UNIVERSIDADE DE LISBOA
Faculdade de Ciências
Departamento de Biologia Animal

Biodiversity and Conservation Planning of the Amphibians and Reptiles in the Western Mediterranean Basin

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Sílvia Ricardo Benoliel de Carvalho

Doutoramento em Biologia
Especialidade Biodiversidade
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Doutoramento em Biologia
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Aos meus pais e às minhas avós
To my parents and to my grannies

Foreword

According to the Article 41 nrº 1 of the Post-graduate studies Regulation (Diário da República Nº 1506 de 2006, II série de 30 de Outubro de 2006), the present thesis integrates manuscripts published or submitted listed below, in collaboration with co-authors. The candidate declares that she contributed to conceiving the ideas, compiling the data, producing the databases and analyzing the data. The candidate also declares that she led the writing of all chapters, with exception of chapter 4.

List of papers

Chapter 4

Harris, D.J., Carretero, M.A., Brito, J.C., Kaliontzopoulou, A., Pinho, C., Perera, A., Vasconcelos, R., Barata, M., Barbosa, D., Batista, V., Carvalho, S., Fonseca, M.M., Pérez-Lanuza, G., Rato, C., 2008. Data on the distribution of the terrestrial herpetofauna of Morocco: records from 2001-2006. Herpetological Bulletin 103, 19-28.

Chapter 5

Carvalho, S.B., Brito, J.C., Pressey, R.L., Crespo, E., Possingham, H.P., 2010. Simulating the effects of using different types of species distribution data in reserve selection. Biological Conservation 143, 426-438.

Chapter 6

Carvalho, S.B., Brito, J.C., Crespo, E.J., Possingham, H.P. (submited) Incorporating evolutionary processes into conservation planning using species distribution data: a case study with the western Mediterranean herpetofauna. Diversity and Distributions.

Chapter 7

Carvalho, S.B., Brito, J.C., Crespo, E.J., Possingham, H.P., 2010. From climate change predictions to actions – conserving vulnerable animal groups in hotspots at a regional scale. Global Change Biology, doi: 10.1111/j.1365-2486.2010.02212.x

Chapter 8

Carvalho, S.B., Brito, J.C., Crespo, E.J., Watts, M. Possingham, H.P. (in prep.) Conservation Planning under Climate Change: accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. Biological Conservation.

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Resumo

A biodiversidade apresenta um valor inestimável, dado que contribui directamente para o bem-estar da humanidade. No entanto, actualmente vive-se uma crise de biodiversidade sem precedente, estimando-se que as actuais taxas de extinção sejam cerca de 100 vezes superiores às verificadas no registo fóssil. Esta perda de biodiversidade reduz a capacidade dos ecossistemas fornecerem uma oferta estável e sustentável de bens e serviços à sociedade. As causas da actual acelerada extinção de biodiversidade são bem conhecidas, encontrando-se estreitamente relacionadas com a actividade humana e manifestando-se como uma consequência directa da globalização económica.

Reconhecendo a importância da biodiversidade, mais de 180 países comprometeram-se em implementar as medidas necessárias para travar a perda de biodiversidade até ao presente ano de 2010. No entanto, foi já reconhecido que esse objectivo não foi atingindo, sendo que as taxas de extinção e os factores de ameaça de muitas espécies continuam a aumentar. Torna-se assim imperativo definir medidas de conservação mais eficazes e eficientes. Para esse efeito, será necessário incrementar o conhecimento sobre os padrões de biodiversidade e os processos que os regulam, assim como implementar medidas de conservação mais eficientes do ponto de vista custo/benefício.

Uma das principais estratégias necessárias para reduzir a perda de biodiversidade é a criação e gestão adequada de áreas protegidas. O Planeamento Sistemático para a Conservação (PSC) consiste num conjunto de metodologias de apoio a decisões estratégicas no âmbito da identificação de áreas e acções prioritárias para a conservação. De um modo geral, o objectivo deste ramo da ciência é o de identificar espacialmente um conjunto óptimo de áreas e acções para a conservação, orientadas por objectivos quantitativos de representação e sobrevivência a longo termo da biodiversidade, tendo em consideração constrangimentos socio-económicos.

Nas últimas três décadas tem-se assistido a um desenvolvimento crescente de metodologias e de ferramentas computacionais no âmbito da identificação de áreas prioritárias para a conservação. No entanto, existem ainda várias limitações metodológicas que necessitam de ser ultrapassadas e aperfeiçoadas por forma a tornar a abordagem mais eficiente e realista. Nesta tese de doutoramento procurou-se abordar alguns dessas limitações utilizando como caso-estudo a região Oeste da Bacia Mediterrânica, com particular enfoque nos anfíbios e répteis.

A região Oeste da Bacia Mediterrânica foi seleccionada dado tratar-se de uma das regiões a nível mundial que alberga maior concentração de espécies ameaçadas e endémicas,

sendo por isso considerada de elevada importância para a conservação da biodiversidade global. Acresce ainda que se trata de uma região com uma ocupação humana antiga e com crescentes pressões antropogénicas sobre a diversidade biológica. Trata-se ainda de uma região com características geográficas, climáticas e evolutivas muito peculiares, que lhe conferem o estatuto de "laboratório natural" para o estudo dos processos biológicos e evolutivos. Os anfíbios e répteis, em particular, apresentam uma diversidade notável nesta região, ocorrendo um elevado número de espécies endémicas e ameaçadas. Estes grupos constituem ainda modelos excepcionais para os estudos biogeográficos tendo em conta a sua fisiologia ectotérmica e a sua capacidade de dispersão relativamente limitada.

Assim, os objectivos específicos deste trabalho consistiam em: 1) incrementar o conhecimento sobre os padrões de distribuição dos anfíbios e répteis no Oeste da Bacia Mediterrânica, 2) avaliar qual o tipo de dados de distribuição das espécies mais adequados em diferentes circunstâncias para utilização no PSC; 3) desenvolver novas abordagens para a incorporação de processos evolutivos no PSC; 4) prever como a distribuição actual das diferentes espécies será afectada pelas alterações climáticas nas próximas décadas; e 5) desenvolver novas abordagens para considerar a incerteza inerente à distribuição das espécies (actual e futura) no PSC, de forma a desenvolver estratégicas de conservação mais eficientes no tempo e no espaço.

Dados sobre a distribuição dos anfíbios e répteis no Oeste da Bacia Mediterrânica encontram-se já publicados em atlas nacionais de Portugal, Espanha e Marrocos. No entanto, esses dados advêm de uma compilação de observações feitas por diferentes observadores, ao longo de diferentes décadas, sem que tenha sido aplicada uma metodologia de amostragem sistemática. Assim, grande parte dos dados dos atlas encontravam-se significativamente enviesados, tendo sido mais amostradas áreas de fácil acesso e localizadas em áreas protegidas, e sendo que a Península Ibérica foi provavelmente alvo de um esforço de amostragem bastante mais intenso do que Marrocos. De forma a tornar estes dados de distribuição mais informativos para as estratégias de conservação, tornou-se necessário identificar as áreas potenciais de ocorrência de cada uma das espécies através de modelação estatística e completar a informação sobre a distribuição das espécies, através da realização de campanhas de amostragem em Marrocos.

A modelação estatística da distribuição das espécies permitiu identificar as áreas potenciais de ocorrência de cada uma das espécies, bem como identificar as principais variáveis ecológicas que mais se relacionam com a distribuição das mesmas. Esta informação é de extrema relevância para a compreensão dos requisitos ecológicos que permitem a persistência das espécies e prever a resposta das mesmas a perturbações ambientais. A identificação das áreas potenciais de distribuição das espécies permitiu ainda identificar as áreas provavelmente menos prospectadas, servindo de instrumento orientador de futuras amostragens.

De forma a completar os dados de distribuição de anfíbios e répteis em Marrocos, diversas campanhas de amostragem foram realizadas durante o período compreendido entre 2001 e 2006. Nessas campanhas foram observadas nove espécies de anfíbios e 57 de répteis, totalizando 427 observações, em 159 locais. Estas observações corresponderam a um incremento em 7% do total de registos publicados no atlas de anfíbios e répteis de Marrocos. As observações efectuadas ampliaram a distribuição previamente conhecida das espécies *Discoglossus scovazzi*, *Ptyodactylus oudrii* e *Spalerosophis dolichospilus*.

Foram realizadas diferentes simulações computacionais com o intuito de testar qual o tipo de dados de distribuição das espécies mais adequado para a identificação de áreas prioritárias para a conservação. Para o efeito, foram construídos diferentes bases de dados de distribuição das espécies contendo a) dados observados; b) dados potenciais probabilísticos; c) dados potenciais binários; e c) dados mistos (observados ou potenciais binários, de acordo com as características ecológicas de cada espécie e o seu nível de ameaça). As simulações foram efectuadas tendo em conta diferentes cenários nos quais se combinaram distintos níveis de conhecimento da distribuição das espécies, diferentes níveis pretendidos de representação das espécies e diferentes custos (em termos de área total a proteger). As simulações foram ainda realizadas de acordo com as duas principais abordagens matemáticas utilizadas para identificar o conjunto óptimo de áreas prioritárias: "área mínima" e "máxima cobertura". Os resultados obtidos indicaram que a qualidade do desempenho obtido na selecção de áreas prioritárias varia com o tipo de dados utilizado, sendo que o tipo de dados mais eficiente depende sobretudo da abordagem matemática utilizada e do nível de conhecimento inicial sobre a distribuição das espécies. No entanto, os resultados obtidos quando se utilizaram dados potenciais binários e dados mistos superaram, em termos de eficiência, os resultados obtidos com os dados observados e potenciais probabilísticos na maioria dos cenários testados.

O planeamento sistemático para a conservação tem-se centrado mais extensivamente no objectivo de representação das espécies em áreas protegidas, do que em assegurar a sua sobrevivência a longo prazo ou dos processos evolutivos que geram e mantêm a biodiversidade. A fundamentação para este facto centra-se na escassez de dados filogenéticos que permitam identificar padrões espaciais na diversidade genética para um número significativo de espécies. De forma a ultrapassar esta limitação, procurou-se desenvolver uma metodologia baseada na distribuição das espécies que permitisse incorporar critérios de representação dos dois eixos da diversidade genética: neutral e adaptativa. A abordagem desenvolvida consistiu na utilização de substitutos para estas duas componentes. Para a diversidade genética neutral, identificaram-se grupos de espécies com uma área de distribuição significativamente semelhante (elementos bióticos), enquanto que para a diversidade genética adaptativa, identificaram-se as principais componentes da variação ambiental, tendo em conta a área de estudo total e a área de distribuição ocupada por cada elemento biótico. Utilizando algoritmos de priorização espacial, identificaram-se as áreas prioritárias para a conservação em três cenários distintos: a) considerando apenas a distribuição das espécies; b) considerando a distribuição das espécies e a variação ambiental total da área de estudo; e c) considerando a distribuição das espécies e a variação ambiental intrínseca de cada elemento biótico. As áreas prioritárias encontradas nos diferentes cenários foram semelhantes em termos de área total seleccionada, no entanto, a sua

congruência espacial foi reduzida. Estes resultados enfatizam a necessidade de incorporar os processos evolutivos na identificação de áreas prioritárias para a conservação.

Um outro aspecto focado neste trabalho foi a questão da dinâmica da distribuição das espécies. A identificação de áreas prioritárias para a conservação geralmente assume que os padrões espaciais de biodiversidade são estáticos ao longo do tempo. No entanto, perturbações como a fragmentação do habitat e as alterações climáticas poderão causar alterações das actuais distribuições das espécies. Assim, pretendeu-se prever como os anfíbios e répteis endémicos ou quase endémicos da Península Ibérica irão alterar a sua actual distribuição tendo em conta diversos cenários de alterações climáticas até 2080. Os resultados obtidos indicam que a distribuição de diversas espécies poderá reduzir-se significativamente nas próximas décadas, sendo que 13 espécies poderão mesmo deixar de ter áreas bioclimáticas adequadas para a sua ocorrência na Península Ibérica. Os resultados indicam ainda que as espécies mais vulneráveis são aquelas que actualmente apresentam maiores afinidades às áreas de clima Atlântico, tais como C*hioglossa lusitanica*, *Rana iberica* e *Vipera seoane*i. Também as espécies que actualmente têm a sua distribuição restrita a elevadas altitudes, como *Rana pyrenaica*, *Iberolacerta monticola*, *I. aranica*, *I. aurelioi*, e *I. bonnali*, poderão ser severamente afectadas pelas alterações climáticas. Os resultados sugerem ainda que o período de maior impacto das alterações climáticas sobre a distribuição das espécies será a próxima década, o que reitera a necessidade urgente do desenvolvimento de medidas adequadas à conservação das espécies. No entanto, os resultados obtidos revestem-se de elevada incerteza, pelo que se tornou necessário desenvolver metodologias de identificação de áreas prioritárias para a conservação que tivessem em consideração esta incerteza. Para esse efeito, foram desenvolvidas metodologias inovadoras, tendo-se implementado uma abordagem logarítmica numa nova versão de uma aplicação computacional direccionada para a identificação de áreas prioritárias para a conservação. Esta nova abordagem permitiu identificar áreas prioritárias robustas à dinâmica da distribuição das espécies prevista, bem como à incerteza inerente a essas previsões. Os resultados obtidos indicam que a actual rede de áreas protegidas da Península Ibérica é insuficiente para assegurar a conservação dos anfíbios e repteis nas próximas décadas. As áreas actualmente não-protegidas identificadas como importantes para a conservação no futuro localizam-se sobretudo no Sudoeste de Espanha e na zona Centro-Este de Portugal.

Este trabalho contribuiu para o incremento do conhecimento sobre a biogeografia dos anfíbios e répteis no Oeste da Bacia Mediterrânica, principalmente através do desenvolvimento de metodologias inovadoras no âmbito do Planeamento Sistemático para a Conservação. Foram ainda identificados diferentes aspectos deste ramo das ciências biológicas que poderão vir a ser abordados e desenvolvidos no futuro.

Palavras-chave: biodiversidade, anfíbios, répteis, Península Ibérica, Marrocos, planeamento sistemático para a conservação, modelos de distribuição de espécies, processos evolutivos, alterações climáticas, incerteza.

