Concerning methodological issues, the thesis emphasizes the importance of information sources of species distribution, since it's a key aspect of the quality of SDM outcomes, and also one of the most controversial sections of conservation budgets. To meet these objectives, the thesis include six chapters organised in three thematic blocks. The first block include various examples of SDM application to different conservation backgrounds (Chapters I, II, III, IV and V). Complementarily, the second block explore how to boost SDM outcomes to inform conservation practice (Chapter IV and V). Finally, the third block examines uncertainties of different information sources of species distribution to develop SDM (Chapter VI). The thesis highlight SDM as key tools to improve decision-making in different conservation backgrounds, playing critical roles in almost all steps of the decision-making processes, especially in dealing with decision uncertainties. It also emphasize that an effective implementation of SDM to solve conservation problems has to match SDM goals to specific questions arising from the decision-making process, and also to promote utilisation of SDM outcomes through active communication and clear, valuable and useful spatial products. These two conditions are also sufficient for an effective knowledge-transfer from other scientific developments to inform and improve conservation practice.