Summary

Given the current global biodiversity crisis, prioritizing conservation areas that maximize species representation and enable persistence has been a major goal of systematic conservation planning. Despite the progresses in the field, there are still challenges needed to be overcome. This thesis aims to address some unresolved issues in conservation planning, by using the Western Mediterranean region as study area and the amphibians and reptiles occurring there as biological models.

This thesis contributed to the knowledge and understanding of the distribution of amphibians and reptiles in the Western Mediterranean region. Field sampling in Morocco increased the number of known species occurrences. Species distribution models were developed to predict the occurrences in under-sampled areas, and to improve the understanding on relationships between species ranges and environmental conditions.

The consequences of using different types of distribution data on the performance of reserve selection algorithms were analysed. Several scenarios were simulated, including variable proportions of species distribution data, conservation targets and costs. The recommended type of data to use varies according to scenarios, but data sets with both observed and predicted distributions generally provided good solutions in most circumstances.

Novel approaches were developed to incorporate evolutionary processes into conservation planning, through surrogate use for both the neutral and adaptive components of genetic diversity. The comparison of the results when incorporating or not evolutionary processes showed reduced spatially congruence, which calls for a need of a paradigm shift in conservation planning.

Issues of how to prioritize areas for conservation while accounting for species range shifts and the uncertainty inherent to those predictions were tackled by developing innovative approaches. Priority areas for the conservation of amphibians and reptiles robust to both range shifts and uncertainty were identified.

Finally, future research prospects in the field of conservation planning were identified and discussed.

Key words: biodiversity, amphibians, reptiles, Iberian Peninsula, Morocco, systematic conservation planning, species distribution models, evolutionary processes, climate change, uncertainty.

Photo: Vasco Flores Cruz

“Because we don’t think about future generations, they will never forget us”

Henrik Tikkanen

Chapter 1

Introduction

1.1 The biodiversity crisis

1.1.1 What is biodiversity and why it is important

The term biodiversity describes the overall variety of life and natural processes on Earth, including diversity and interaction within species, between species and ecosystems. Biodiversity underpins the functioning of ecosystems and their services, on which humans depend. Recently, the United Nations conducted the Millennium Ecosystem Assessment (http://www.millenniumassessment.org), ascertaining the outstanding contribution of biodiversity to human well-being, sustainable development, and poverty reduction. Among other things, biodiversity contributes directly or indirectly to human societies by provisioning services such as food, water, timber, and fiber; regulating climate, disease, wastes, and water quality; providing recreation and aesthetic enjoyment; and supporting services such as soil formation, photosynthesis, and nutrient cycling (Balvanera et al. 2006; Díaz et al. 2006; Díaz et al. 2005; Mace et al. 2005; Millennium Ecosystem Assessment 2005). Moreover, biodiversity was declared as extremely important to mitigate global warming effects (Campbell et al. 2008).

1.1.2 The biodiversity crisis

Despite its importance, biodiversity is being lost worldwide at an escalating and unprecedented pace since the last mass extinction, 65 million years ago (Lovejoy 1980; May et al. 1995; Pimm et al. 1995). Current rates of extinction are estimated to be roughly 100 times higher than typical rates in the fossil record (Millennium Ecosystem Assessment

2005). About 36% of the 47 966 assessed species were classified as threatened by the International Union for Conservation of Nature (IUCN 2010). The analysis encompassed only vertebrates and some plants thus the real number of threatened species is probably much higher. The taxonomic groups with higher number of threatened species are the amphibians and the birds. The scenario of biodiversity loss is similar when considering ecosystem trends as a considerable percentage of the world's natural biomes have already been converted to humanized landscapes or damaged beyond repair (Millennium Ecosystem Assessment 2005).

The causes for the current escalating biodiversity loss are well documented. They are mostly human-induced and a primal consequence of economical globalization. Exponential human population growth and increased patterns of consumption have amplified the demand for ecosystem services, resulting in several drivers of biodiversity loss acting synergistically (Brook et al. 2008). Among the most important ones are overexploitation of biological resources, rapid conversion and fragmentation of natural habitats, accelerated climate change, increased dissemination of invasive species, pollution and genetic depletion (Davies et al. 2006; Ehrlich and Pringle 2008; Groom et al. 2006; Parmesan 2006; Purvis et al. 2000; Thomas et al. 2004).

As a consequence of biodiversity loss, approximately 60% of the Earth's ecosystem services have been degraded in the last 50 years (Millennium Ecosystem Assessment 2005). This degradation has been disrupting ecosystem functions and decreasing ecosystem's resilience to disturbances, and is starting to have serious socio-economic impacts (TEEB 2008).

1.1.3 Protected areas

Governments and conservation organizations around the world recognize the urgent need to stop biodiversity loss. Over 180 governments have legally committed to conserve biodiversity by signing the Convention on Biological Diversity (CBD), and committed to achieve a significant reduction in the rate of biodiversity loss by 2010. However, it was already recognized that this target was not met (Secretariat of the Convention on Biological Diversity 2010) and recently reported indicators showed that biodiversity continues to decline rapidly, while pressures on biodiversity have increased (including resource consumption, invasive alien species, nitrogen pollution, overexploitation, and climate change impacts) (Butchart et al. 2010).

The CBD encourages governments to endorse in-situ conservation by establishing a system of Protected Areas (PAs). Protected areas are one of the most effective tools available for long-term biodiversity conservation (Possingham et al. 2006), and governments throughout the world have set aside fractions of their territory for conservation purposes. Although the global network of PAs has been increasing in the last decades, both on terrestrial and marine environments (UNEP 2009) (Figure 1.1), it is still far from achieving sufficient coverage of vertebrate species (Rodrigues et al. 2003), and PAs are often ineffective in halting biodiversity loss (McDonald-Madden et al. 2009; Secretariat of the Convention on Biological Diversity 2010). Thus, if biodiversity loss is to be prevented, further conservation areas have to be designated and managed more efficiently.

Designating new PAs is a complex task because there are several competing land-use options and considerable socio-economic costs associated with PAs implementation (James et al. 2001). For example, there are direct economical costs for purchasing land (Ando et al. 1998; Carwardine et al. 2008), managing protected areas and acquiring data (Grantham et al. 2008, 2009). In many cases there are also costs for compensating land owners and residents for forgone opportunities (Carwardine et al. 2008), or for forgone benefits from alternative land uses (Adams et al. 2010; Naidoo and Iwamura 2007). Because spatial and financial resources constrain PAs designation (James et al. 2001), a prioritization procedure is mandatory (Halpern et al. 2006a; Pearce 2007; Wilson et al. 2009b).

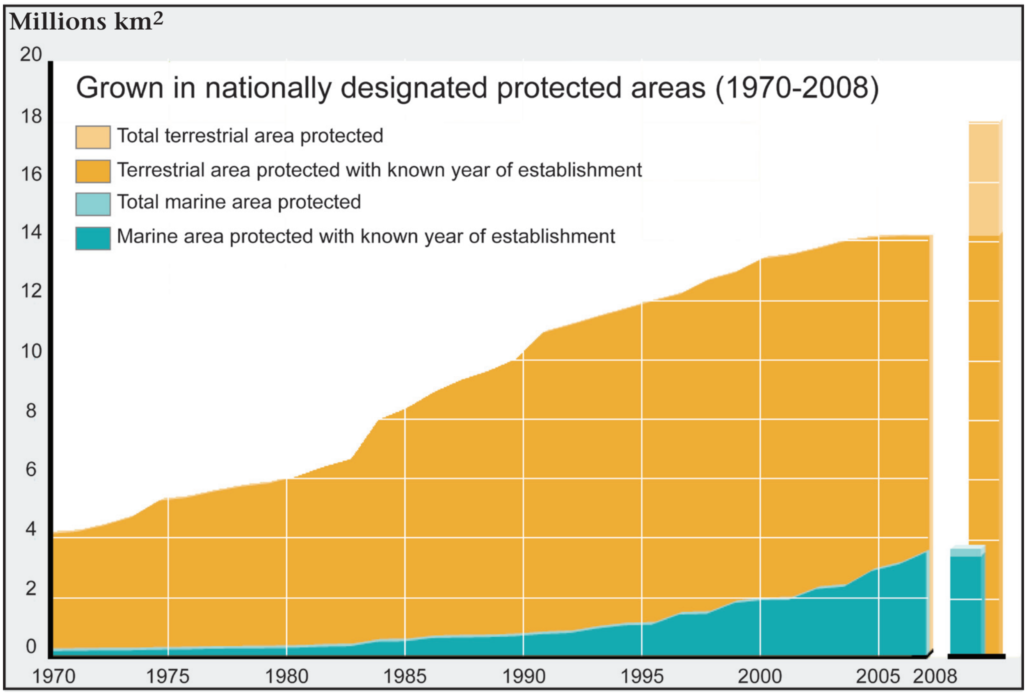


Figure 1.1- Extent of nationally designated protected areas through time. Adapted from Secretariat of the Convention on Biological Diversity (2010).

1.2 The science of conservation planning

Conservation planning is the field of conservation science concerned with the processes of locating and designing conservation areas to promote biodiversity persistence *in situ*. These conservation areas include both strict reserves and off-reserve areas with planed management.

The last two decades have been fruitful in the field of conservation planning. Moving from defining protected areas ad-hoc or based on aesthetic or recreational criteria, conservationist practitioners started to use data on the spatial distribution of biodiversity or its surrogates (Ferrier and Watson 1997; Margules et al. 1988). A common strategy is to use scoring methods to rank areas according to a biodiversity index, or a combinations of indices, such as species richness, rarity, level of endemism or threat (e.g. Margules and Usher 1981; Pressey and Nicholls 1989; Smith and Theberge 1987; Williams et al. 1996). In some cases, other geographic, ecological, economic, and social indices are also included. Such strategies are applied worldwide by many nature conservancy agencies, resulting in the identification of several important areas for conservation (reviewed by Brooks et al. 2006). Global prioritization approaches include, for example, biodiversity hotspots (Myers et al. 2000), crisis ecoregions (Hoekstra et al. 2005), key biodiversity areas (Eken et al. 2004) and Global 200 ecoregions (Olson and Dinerstein 2002). However, these diverse approaches have been criticized for identifying areas with limited consensus (Lamoreux et al. 2006; Orme et al. 2005; Prendergast et al. 1993), duplicating conservation efforts (Mace et al. 2000), excluding economic and social factors (Possingham and Wilson 2005) and, more importantly, for not establishing explicit conservation goals that can be translated into quantitative and operational targets towards which progress can be measured (Wilson et al. 2006). In face of such criticisms, a new field of systematic conservation planning has emerged (Margules and Sarkar 2007; Margules and Pressey 2000), as well as powerful and quantitative tools to address complex spatial prioritization problems that objectively inform the decision-making process (Moilanen et al. 2009c).

1.2.1 Objectives and key principles of systematic conservation planning

Systematic conservation planning is a framework developed to efficiently identify conservation areas that assure species representation and persistence. The objective of achieving species representation requires that all relevant features of biodiversity are covered within the selected conservation areas with a desired target, while the objective of assuring biodiversity persistence involves covering and managing a variety of ecological and evolutionary processes.

Systematic conservation planning has several distinctive characteristics. Probably the most defining one is the use of spatially explicit and quantitative objectives for representation and persistence of biodiversity features. This means that planners must be clear about what they intend to achieve and measure progress towards those objectives. Another important characteristic is being a process guided by a set of key principles described next (Possingham et al. 2006; Wilson et al. 2009a).

Comprehensiveness and representativeness

A comprehensive set of conservation sites is the one that includes a portion of each biodiversity feature. The principle of representativeness is similar to comprehensiveness, but it defines representation at a finer scale. A representative set of conservation sites is the one that assures that each conservation feature is sufficiently represented, for example by including viable populations.

Complementarity and efficiency

These two principles are directly related to the economy of selected conservation sites. Comprehensiveness and representativeness could be achieved by selecting all the available sites, but such strategy is unfeasible in the real world where options are constrained by limited financial resources. Thus, an efficient set of conservation sites is the one that achieves comprehensiveness and representativeness at the lowest possible cost. The complementarity principle (see Justus and Sarkar 2002; Kirkpatrick et al. 1983; Vane-Wright et al. 1991) ensures that the sites selected complement each other in terms of the type and amount of conservation features that they cover. Thus, maximising complementarity allows identifying conservation areas that overall add as much biodiversity as possible to the complete set of selected conservation areas .

Flexibility and irreplaceability

Flexibility refers to the amount of possible combinations of conservation sites that can be selected to achieve the representation goals efficiently. Flexibility is desirable because it allows for negotiations with land-owners and stakeholders, and for reductions in socio-economical conflicts. In contrast, irreplaceability refers to how essential a given site is to achieve representativeness. A site is highly irreplaceable when it includes at least one rare or endemic feature. Thus, irreplaceability identifies the non-negotiable conservation areas (Carwardine et al. 2006; Ferrier et al. 2000; Pressey et al. 1994).

Adequacy

Adequacy refers to the ability of a set of conservation areas to promote persistence and continued evolution of all biological features represented. This principle is usually neglected probably due to a lack of adequate data or to the limited understanding of the ecological and evolutionary processes underlying species persistence. Common approaches of addressing adequacy include the setting of ecologically meaningful conservation targets and the incorporation of spatial configuration criteria. For example, targets can be set based on population viability analyses (Carroll et al. 2003; Soulé 1987) or using probabilities of persistence (Araújo and Williams 2000; Williams and Araújo 2000). Spatial configuration criteria can include reserve size, number of reserves, reserve proximity, connectivity and shape, and rules about establishing core and buffer zones (Briers 2002; Williams et al. 2005a,b). Additionally, some authors have explicitly addressed ecological and evolutionary processes by identifying spatial surrogates. For example, targets have been set for edaphic and upland–lowland interfaces, for sand movement and inter-basin riverine corridors, and for macroclimatic gradients (Pressey et al. 2003; Rouget et al. 2003). Others have used sub-catchments as planning units, thereby grouping priority areas along vegetated waterways (Klein et al. 2009). There have also been some attempts to integrate information on phylogenetic diversity directly (e.g. Faith et al. 2004; Forest et al. 2007).

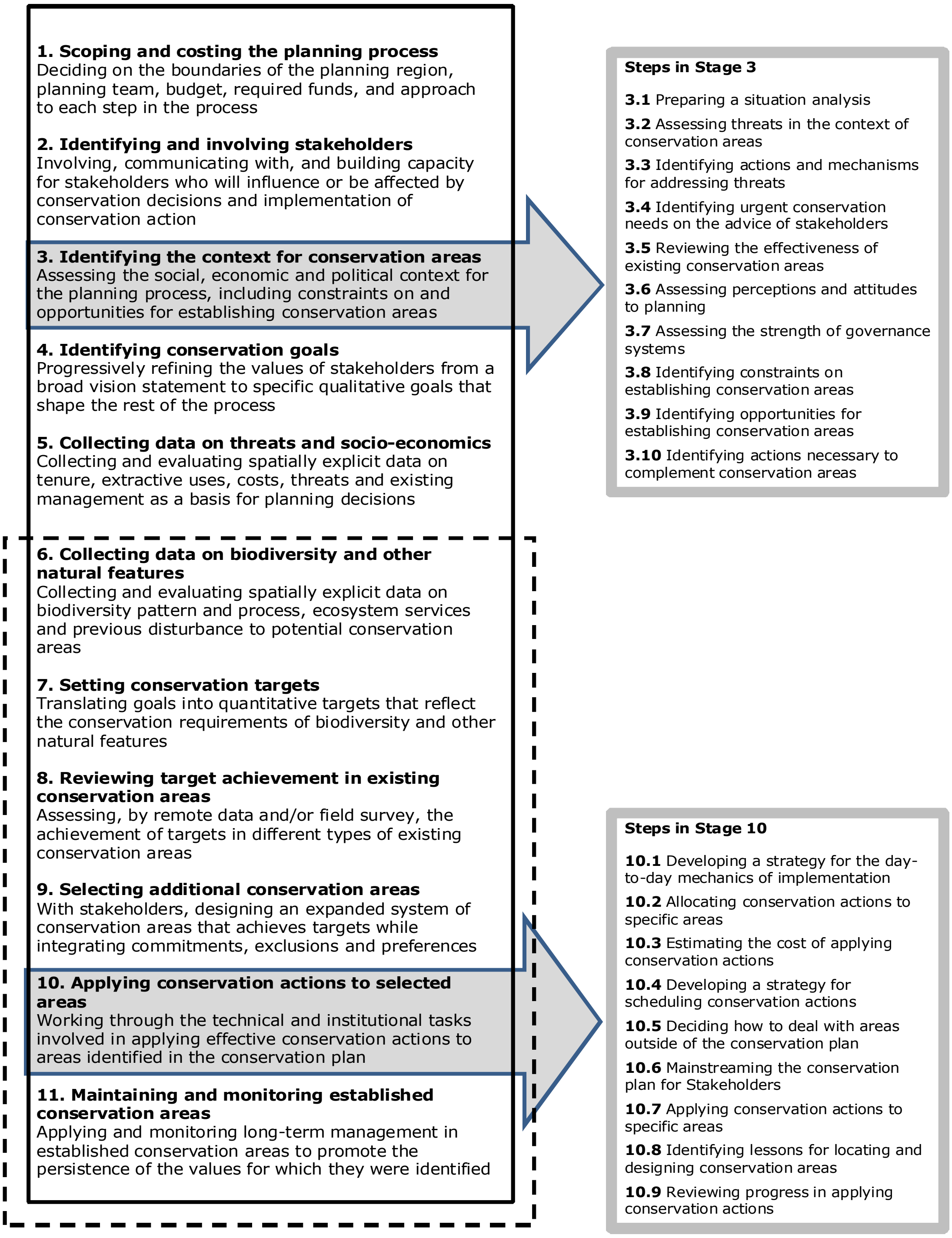
1.2.2 Stages and conceptual framework of systematic conservation planning

An effective conservation planning approach follows a well defined series of steps. The original framework proposed by Margules and Pressey (2000) comprised six steps, however, it has been extended throughout time with main contributions from Cowling and Pressey (2003) and Pressey and Bottrill (2008) (Figure 1.2).

Systematic conservation planning can be represented with a conceptual framework which can be divided into three main subgroups: objectives, constraints and solutions (Moilanen 2008) (Figure 1.3). Representation and persistence objectives require clear choices on how biodiversity is to be included in the process, which taxa should be targeted, which ecological and evolutionary processes are necessary to promote biodiversity persistence and which are the conservation targets. These tasks, in turn, imply compiling accurate data on the distribution of the conservation features and to apply appropriate statistical procedures to improve spatial consistency or derive surrogates. Data quality and accuracy are regulated by three interrelated concepts: uncertainty, dynamics and threats. Data uncertainty can arise from multiple sources, including data sampling and statistical uncertainty. Moreover, uncertainty can be exacerbated by shifts in species ranges with time, which in turn can be determined by ecological disturbances or anthropogenic threats.

The “constraints” subgroup refers to the restrictions of possible conservation strategies and may include economical costs, unavailable lands and spatial configurations requirements. The “solutions” subgroup relates to the methods used to identify and implement a set of conservation actions required to achieve the conservation objectives.

The identification of optimal solutions is guided by the set of key principles described above, which can be expressed in a mathematical manner and included in prioritization algorithms. However, the implementation of algorithmic solutions is also subject to a decision-making process that involves the opinions of experts, stakeholders and politicians, and is guided through socio-economical pressures.



1. Scoping and costing the planning process
Deciding on the boundaries of the planning region, planning team, budget, required funds, and approach to each step in the process

2. Identifying and involving stakeholders
Involving, communicating with, and building capacity for stakeholders who will influence or be affected by conservation decisions and implementation of conservation action

3. Identifying the context for conservation areas
Assessing the social, economic and political context for the planning process, including constraints on and opportunities for establishing conservation areas

4. Identifying conservation goals
Progressively refining the values of stakeholders from a broad vision statement to specific qualitative goals that shape the rest of the process

5. Collecting data on threats and socio-economics
Collecting and evaluating spatially explicit data on tenure, extractive uses, costs, threats and existing management as a basis for planning decisions

6. Collecting data on biodiversity and other natural features
Collecting and evaluating spatially explicit data on biodiversity pattern and process, ecosystem services and previous disturbance to potential conservation areas

7. Setting conservation targets
Translating goals into quantitative targets that reflect the conservation requirements of biodiversity and other natural features

8. Reviewing target achievement in existing conservation areas
Assessing, by remote data and/or field survey, the achievement of targets in different types of existing conservation areas

9. Selecting additional conservation areas
With stakeholders, designing an expanded system of conservation areas that achieves targets while integrating commitments, exclusions and preferences

10. Applying conservation actions to selected areas
Working through the technical and institutional tasks involved in applying effective conservation actions to areas identified in the conservation plan

11. Maintaining and monitoring established conservation areas
Applying and monitoring long-term management in established conservation areas to promote the persistence of the values for which they were identified

Steps in Stage 3

3.1 Preparing a situation analysis

3.2 Assessing threats in the context of conservation areas

3.3 Identifying actions and mechanisms for addressing threats

3.4 Identifying urgent conservation needs on the advice of stakeholders

3.5 Reviewing the effectiveness of existing conservation areas

3.6 Assessing perceptions and attitudes to planning

3.7 Assessing the strength of governance systems

3.8 Identifying constraints on establishing conservation areas

3.9 Identifying opportunities for establishing conservation areas

3.10 Identifying actions necessary to complement conservation areas

Steps in Stage 10

10.1 Developing a strategy for the day-to-day mechanics of implementation

10.2 Allocating conservation actions to specific areas

10.3 Estimating the cost of applying conservation actions

10.4 Developing a strategy for scheduling conservation actions

10.5 Deciding how to deal with areas outside of the conservation plan

10.6 Mainstreaming the conservation plan for Stakeholders

10.7 Applying conservation actions to specific areas

10.8 Identifying lessons for locating and designing conservation areas

10.9 Reviewing progress in applying conservation actions

Figure 1.2 - An evolving framework for conservation planning with 11 main stages. Text under the heading for each stage summarizes the main issues to be addressed (see Margules and Pressey 2000 and Cowling and Pressey 2003 for more detail on most stages). For convenience, the process is depicted as a linear sequence, but in reality some stages are undertaken simultaneously and there are many feedbacks from later to earlier stages. The dashed rectangle contains the stages described by Margules and Pressey (2000). Shown on the right are the steps involved in stages 3 and 10. Adapted from Pressey and Botrill (2008).

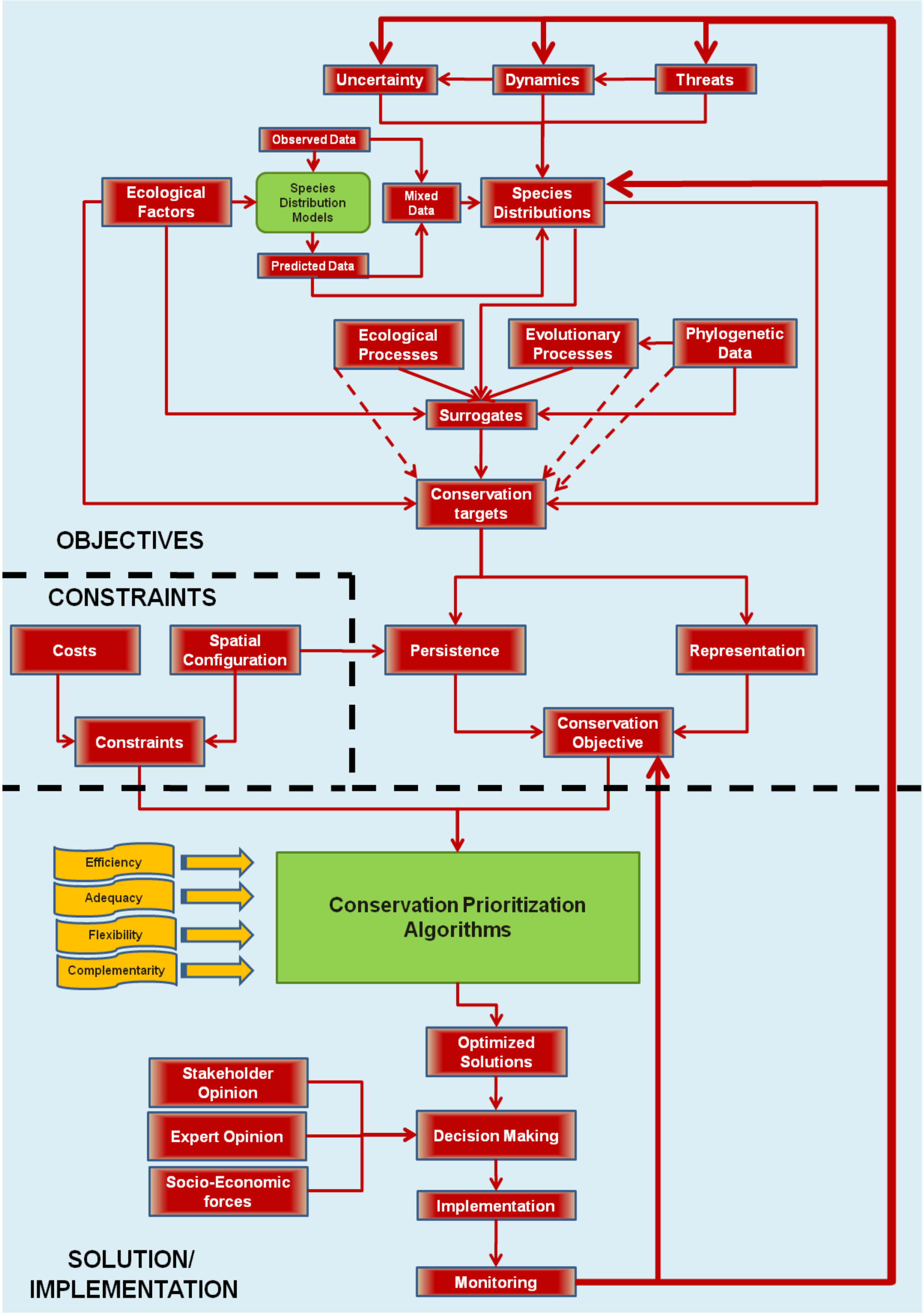


Figure 1.3 - A schematic overview of the systematic conservation planning process. Arrows show the direction of the relation between concepts. Green boxes represent analytical/ computational processes. Yellow boxes represent systematic conservation planning concepts underlying conservation prioritization algorithms. Based on Moilanen (2008) and Arponen (2009)

1.2.3 Algorithms and computational tools for spatial prioritization

Conservation planning has made extensive use of computational tools to assist the decision making process. Their purpose is not to impose a course of action, but rather to inform decision-making (Possingham et al. 2001; Pressey and Cowling 2001). In general, there are two major classes of conservation prioritization problems: the "minimum set" and the "maximal cover" (see Cabeza and Moilanen 2001; Moilanen et al. 2009a; Sarkar et al. 2006; Williams et al. 2004 for reviews). In the "minimum set" problem, the objective is to minimize the total cost of selected sites such that each species is represented at or above a pre-determined target (Kirkpatrick 1983; Pressey 2002; Pressey et al. 1993). In the "maximal cover" problem, the objective is to find a reserve system that contains the largest number of species meeting their targets, subject to a limit on the total cost of the selected planning units (Arthur et al. 1997; Camm et al. 1996; Church et al. 1996). These problems can be mathematically formalized and solved using heuristics, meta-heuristics and optimal algorithms. (Possingham et al. 2000, 1993; Pressey et al. 1996, 1997; Rodrigues and Gaston 2002b; Underhill 1994). Some of these mathematical approaches were implemented in computational tools, such as Marxan (Ball et al. 2009) and Zonation (Moilanen et al. 2009b).

1.3 Challenges in conservation planning

Despite the immense progress that conservation planning has achieved in the last decades, there are still many challenges to overcome. The next paragraphs describe some of the issues addressed in this thesis.

1.3.1 Issues about species' distribution data

Systematic conservation planning requires spatially explicit data on the distribution of natural features (Brooks et al. 2004; Ferrier 2002b; Margules and Pressey 2000). These natural features can include biodiversity in any of its forms (ecosystems, communities, species and genetic diversity), natural processes related to biodiversity origin and persistence (such as dispersion, migration, ecological and evolutionary refugia and disturbance regimes), or even ecosystem services (such as flood control from wetlands and carbon sequestration from forests).

Our understanding of the spatial distribution of natural features has increased substantially in recent years. However, there is still limited knowledge on biodiversity levels since most species have not been formally described yet (the Linnean shortfall), and the geographical distributions for the majority of taxa are insufficiently understood (Wallacean shortfall) (Whittaker et al. 2005). On the other hand, the available data also poses some challenges because it is usually biased towards developed countries, charismatic species, easily accessible sites, field stations or areas close to major universities or museums (Grand et al. 2007; Harris and Froufe 2005; Possingham et al. 2000).These biases can affect the accuracy of conservation planning outcomes and introduce uncertainty and subjectivity into the planning process.

Prior to the planning process it is important to decide when the available data is sufficient and when investment in data acquisition is needed (Grantham et al. 2008, 2009). Nevertheless, the development of conservation plans should not be hindered by limited data on biodiversity (Pressey 2004) as conservation prioritization based on scarce data can be highly effective in representing species (Gaston and Rodrigues 2003), and several biodiversity surrogates can be used instead (Ferrier 2002a; Rodrigues and Brooks 2007).

The emergence and the relatively fast progress of species' distribution models (SDMs) have been paramount in conservation planning as ways to address the paucity and biases in species' distribution data (Elith and Leathwick 2009a; Rodríguez et al. 2007). Species' distribution models aim to determine and map the components of a species' ecological niche through space by using spatial environmental data to make inferences on species' limits and habitat suitability. Suitable environmental conditions for any given species may be characterized using either mechanistic or correlative approaches. Mechanistic models aim to incorporate physiologically limiting mechanisms in a species' tolerance to environmental conditions. Such models require a detailed understanding of the physiological response of the species to environmental factors and are therefore complex to develop for all but the most well-studied species. Thus, correlative approaches are more widely used than mechanistic ones. Correlative SDMs are statistical or machine-learning tools that combine scattered, biased and incomplete observations of species occurrences or abundances with environmental variables to predict the complete distribution of the species (Elith and Leathwick 2009b; Guisan and Thuiller 2005; Guisan and Zimmermann 2000). Correlative models have been developing at an accelerated pace, with several statistic methods emerging in the last two decades as well as evaluation procedures and computational tools (Franklin 2009) (Table 1.1).

Differences between SDM methods rely mostly on the type of algorithm used to make the predictions, the type of occurrence data needed and the type of output prediction. SDMs also differ in their ability to predict uncertainty and to ensemble different predictions. However, one of the major distinctive characteristics of SDMs methods is the type of input data. Some algorithms operate by comparing sites according to the presence/absence of a species, although reliable absence data is usually not available. In contrast, presence-only methods do not require absence data. While some of these presence-only methods require only presence records (such as BIOCLIM or ENFA), others require presence data and background points to contrast them (e.g. Maxent). In extreme, all presence-absence methods can operate by generating pseudo-absences, i.e. by assuming that some of the locations where the species is not known to occur are true absences. Another important characteristic is in the form of their output, with options usually being either a continuous probability of occurrence values (ranging from 0 to 1) or a binary prediction (0 or 1 values, standing for unsuitable or suitable environmental conditions, respectively). However, continuous probability outputs can be transformed into binary predictions by setting a threshold above which the environmental conditions would be assumed as suitable. There are several possible methods to set this threshold (e.g. Liu et al. 2005).

Table 1.1 - Frequently used species' distribution model methods, their main characteristics and key references. PO – presence-only methods; PA – presence-absence methods. Adapted from Elith and Leathwick (2009a) and Guisan and Thuiller (2005).

Name	Algorithm	Input data	Output type	References
BIOCLIM	Envelope	PO	Rank	Busby 1991
DOMAIN	Similarity	PO	Continuous	Carpenter et al. 1993
Ecological Niche Factor Analysis (ENFA)	Factor Analysis	PO	Continuous	Hirzel et al. 2002
Genetic Algorithm for Ruleset Production (GARP)	Genetic algorithm	PO	Rank	Stockwell et al. 1999
Maxent	Maximum entropy	PO	Continuous	Phillips et al. 2006, 2004; Phillips and Dudík 2008
Generalized Linear Model (GLM)	Regression	PA	Continuous	McCullagh and and Nelder 1989
Generalized Additive Model (GAM)	Regression	PA	Continuous	Hastie and Tibshirani 1990
Multivariate Adaptative Regression Splines (MARS)	Machine learning/ Regression	PA	Continuous	Friedman 1991
Nonparametric Multiplicative Regression (NPMR)	Machine learning/ Regression	PA	Continuous	McCune 2006
Artificial neuronal networks (ANN)	Machine learning/ Regression	PA	Continuous	Ripley 1996
Boosted regression trees (BRT) or Generalised Boosting Model (GBM)	Machine learning/ Tree/ Regression	PA	Continuous	Elith et al. 2008; Friedman 2001; Ridgeway 2004
Random Forests (RF)	Machine learning/ Tree	PA	Continuous	Breiman 2001; Prasad et al. 2006
Classification Tree Analysis (CTA)	Machine learning/ Tree	PA	Continuous	Breiman et al. 1984
Mixture Discriminant Analysis (MDA)	mixture models/ linear discriminant analysis	PA	Continuous	Hastie and Tibshirani 1996; Hastie et al. 1995

Several studies have attempted to evaluate the performance of different methods for modeling species' distributions and have demonstrated that discrepancies between different techniques can be very large (e.g. Elith et al. 2006; Elith and Leathwick 2009b; Hernandez et al. 2006; Segurado and Araújo 2004; Tsoar et al. 2007). The efficacy of the methods depends of several factors such as the quantity and quality of occurrence data, the choice of environmental predictors, the species' ecological characteristics, the scale of analysis and the biotic interactions (Araújo and Luoto 2007; Costa et al. 2010; Franklin et al. 2009; Graham et al. 2008; Guisan et al. 2007a,b; Hernandez et al. 2006; Kriticos and Leriche 2010; Lassueur et al. 2006; Loiselle et al. 2008; McPherson and Jetz 2007; Peterson and Nakazawa 2008; Pöyry et al. 2008; Seo et al. 2009; Stockwell and Peterson 2002; Syphard and Franklin 2009). No single method is currently considered to perform better in every condition, although some methods consistently outperform others. In general, methods with higher performance are able to identify complex relationships in the data including interactions between environmental variables. Among the best performing methods, Maxent has been one of the most used because it generally has high predictive performance even with a small number of occurrence records (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008). Other advantages of Maxent include operating with presence-only data sets and allowing for category predictors (Elith and Leathwick 2009a).

The application of SDMs in conservation planning goes beyond the prediction of current species' ranges in data deficient situations (Guisan and Thuiller 2005). For example, SDMs allow the prediction of sites of different suitability within the predicted distribution of the species, which in turn can be used to select sites where the species persistence is more likely (Araújo and Williams 2000; Cabeza 2004). SDMs also allow the reconstruction of past species' distributions (e.g Araújo et al. 2008; Carnaval and Moritz 2008) and the prediction of future species' ranges (e.g. Coetzee et al. 2009; Hannah et al. 2007; Hole et al. 2009; Thuiller et al. 2005). SDMs can even be used to assist conservation of species that have not been described (Bini et al. 2006; Possingham et al. 2007). Indirect applications of SDMs to conservation planning include their ability to predict invasion and proliferation of exotic species (e.g. Jeschke and Strayer 2008; Roura-Pascual et al. 2008), to identify areas of possible expansion or reintroduction of endangered species (Cianfrani et al. 2010), to improve the sampling of rare species (Guisan et al. 2006), and to predict the expansion of vectors of wildlife diseases (e.g. Puschendorf et al. 2009). But despite the usefulness of SDMs, caution is needed in its application to conservation planning because all models contain some degree of mismatch between their predictions and the actual distribution of species.

There are several sources of error that can lead to uncertainty in model predictions (Barry and Elith 2006; Elith et al. 2002). Occurrence samples can contain errors when species are misidentified, when there are inaccurate records of the geographic location of observations (Graham et al. 2008), or when using out-dated historical references (Hortal et al. 2008). Other frequently detected limitations related with occurrence samples is sample size, since most modeling methods require a minimum number of occurrence samples to produce robust predictions. In general, the minimum number of records required depends on the complexity of the pattern being modeled (Barry and Elith 2006). Some methods also require a minimal number of true absences. Additionally, occurrence data is usually biased towards particular features (as discussed above) and do not cover the full range of the environmental gradients, which can induce biases in model fitting (Hortal et al. 2008).

Uncertainty in SDM outcomes can also derive from the predictors used to fit the model, for example, when there is a lack of knowledge of which environmental factors constrain the distribution of a species. In addition, inaccurate predictions can arise when that knowledge exists but the required data are not available, are not mapped at an ecologically significant scale (Seo et al. 2009; Trivedi et al. 2008), or contain measurement errors (Graham et al. 2008). Finally, uncertainties related to ecological assumptions, such as biotic interactions, dispersion abilities, geographic factors (such as geographic barriers) or historical constraints can also induce inaccurate model predictions (Lomolino et al. 2005).

Because both observed occurrence and predicted species distribution data contain uncertainty, it is debatable which data type will be most suited to use in conservation planning. Advantages and disadvantages of using different types of occurrence data or SDMs predictions in conservation planning have been discussed previously (e.g. Freitag et al. 1996; Pressey et al. 1999; Rondinini et al. 2006; Underwood et al. 2010; Wilson et al. 2005). In theory, observed data contain higher confidence in validity of species occurrences, but a large proportion of false species absences, i.e. omission errors. When used for conservation planning, this type of data is more reliable because the selected priority sites will actually represent the species' presence. However, there will be less options of possible sites combinations resulting in more selected areas, higher costs, and limited negotiation opportunities with stakeholders. In contrast, predicted distribution data contain a high proportion of false occurrences (commission errors), because models tend to over predict species' distributions. Consequently, sites where species do not occur can be mistakenly selected for conservation.

Several factors have been reported to influence the type of species' distribution data chosen for conservation purposes. These include, for example, the amount of data availbale when the planning process starts (Freitag and van Jaarsveld 1998; Grand et al. 2007), the level of the representation target to be achieved (Justus et al. 2008; Warman et al. 2004), and the size (Warman et al. 2004) and costs (Bode et al. 2008) of the planning units. However, the impact of these factors to the conservation planning processes remains largely unknown. Thus, it is important to understand how sensitive the prioritization algorithms are to these factors and to variations in data type and quality .

1.3.2 Incorporating evolutionary processes into conservation planning

Conservation planning has focused more on the biodiversity patterns (representation) than on the evolutionary processes that generate and maintain biodiversity (Pressey et al. 2007). However, it is essential to understand the processes that affect the amount and distribution of biological variability, and the ability of organisms to adapt and evolve (Crandall et al. 2000; Mace and Purvis 2008). Evolutionary tools can support conservation planning by discovering and documenting biodiversity, understanding the causes of diversification and evaluating evolutionary responses to ecological disturbances (Hendry et al. 2010 and references therein).

Evaluating evolutionary distinctiveness and adaptation potential

Several methodologies have been suggested to address the representation of evolutionary history and processes using diverse biodiversity levels. One way to address evolutionary history is to consider that species are not discrete biologic units. Species differ substantially in the amount of unique evolutionary history they embody, reflecting the time and mode of divergence. Some biologic features are shared among species, while others are exclusive of a particular species. Thus, the principle of complementarity, which in conservation planning is usually applied to areas, can be extended to taxa (Faith et al. 2004). Evolutionary distinct taxa are expected to have a higher diversity of biological features, and consequently, to make a larger contribution to some overall measure of diversity. Thus, the extinction of a species in an old, monotypic or species-poor clade would result in a greater loss of biodiversity than that of a young species with many close relatives (Mace et al. 2003). The “uniqueness” of a particular taxa relative to the others can be measured and taxa with unique evolutionary histories should be given higher priority for conservation (Avise 2005).

One of the most used diversity metric for measuring evolutionary distinctiveness is phylogenetic diversity (PD) (Faith 1992; Vane-Wright et al. 1991). Phylogenetic diversity is a biodiversity index that measures the length of the evolutionary pathways that connect a given set of taxa (Figure 1.4). In other words, PD represents the sum of the branch lengths of a phylogenetic tree containing a set of species and the root.

Originally, PD was formulated to be measured on cladograms where distances between branches represented changes among phenotypic characteristics of distinct taxa. The procedure evolved to incorporate genetic differences among taxa given the advances in molecular ecology (e.g. Avise 2005; Crozier 1992). The rationale in using molecular divergence to build phylogenetic trees is the correlation of branch length with time since divergence, and the fact that phenotypic characters also change according to a clock-like anagenetic model (Moritz and Faith 1998).

The complementarity principle of conservation planning can be applied to phylogenetic diversity by selecting a set of species that maximize PD using several algorithms developed for this purpose (e.g. Rodrigues and Gaston 2002a; Steel 2005). In general, in a balanced tree, PD would be higher if one selects a set of species from branches separated

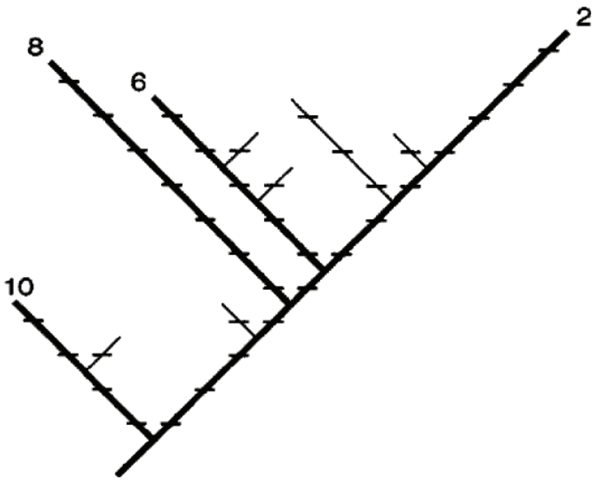


Figure 1.4 - A hypothetical phylogenetic tree. The path connecting the four taxa (2,6,8 and 10) with maximum expected feature diversity is shown by the thickened lines. The number of transverse tick marks in this path is 28 indicating the relative feature diversity for the set. Adapted from Faith and Baker (2006).

by the main splits in the tree, i.e. by selecting sample taxa of the main phylogenetic lineages (Rodrigues and Gaston 2002a, Avise 1992). These main lineages are probably the result of extensive historical isolation periods, such as vicariance events, (Avise 1992). While this approach maximizes the representation component of conservation planning (by including the highest genetic diversity), it has been criticized on the grounds that it disregards important areas of recent diversification. These areas comprise highest adaptive genetic variation among populations, where phenotypes and ecological traits are more distinct. Therefore they are important for conservation because they influence fitness and population viability in current and future environments (Smith et al. 2000, 2005). Consequently, it has been recognized that both the neutral and the adaptive components of genetic diversity need to be preserved while targeting conservation of evolutionary processes (Brooks et al. 1992; Moritz 2002) (Figure 1.5). However, despite the growing body of literature focusing on conservation of evolutionary processes, few have objectively focused on these two aspects simultaneously.

Identifying evolutionary processes in space

One of the challenges of integrating evolutionary processes in conservation planning resides on the fact that conservation planning is spatially explicit, making it necessary to spatially identify the two components of genetic diversity. Additionally, the selection of areas of conservation priority is constrained by combinations of co-occurring species (and corresponding genetic diversity). The aim of conservation planning should be to conserve the minimum set of areas that maximize representation of both neutral divergent and adaptive genetic variation. Hence, genetic diversity conserved by a given set of protected areas will depend on the structure of phylogenetic trees, on the spatial structure of genetic diversity, and on the relationships between the two.

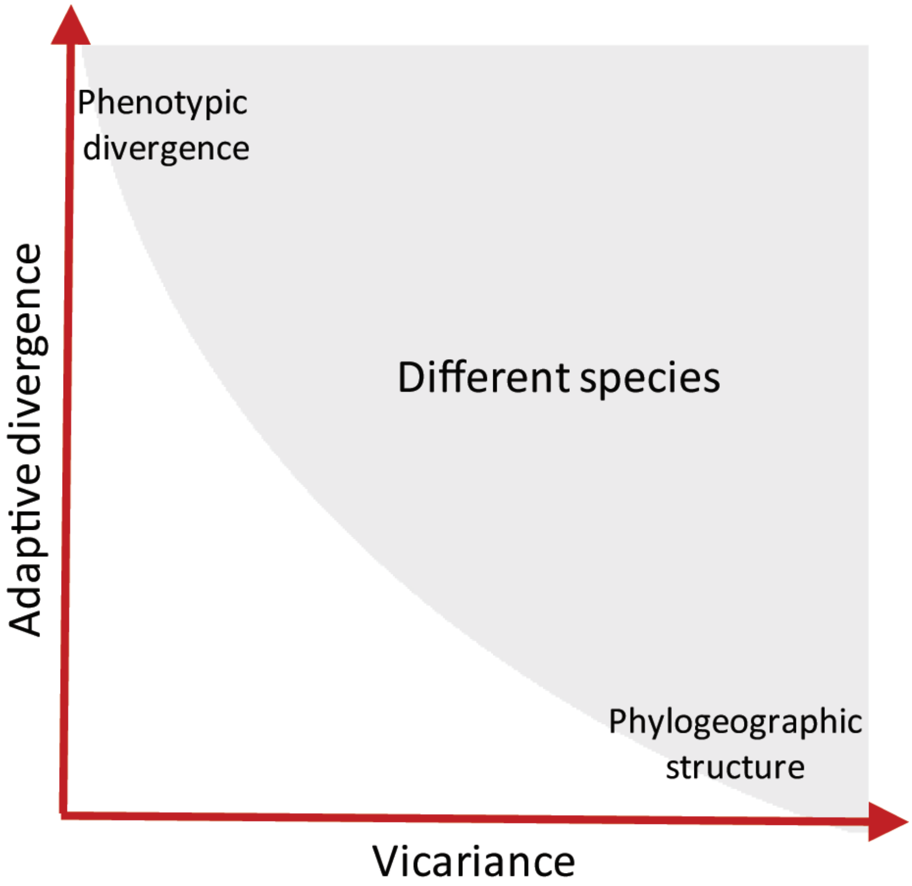


Figure 1.5 - Separation of genetic diversity into two components: adaptive variation that arises through natural selection, and neutral divergence due to vicariant evolution. The former is typically assayed through analysis of phenotypes and the later through molecular plylogeography. The areas in grey mean conditions where populations are likely to be considered as separate species under most concepts. Adapted from Moritz (2002).

Previous studies attempted to represent the neutral divergent component of genetic diversity in a spatial framework. For example, some authors (e.g. Moritz and Faith 1998; Smith et al. 2000) used comparative phylogeography to identify sets of species sharing a common vicariance history, and subsequently used Venn diagrams to identify areas representing unique lineages that were range-restricted (Figure 1.6). Another approach was to identify areas with higher concentrations of lineage breaks to reveal endemic areas at the subspecific level (Rissler et al. 2006). Other approaches combined phylogenetic diversity directly with other endemicity metrics (Faith et al. 2004; Posadas et al. 2001; Rosauer et al. 2009). On the other hand, the adaptive component of genetic diversity have been addressed by identifying areas where recently diverged endemic species co-occur, as a proxy for rapid diversification areas or evolutionary hotspots (Davis et al. 2007; Vandergast et al. 2008). The two components of genetic diversity have only recently been taken into account by modelling relationships between environmental heterogeneity and genetic and phenotypic variation (Thomassen et al. 2010).

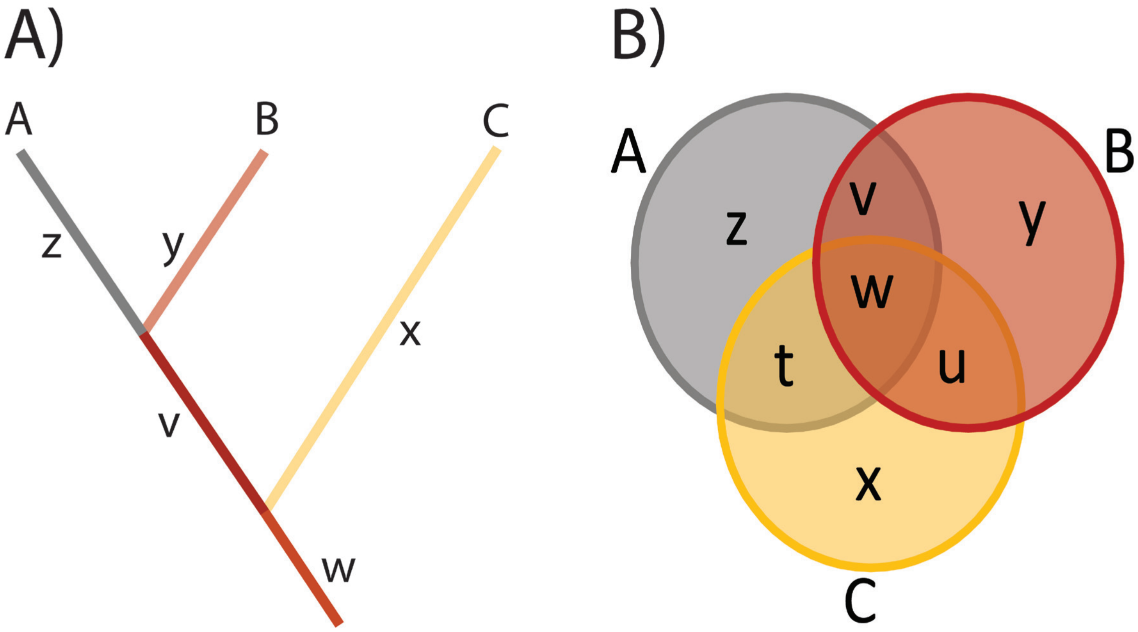


Figure 1.6 - Hypothetical phylogenetic tree for three alleles, each restricted to one area (A-C) with estimated branch lengths of v – z, and a corresponding Venn diagram indicating the components of branch length that are unique to areas or shared by one or more areas. Adapted from Moritz and Faith (1998)

Spatial surrogates for genetic diversity

Most attempts to integrate genetic diversity into conservation planning have focused on a limited number of taxa. Although there has been a boom of phylogenetic studies in the last decades, the information is difficult to integrate in conservation plans when targeting multiple taxa. The main reason underlying this difficulty may be that the available molecular data for different taxa has often been collected using different molecular markers and statistical methods, hindering their integration into consensual phylogenies. Moreover, molecular data is still lacking or is insufficient for most taxa, and processes driving adaptive variation have only recently begun to be understood. Therefore, using surrogates for evolutionary processes is often necessary in conservation planning, as well as identifying their spatial components.

Previous studies have called attention for multiple possible surrogates for evolutionary processes. For example, considering the neutral component of genetic diversity, Rodrigues et al. (2005) found that species richness was an adequate surrogate for phylogenetic diversity (PD) under a diversity of scenarios, particularly when taxonomy complementarity was accounted. A less explored surrogate for evolutionary processes is community structure. There is a growing recognition that evolutionary processes (speciation, vicariance, dispersal and extinction) interact with ecological processes (competition, predation and environmental filtering) to influence the distribution of species and traits in communities and vice versa (Cavender-Bares et al. 2009; Emerson and Gillespie 2008; Johnson and Stinchcombe 2007; Losos 1996; Vamosi et al. 2009;

Webb et al. 2002; Wiens and Donoghue 2004). Most of these studies have not addressed the potential of comparative phylogeography to understand community structure, probably due to a lack of molecular data fo multiple species (Hickerson et al. 2010). Nonetheless, a consistent finding in comparative phylogeography is that species with similar ranges tend to be genealogically structured in similar ways (Avise 2000, 2009). The explanation for this finding is that emergence of geographic barriers, such as mountains uplifts or marine gaps derived from continental drift can induce vicariance and subsequent allopatric speciation in several taxa (Hickerson et al. 2010). Consequently, deeply separated phylogroups are often confined to biogeographical regions as identified from current species assemblages (Avise 2000; Crisci et al. 2003). In other words, the vicariance model predicts that the ranges of the species originating by the same vicariant events will be, on average, more similar to each other (Hausdorf 2002). A classic example where genetic surveys have provided strong evidence for phylogeographic concordance is represented by the Mediterranean Peninsulas (Iberian, Italian and Balkan), which include several Pleistocene refugia for many taxa (Hewitt 2000; Taberlet et al. 1998; Weiss and Ferrand 2006). Further evidence of the vicariance role in structuring biotas is revealed by the concordance of Pleistocene refugia with current biodiversity hotspots, which represent areas where several endemic species co-occur (Carnaval et al. 2009; Médail and Diadema 2009). Thus, in areas where vicariance events played an important role in structuring biotas, the identification of groups of species with significantly co-occurring ranges may surrogate for the neutral divergent component of genetic diversity.

Regarding the adaptive component of genetic diversity, some studies used ecological and climatic gradients as surrogates, e.g, by identifying and targeting edaphic, upland–lowland and macroclimatic gradients (Cowling et al. 2003; Rouget et al. 2003). The rationale to use these surrogates is that ecology plays a major role in speciation (e.g. through adaptive radiation) (Smith et al. 2005) and because environmental gradients facilitate genetic differentiation and character displacement (Doebeli and Dieckmann 2003). Thus, adaptive speciation is expected to be greatest along steep environmental transitions, such as ecotones (Smith et al. 2001), which often coincide with areas with high beta diversity where different species assemblages co-occur (Spector 2002). However, crossroads constitute marginal areas of species distributions, where overall genetic diversity within populations is generally lower (Emerson and Gillespie 2008).

Ideally, conservation strategies should aim to preserve both neutral and adaptive components of genetic diversity. In face of inadequate molecular data, these could be achieved by protecting a proportion of all species assemblages and, within them, the contiguous habitats across major environmental gradients that potentially represent a variety of selective regimes, and guarantee maximum potential of species to respond to environmental changes (Moritz 2002; Smith and Grether 2008). However, such strategies have seldom been applied in conservation planning.

1.3.3 Dynamics in conservation planning: dealing with shifts in species' ranges derived by climate change

The conventional approach of systematic conservation planning assumes that both economic systems and biodiversity are static. Priority areas are often identified based on biodiversity distribution patterns at a given time and it is assumed that conservation implementation occurs immediately and that once implemented it will assure a perpetual persistence of biodiversity (Meir et al. 2004). However, a static approach may become inefficient (Leroux et al. 2007) because the attributes of the system may change between the planning and implementation phases, which is often the case in the currently complex and dynamic world (Drechsler 2005; Possingham et al. 2009; Pressey et al. 2007).

Methods used to target areas for conservation often disregard land market dynamics (Armsworth et al. 2006; McDonald-Madden et al. 2008b), social dynamics such as political instability and corruption, financial opportunities and budget continuity (McBride et al. 2007). Moreover, several human-induced changes in the environment are threatening biodiversity, leading to a dynamic geographic rearrangement of species distributions and to extinctions (McCarty 2002; Root et al. 2003; Sala et al. 2000; Thomas et al. 2004; Walther et al. 2002). Thus, dynamic threats to biodiversity change conservation priorities through space and time (Pressey et al. 2007; Visconti et al. 2010; Wilson et al. 2007)

Climate change as a driver of shifts in biodiversity distribution

Climate change has been declared as one of the major threats to biodiversity (Jetz et al. 2007; Lee and Jetz 2008; Sala et al. 2000) and it is already driving changes in species distributions (Parmesan and Yohe 2003; Walther et al. 2005). Such changes pose major challenges to conservation planning, because it may cause species to shift their range away from current protected areas, and additional areas may become required to achieve sufficient species representation in the future (e.g. Araújo 2009; Araújo et al. 2004; Hannah et al. 2007; Lee and Jetz 2008). Thus, the scientific community is being asked to forecast changes in species distributions and to take proactive actions to facilitate biodiversity adaptation to climate change.

Species distribution models (SDMs) (see topic 1.3.1) are the most commonly used tools for forecasting the potential impacts of climate change on species distributions (e.g. Hannah et al. 2002; Pearson and Dawson 2003). These tools assess species-climate relationships by relating current species distributions with present climate and then project those relations into future climate scenarios. This way, information on current and future distribution of species can be integrated into reserve selection algorithms and taken into account in conservation planning strategies.

Uncertainties in projections of future species distributions

The ability of SDM to realistically predict future species distributions has been challenged to the point of jeopardizing its usefulness in informing conservation decisions. Criticisms to SDMs arise mostly from its multiple sources of uncertainty, which become particularly worrying in the context of climate change. The major sources of uncertainty can be categorized into three groups: climatic, biological, and statistical (Beaumont et al. 2008; Dormann et al. 2008; Heikkinen et al. 2006).

Climatic uncertainty arises from projections of future climate which are usually accomplished by integrating global circulation models (GCMs) with projections of greenhouse gas concentrations. GCMs are based on equations that describe physical processes of atmosphere or ocean dynamics and allow simulating the response of the global climate to increasing greenhouse gas concentrations. Several GCMs have been developed by distinct meteorological research centres with different parameterizations and performances (Randall et al. 2007). Conversely, future greenhouse gases concentrations are also uncertain with estimates based on different scenarios of driving forces such as demographic grow, socio-economical and environmental developments, and technological and energetic changes (Nakicenovic and Swar 2000). Hence, combinations of GCMs and storylines retrieve fairly different estimates of future climate conditions. Moreover, uncertainty in future climate conditions also arise from methods used to downscale climate scenarios and from uncertainties in current climate data (Beaumont et al. 2008).

Biological uncertainty is related to the insufficient knowledge on biodiversity distribution and with the way that different species will respond to climate change. Beyond biological uncertainties related with predicting current species distributions already discussed (topic 1.3.3), there are additional ones related with future predictions (Zurell et al. 2009).These include, for example, uncertainties in a) biotic interactions (Araújo and Luoto 2007); b) in interactions between population processes, and between demographic and landscape dynamics (Brook et al. 2009; Keith et al. 2008); c) in species ability to disperse (Thuiller 2004; Thuiller et al. 2008); and d) in species ability to adapt and persist (Thuiller et al. 2008; Williams et al. 2008).

If the outcome of SDMs is to be useful for decision-makers, uncertainty related to projections of future distributions needs to be understood and quantified (Pearson et al. 2006). Recently, it has been argued that the use of multiple model techniques and several combinations of GCMs-storylines is recommended to achieve more robust forecasts (Araújo and New 2007; Araújo et al. 2005; Leutbecher and Palmera 2008). The approach consists in finding a consensus that summarizes the variability within the multiple predictions and is often referred to as ensemble forecasting. There are multiple ways to find a consensual forecast, for instance, averaging the predictions of multiple models was found to increase significantly the accuracy of predictions (Marmion et al. 2009). Using multiple SDMs and future climate scenarios also allows the determination of the variability between models, which can be used as a measure of uncertainty (Buisson et al. 2010). In turn, uncertainty measurements allows the discrimination of the contribution of individual sources of variation entering the models (Diniz-Filho et al. 2009).

In general, SDMs' predictions can be useful as indicators of species' distribution trends, but they should be analyzed with other biological parameters such as physiological tolerance to temperature and precipitation extremes, geographical range sizes, local abundances, life cycles, behavioural and phenological adaptations, evolutionary potential and dispersal abilities (Bradshaw and Holzapfel 2006; Calosi et al. 2008; Isaac et al. 2008; Kearney and Porter 2009; Massot et al. 2008; Parmesan 2006, 2007; Thuiller 2004; Williams et al. 2008).

1.3.4 Dealing with uncertainty to improve conservation decisions

Several sources of uncertainty are associated with conservation planning, including uncertainty about the objectives, and the likelihood of success of conservation actions, uncertainty in costs, and in the impact of threats, and in biological data uncertainty (Game et al. 2008; Halpern et al. 2006b; Langford et al. 2009; McDonald-Madden et al. 2008a; Nicholson and Possingham 2007; Regan et al. 2009). Failure to acknowledge and treat uncertainty may lead to unsuccessful or sub-optimal conservation decisions or expensive failures. Only recently conservation planners have started to acknowledge the need to deal with uncertainty, although such practice has long been adopted in other fields such as engineering, finance and risk analysis.

In some cases, uncertainty can be naturally resolved or removed, for example, by improving knowledge or gathering additional data, and by refining parameter estimates. However, this is not always feasible, such as when predicting future species distributions (see topic 1.3.3). In cases such as these, uncertainty analysis will be necessary to ensure reliable decisions.

There are several methods available to treat uncertainty, including Monte-Carlo methods, interval analysis, sensitivity analysis, Bayesian analysis, info-gap decision theory and scenario analysis (reviewed by Regan et al. 2002, 2009). The choice of the appropriate method depends on the type and severity of uncertainty and the degree to which a system can be controlled. In conservation planning, info-gap uncertainty analysis and scenario analysis are most commonly used because they are the most appropriate to deal with severe uncertainty and uncontrollable systems (Peterson et al. 2003; Regan et al. 2009).

An important question in conservation planning is how uncertainty will change decisions (Possingham et al. 2001). In general, uncertainty analysis evaluates trade-offs between conservation value and the certainty of the information. For example, areas that are certain to have high or low biological value do not pose decision challenges: the former are most important for conservation, while the later should be avoided. However, areas with high conservation value but also high level of uncertainty can potentially lead to unsuccessful conservation investments ("negative surprises") and thus these are the areas requiring uncertainty analysis. Conversely, areas with low conservation value and high uncertainty can potentially become good candidates for conservation investment ("positive surprises") (Figure 1.7).

Dealing with uncertainty becomes more complex when dealing with multiple species in a dynamic context. This can be the case, for example, when attempting to resolve the minimum set problem in a context where species distributions change throughout time and where there is severe uncertainty about the probabilities of occurrence of each species in each location and time. For instance, a site can have a high certainty that a species occurs at present,but high uncertainty that it will occur in the future. The same site can be highly uncertain regarding the current and future occurrence of other species. When the conservation planning problem involves thousand of sites and species, finding a robust set of sites that represents all species throughout time for a minimum cost is a massive challenge. Adequate solutions to face complex uncertainty problems have been slow to emerge, but recently there have been a few attempts to do so (e.g. Carroll et al. 2009; Fuller et al. 2008; Moilanen et al. 2006b). However, new strategies are still required to face uncertainty and to improve conservation decisions.

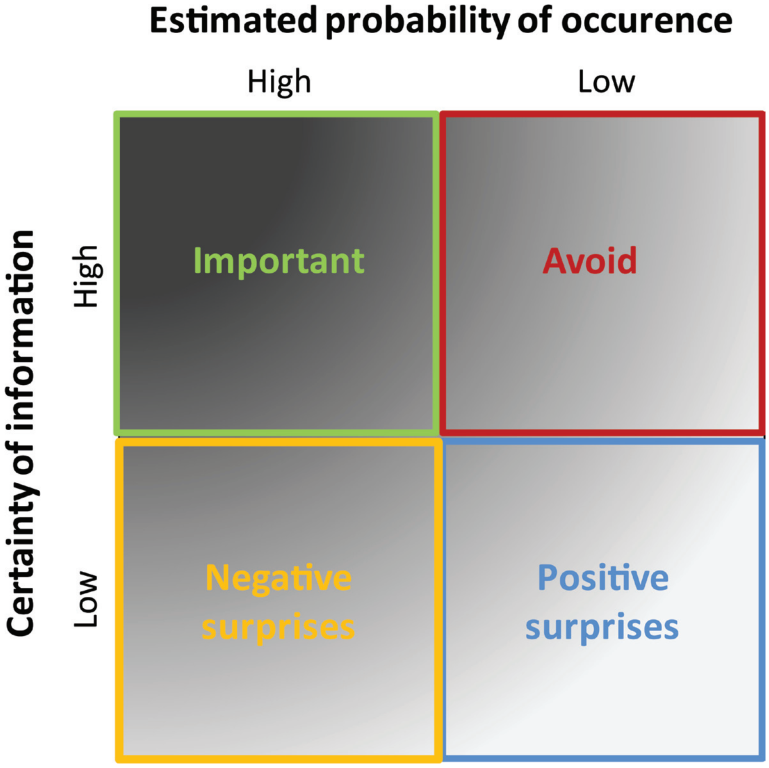


Figure 1.7 - A categorization of four kinds of sites with different implications for conservation decision making. Adapted from Moilanen et al. (2006a)

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Photo: Vasco Flores Cruz

"Look! Look! Look deep into nature and you will understand everything".

Albert Einstein

Chapter 2

Study Area

2.1 Current patterns of biodiversity in the Mediterranean region

The terrestrial Mediterranean Basin is one of the most biodiversity rich regions of the world, holding approximately 25000 plant species (13000 of each are endemic), and around 770 vertebrate species (235 of each are endemic) (Myers et al. 2000).

The high biodiversity of the Mediterranean Basin is a consequence of paleogeographic, biogeographic and ecological events, along with human activities, which turn this region into a biogeographic crossroad and into a melting pot of biodiversity (Blondel and Aronson 1999). Several global conservation assessments recognize the Mediterranean Basin as priority for the conservation of the world's biodiversity (Hoekstra et al. 2005; Myers et al. 2000; Olson and Dinerstein 2002; Shi et al. 2005).

Biodiversity is unevenly distributed across the Mediterranean Basin. For example, several hotspots were identified within the Mediterranean Basin based on plant endemism and richness (Médail and Quézel 1997). For animal species, the International Union for Conservation of Nature (IUCN) has identified patterns of species richness for several groups, including crabs, dragonflies, freshwater fishes, freshwater amphibians, reptiles and mammals. Overall higher species richness was identified along the Italian Peninsula and the Alps, and other smaller areas on the Balkans and the Iberian Peninsula. Areas with highest number of threatened species were identified in the Iberian Peninsula and the Eastern Mediterranean coastal areas. (Figure 2.1).

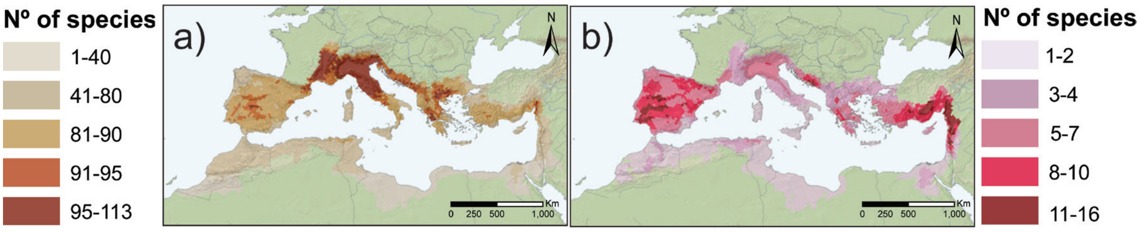

Figure 2.1 – a) Species richness of crabs, dragonflies, endemic freshwater fishes, freshwater amphibians, reptiles and mammals, in the Mediterranean Basin. b) Species richness of threatened species of crabs, dragonflies, endemic freshwater fishes, freshwater amphibians, reptiles and mammals, in the Mediterranean Basin. Source: Cuttelod et al. (2008)

2.2 Amphibians and reptiles in the Western Mediterranean region – current patterns

This thesis focuses on the amphibians and reptiles of the Western Mediterranean, and particularly on the Iberian Peninsula, for several reasons. The Western Mediterranean region was chosen as a study area because of its high conservation importance and because this region presents a remarkable rich geologic and biogeographic history. Indeed, multiple historical events caused changes in climate and in the physical environment since the Mesozoic, which turned it into a natural laboratory to study the influence of current and historical factors on the patterns of species distributions and its importance to conservation planning (De Jong 1998; Hewitt 1996; Weiss and Ferrand 2006). The amphibians and reptiles were chosen as focal groups because they represent a remarkable diverse group in the Western Mediterranean but, at the same time, several species are considered threatened. Moreover, amphibians and reptiles are suitable groups for modeling species distributions, since they have a tight relation with environmental and climatic variables due to their ectothermic physiology and low vagility (Zug et al. 2001). An additional reason to select these groups relies on the availability of comprehensive and reliable data set of species distributions in the Western Mediterranean (e.g. Bons and Geniez 1996; Loureiro et al. 2008; Pleguezuelos et al. 2002), along with availability of published phylogenies and phylogeographies for several taxa.

Approximately 106 amphibian and 355 reptiles species occur in the Mediterranean Basin, being 68 and 170 endemic of this region, respectively (Cox et al. 2006). However, spatial patterns of species richness are dissimilar among amphibians and reptiles, both when considering the total number of species occurring or only the ones classified as threatened (i.e. considered critical endangered, endangered or vulnerable by IUCN) (Figure 2.2). Such differences probably reflect contrasted ecology and physiology of the two groups, which constrains species occurrence to areas with favorable ecological characteristics. In general, amphibian species are more dependent on water, therefore, more species occur in humid regions, which are mainly represented at the western and northern portions of the Basin. In contrast, reptiles are well adapted to dry environments,

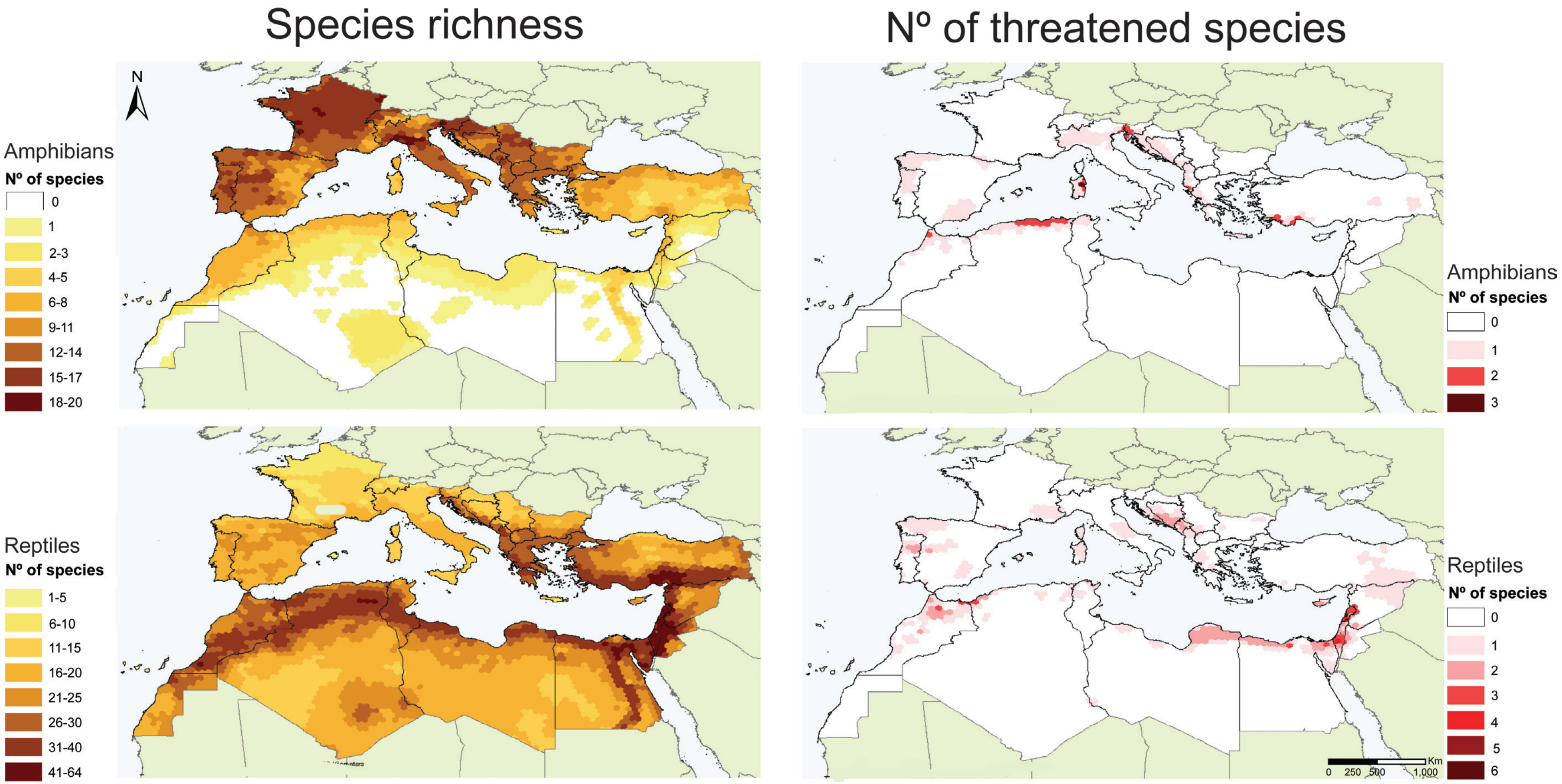

Figure 2.2 – Spatial patterns of amphibian and reptile species richness and number of threaten species in the Mediterranean Basin. Adapted from Cox et al. (2006).

thus, the aridity gradient favors reptile species richness at the east and southern regions of the Mediterranean Basin (Blondel and Aronson 1999).

The western part of the Mediterranean Basin, including the Iberian Peninsula and Morocco (Figure 2.3), holds a high number of species whose ranges are restricted to this region of the Mediterranean Basin, comprising 13 amphibian and 35 reptile endemics (Tables 2.1 and 2.2).

This unique diversity probably derives from a current heterogeneous landscape and climate, and from an eventful and diverse geological and climatic history of the Western Mediterranean, which led to repeated isolation of the biota and provided opportunities for evolutionary divergence and speciation events (Blondel and Aronson 1999).

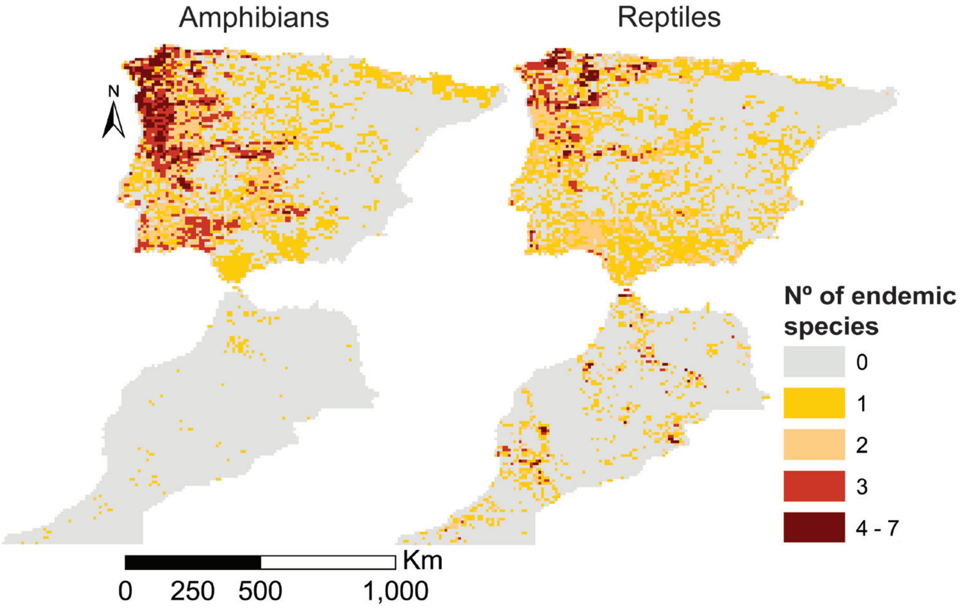

Figure 2.3 - Spatial patterns of endemic amphibian and reptile species in the Western Mediterranean region. Maps based on data from Bons and Geniez (1996), Loureiro et al. (2008) and Pleguezuelos et al. (2002).

2.3 The Western Mediterranean region: determinants of amphibian and reptile diversity

In the Western Mediterranean area, the historical processes that most affected the distribution of current herpetofauna, occurred in the past 35 Million Years (MY) (Rosembaum et al. 2002). Some of the most important events included the formation and evolution of the Mediterranean Sea, the uplift of mountain ranges, the geologic dynamics around the Strait of Gibraltar and climatic oscillations. At present, the Western Mediterranean is a heterogeneous area, both topographically and climatically, which allows the coexistence of species with very different biogeographic affinities and evolutionary histories (Gómez and Lunt 2006).

Table 2.1 – List of amphibian species occurring in the area comprised by the continental territories of Portugal, Spain and Morocco. Endemic species (END) to this region are marked with an "X" and conservation status (CS) according to Cox et al. (2006).

Order	Family	Species	END	CS
Anura	Alytidae	Alytes cisternasii Boscá, 1879	X	NT
		Alytes dickhilleni Arntzen & García-París, 1995	X	VU
		Alytes maurus Pasteur & Bons, 1962	X	NT
		Alytes obstetricans (Laurenti, 1768)		LC
		Discoglossus galganoi Capula, Nascetti, Lanza, Bullini & Crespo, 1985	X	LC
		Discoglossus jeanneae Busack, 1986	X	NT
		Discoglossus scovazzi Camerano, 1878		LC
	Bufonidae	*Bufo brongersmai* Hoogmoed, 1972	X	NT
		Bufo bufo (Linnaeus, 1758)		LC
		Bufo calamita Laurenti, 1768		LC
		Bufo mauritanicus Schlegel, 1841		LC
		Bufo viridis Laurenti, 1768		LC
	Hylidae	*Hyla arborea* (Linnaeus, 1758)		LC
		Hyla meridionalis (Boettger, 1874)		LC
	Pelobatidae	*Pelobates cultripes* (Cuvier, 1829)		NT
		Pelobates varaldii Pasteur & Bons, 1959	X	EN
		Pelodytes punctatus (Daudin, 1802)		LC
		Pelodytes ibericus (Sánchez-Herráiz,Barbadillo, Machordom & Sanchiz, 2000)	X	LC
	Ranidae	*Pelophylax perezi* (Seoane, 1885)		LC
		Rana saharica Boulenger, 1913		LC
		Rana dalmatina Fitzinger in Bonaparte, 1838		LC
		Rana iberica Boulenger, 1879	X	NT
		Rana pyrenaica Serra-Cobo, 1993	X	EN
		Rana temporaria Linnaeus, 1758		LC
Urodela	Salamandridae	*Chioglossa lusitanica* Bocage, 1864	X	VU
		Calotriton asper (Dugès), 1852	X	NT
		Lissotriton boscai (Lataste, 1879)	X	LC
		Lissotriton helveticus (Razoumowsky, 1789)		LC
		Mesotriton alpestris (Laurenti, 1768)		LC
		Pleurodeles waltl Michahelles, 1830		NT
		Salamandra algira Bedriaga, 1883		VU
		Salamandra salamandra (Linnaeus, 1758)		LC
		Triturus marmoratus (Latreille, 1800)		LC
		Triturus pygmaeus Wolterstorff, 1905		NT

Table 2.2 - List of reptile species occurring in the area comprised by the continental territories of Portugal, Spain and Morocco. Endemic species (END) to this region are marked with an "X" and conservation status (CS) are according to Cox et al. (2006).

Order	Family	Species	END	CS
Chelonia	Bataguridae	*Mauremys leprosa* (Schweigger, 1812)		LC
	Emydidae	*Emys orbicularis* (Linnaeus, 1758)		NT
	Testudinidae	*Testudo graeca* Linnaeus, 1758		LC
		Testudo hermanni Gmelin, 1789		NT
Ophidia	Boidae	*Eryx jaculus* (Linnaeus, 1758)		LC
	Colubridae	*Coronella austriaca* Laurenti, 1768		LC
		Coronella girondica (Daudin, 1803)		LC
		Dasypeltis scabra (Linnaeus, 1758)		LC
		Hemorrhois algirus (Jan, 1863)		LC
		Hemorrhois hippocrepis (Linnaeus, 1758)		LC
		Hierophis viridiflavus (Lacépède, 1789)		LC
		Lamprophis fuliginosus (Boie, 1827)		LC
		Lytorhynchus diadema (Duméril, Bibron & Duméril, 1854)		LC
		Macroprotodon abubakeri Wade, 2001		DD
		Macroprotodon brevis (Günther, 1862)		NT
		Macroprotodon cucullatus (Geoffroy Saint-Hilaire, 1827)		LC
		Malpolon insignitus (Geoffroy Saint-Hilaire, 1827)		-
		Malpolon moilensis (Reuss, 1834)		LC
		Malpolon monspessulanus (Hermann, 1804)		LC
		Natrix maura (Linnaeus, 1758)		LC
		Natrix natrix (Linnaeus, 1758)		LC
		Psammophis schokari (Forskål, 1775)		LC
		Rhinechis scalaris (Schinz, 1822)		LC
		Spalerosophis cliffordi Schmidt, 1939		-
		Spalerosophis dolichospilus (Werner, 1923)		DD
		Telescopus guidimakaensis (Chabanaud, 1916)		LC
		Zamenis longissima (Laurenti, 1768)		LC
	Elaphidae	*Naja haje* (Linnaeus, 1758)		LC
	Leptotyphlopidae	*Leptotyphlops macrorhynchus* (Jan, 1862)		LC
	Viperidae	*Bitis arietans* (Merrem, 1820)		LC
		Cerastes vipera (Linnaeus, 1758)		LC
		Daboia mauritanica (Duméril & Bibron, 1848)		NT
		Echis leucogaster Roman, 1972		LC
		Vipera aspis (Linnaeus, 1758)		LC
		Vipera latastei Boscá, 1878		NT
		Vipera monticola Saint Girons, 1954	X	NT
		Vipera seoanei Lataste, 1879	X	LC
Sauria	Agamidae	*Agama impalearis* Boettger, 1874		LC
		Trapelus mutabilis (Merrem, 1820)		LC
		Uromastyx acanthinura Bell, 1825		NT
	Anguidae	*Anguis fragilis* Linnaeus, 1758		LC
		Hyalosaurus koellikeri (Günther, 1873)	X	LC
	Blanidae	*Blanus cinereus* (Vandelli, 1797)	X	LC
		Blanus mettetali Bons, 1963	X	LC
		Blanus tingitanus Busack, 1988	X	LC
	Chamaeleonidae	*Chamaeleo chamaeleon* (Linnaeus, 1758)		LC
	Gekkonidae	*Hemidactylus turcicus* (Linnaeus, 1758)		LC
		Ptyodactylus oudrii Lataste, 1880		LC
		Quedenfeldtia trachyblepharus (Boettger, 1873)	X	NT

Table 2.2 (continued)

Order	Family	Species	END	CS
		Quedenfeldtia moerens (Chabanaud, 1916)	X	LC
		Saurodactylus brosseti Bons & Pasteur, 1957	X	LC
		Saurodactylus fasciatus Werner, 1931	X	VU
		Saurodactylus mauritanicus (Duméril & Bibron, 1836)		LC
		Stenodactylus petrii Anderson, 1896		LC
		Stenodactylus sthenodactylus Lichtenstein, 1823		LC
		Tarentola annularis (Geoffroy Saint-Hilaire, 1827)		LC
		Tarentola boehmei Joger, 1984	X	LC
		Tarentola chazaliae (Mocquard, 1895)		LC
		Tarentola deserti Lataste, 1891		LC
		Tarentola ephippiata O'Shaughnessy, 1875		LC
		Tarentola mauritanica (Linnaeus, 1758)		LC
		Tropiocolotes tripolitanus Peters, 1880		LC
	Lacertidae	*Acanthodactylus aureus* Günther, 1903		LC
		Acanthodactylus boskianus (Daudin, 1802)		LC
		Acanthodactylus busacki Salvador, 1982	X	LC
		Acanthodactylus dumerilii Salvador, 1982		LC
		Acanthodactylus erythrurus (Schinz, 1833)		LC
		Acanthodactylus lineomaculatus Duméril & Bibron, 1839	X	LC
		Acanthodactylus longipes Boulenger, 1918		LC
		Acanthodactylus maculatus (Gray, 1838)		LC
		Algyroides marchi Valverde, 1958	X	EN
		Iberolacerta aranica (Arribas, 1993)	X	CR
		Iberolacerta aurelioi (Arribas, 1994)	X	EN
		Iberolacerta bonnali Lantz,1937	X	NT
		Iberolacerta cyreni (Müller & Hellmich, 1937)	X	EN
		Iberolacerta martinezricai (Arribas, 1996)	X	CR
		Lacerta agilis Linnaeus, 1758		LC
		Lacerta andreanszkyi Werner, 1929	X	NT
		Lacerta bilineata (Daudin, 1802)		LC
		Lacerta monticola Boulenger, 1905	X	VU
		Lacerta pater Lataste, 1880		-
		Lacerta schreiberi Bedriaga, 1878	X	NT
		Lacerta tangitanus (Boulenger, 1887)		LC
		Mesalina guttulata (Lichtenstein, 1823)		LC
		Mesalina olivieri (Audouin, 1829)		LC
		Mesalina pasteuri (Bons, 1960)		DD
		Mesalina rubropunctata (Lichtenstein, 1823)		LC
		Mesalina simoni (Boettger, 1881)		LC
		Ophisops occidentalis Boulenger, 1887		LC
		Podarcis bocagei (Seoane, 1884)	X	LC
		Podarcis carbonelli Pérez Mellado, 1981	X	EN
		Podarcis hispanica (Steindachner, 1870)		LC
		Podarcis muralis (Laurenti, 1768)		LC
		Podarcis vaucheri (Boulenger, 1905)		LC
		Psammodromus algirus (Linnaeus, 1758)		LC
		Psammodromus blanci (Lataste, 1880)		NT
		Psammodromus hispanicus Fitzinger, 1826		LC
		Psammodromus microdactylus (Boettger, 1881)	X	EN
		Teira perspicillata (Duméril & Bibron, 1839)		LC
		Timon lepida (Daudin, 1802)		NT
		Zootoca vivipara (Jacquin, 1787)		LC

Table 2.2 (continued)

Order	Family	Species	END	CS
	Scincidae	*Chalcides bedriagai* (Boscá, 1880)	X	NT
		Chalcides colosii Lanza, 1957	X	LC
		Chalcides ebneri Werner, 1931	X	CR
		Chalcides lanzai Pasteur, 1967	X	NT
		Chalcides manueli Hediger, 1935	X	VU
		Chalcides mauritanicus (Duméril & Bibron, 1839)		EN
		Chalcides minutus Caputo, 1993	X	VU
		Chalcides mionecton (Boettger, 1873)	X	LC
		Chalcides montanus Werner, 1931	X	NT
		Chalcides ocellatus (Forskål, 1775)		LC
		Chalcides parallelus Caputo & Mellado, 1992		EN
		Chalcides polylepis Boulenger, 1896	X	LC
		Chalcides pseudostriatus Caputo, 1993	X	NT
		Chalcides striatus (Cuvier, 1829)		LC
		Eumeces algeriensis Peters, 1864		LC
		Scincopus fasciatus (Peters, 1864)		DD
		Scincus albifasciatus Boulenger, 1890		LC
		Sphenops boulengeri (Anderson, 1892)		LC
		Sphenops sphenopsiformis (Duméril, 1856)		LC
	Trogonophidae	*Trogonophis wiegmanni* Kaup, 1830		LC
	Varanidae	*Varanus griseus* (Daudin, 1803)		LC

2.3.1 Historical geography

The physical geography of the area that nowadays corresponds to the Mediterranean Basin changed continuously throughout the geological history of Earth, due to the movement of tectonic plates and continental drift. The origin of the Mediterranean Basin resulted from tectonic interactions between the North African and the Eurasian plates (Mather 2009; Rosembaum et al. 2002). The Iberian Peninsula originated from multiple geologic events related to the convergence of the Eurasian and African plates in the upper Oligocene (28 MY ago) (Jolivet and Faccenna 2000; Mather 2009). In the Oligocene and Early Miocene, a wide zone in the interface between Africa and Europe extended, driven by subduction rollback. This resulted from a slower rate of convergence between the Eurasian and African plates starting about 30 MY ago (Rosembaum et al. 2002) (Figure 2.4 a). As a result of subduction rollback, extension in the Early Miocene led to the breakup and drifting of continental fragments formerly attached to southern France and Iberia, which are now scattered throughout the Western Mediterranean (the Betic region, in the Iberian Peninsula, the Rif in North Africa, and also the Balearic Islands, Sardinia, Corsica and part of the Italian Peninsula). The land mass currently forming the Betic and Rif regions eventually collided with South Iberia and North Africa during the Miociene (Figures 2.4b and 2.5a).

The continuity of the tectonic dynamics of the Mediterranean area gave rise to successive periods where the African plate was connected to the Iberian Peninsula, intercalated with periods where it was disconnected. One of the most dramatic historical

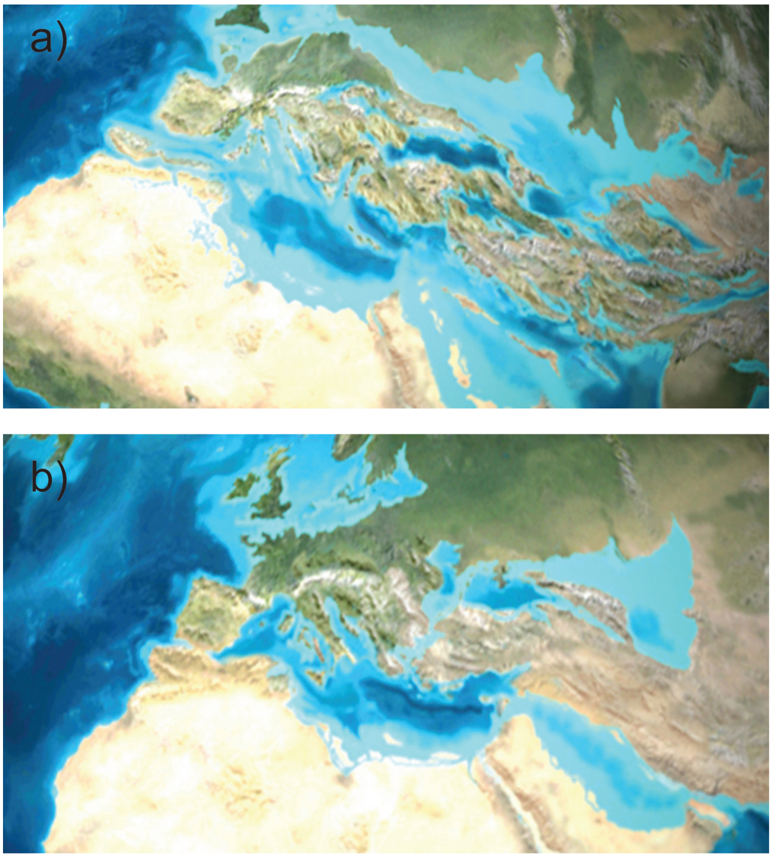

Figure 2.4 – Reconstruction of Mediterranen area geography showing the convergence of the Eurasian and African plates during a) the Oligocene (35 MY ago) and b) the Miocene (25 MY ago). Adapted from Don Blakey, NAU Geology.

events was the Messinian Salinity Crisis (MSC), which triguered around 5.96 MY ago (Duggen et al. 2003; Hsü et al. 1977; Krijgsman et al. 1999; Rouchy and Caruso 2006). The MSC resulted from a complex combination of tectonic and glacio-eustatic processes which progressively reduced the seaways from deep sea to shallow waters (Braga et al. 2003; Krijgsman et al. 2000) and finally isolated the Mediterranean Sea from the Atlantic ocean (Krijgsman et al. 1999). This isolation occurred between 5.9-5.33 MY ago, with the complete formation of the Betic corridor (Figure 2.5b) (Duggen et al. 2003; Hsü et al. 1977; Krijgsman et al. 1999; McKenzie 1999; Rouchy and Caruso 2006). The closure of the Betic Strait endorsed a relatively fast drying of the Mediterranean Sea, resulting in subsequent several land connections between Africa and Europe, and allowing dispersal of terrestrial amphibians and reptiles from the Eurasian plate to the African and vice versa (Pleguezuelos et al. 2008) (Figure 2.5c). Around 5.3 MY ago, a new series of tectonic activity broke the land bridge between Africa and the Iberia, opening the current Strait of Gibraltar, and allowing the Atlantic ocean to surge into the Mediterranean (Hsü et al. 1977; Rouchy and Caruso 2006). After the refilling of the Mediterranean, the Strait of Gibraltar became once again a geographical barrier to the dispersal of Iberian and Moroccan biotas (Figure 2.5d).

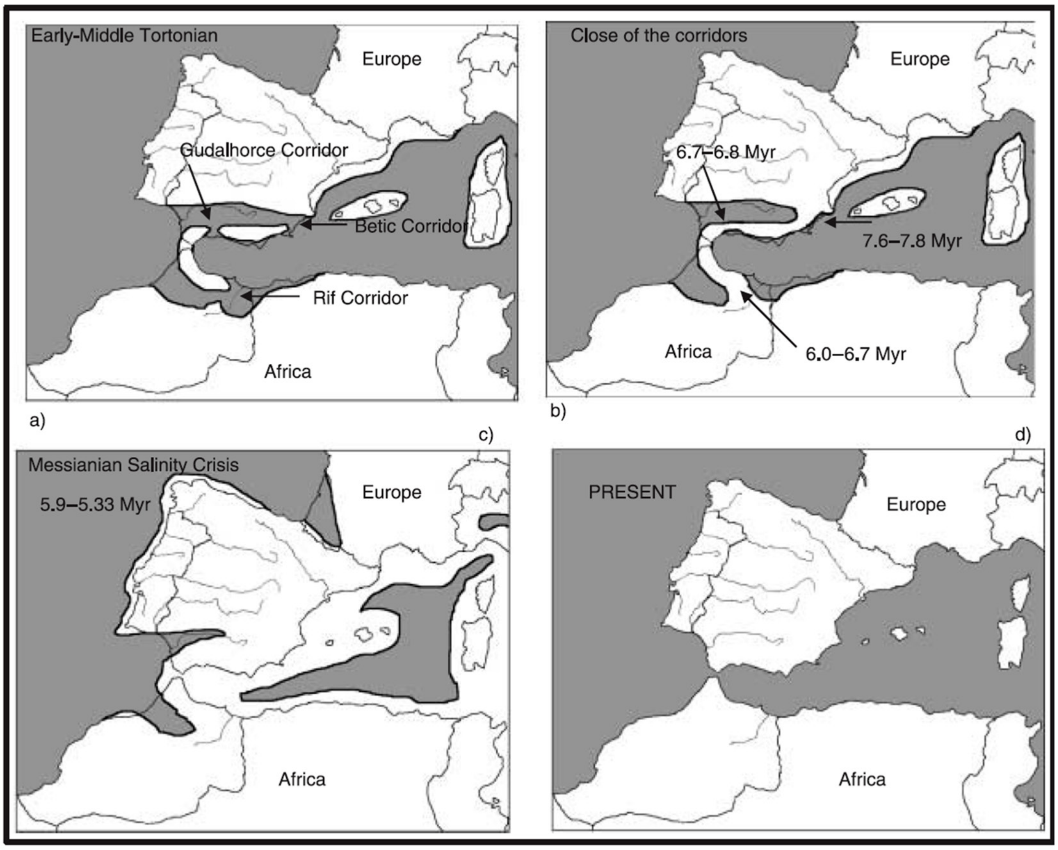

Figure 2.5 - A simplified schematic of the evolution of the Western Mediterranean region from the middle-Tortonian age (~7.2 MY) until present. (a) Middle-Tortonian age, arrows indicate the three corridors between Mediterranean and the Atlantic Ocean, with islands corresponding to the Betic and Rifian zone. (b) Close of the corridors, with estimated closing times of the three corridors. (c) Messinian salinity crisis, 5.9–5.33 MY, a period of wide land connections between Africa and Europe. (d) Present-day situation. For the Balearic and Corsica-Sardinia, the representation is not as accurate as for the Betic-Rif zone. Source: Paulo et al. (2008).

2.3.2 Current topography and hydrography

At present, the Western Mediterranean region is topographically and climatically heterogeneous. Several mountain ranges dominate the landscape, both in Iberia Peninsula and Morocco (Figure 2.6a). In Iberia, the Pyrenean separate the Peninsula from the remaining Europe. Most of the landscape is dominated by a central plateau known as the Central Meseta, with elevations ranging from 610 to 760 m. The Central System divides the Meseta into northern and southern sub-regions. The Meseta is rimed by high mountains on its northern (the Cantabric Mountain Range), eastern (the Iberian System), and southern regions (Morena mountains). The higher peak in the Iberian Peninsula is located in Sierra Nevada, in the Betic System, with 3478 m.

Most mountain ranges in the Iberia Peninsula have a pronounced East-West direction, thus the main rivers flow to the west, including the Tagus, Douro, Guadiana, and the Guadalquivir. A major exception is the Ebro river, which flows to the East. There are also several smaller rivers in the northwestern and northern coastal plains, which drain directly into the Atlantic Ocean. The smaller river Basins of the Mediterranean coast and southwestern Iberia are relatively narrow and most have seasonal water availability. Lowlands dominate southwestern landscapes as well as in most of the Ebro river Basin.

In Morocco, mountains ranges also dominate an important part of the territory, although there are extensive lowlands along the Atlantic Ocean coastal areas. The main mountain range is the Atlas mountain, which extends along North Africa, from Morocco to Algeria and Tunisia, separating the Atlantic and Mediterranean coastlines from the Sahara desert. The Atlas has a dominant southeast-northeast orientation, and is divided into separate ranges: the Middle Atlas, High Atlas, and Anti-Atlas. The highest peak in Morocco has an elevation of 4165 m, located in the High-Atlas range. Another important Mountain range is the Rif, which extends along the Mediterranean coast and was once connected to the Betic System in the Iberian Peninsula. Between the Atlases Mountains and the Atlantic coast there is a region of low plateaus and plains. Inland from the Atlases and throughout the southern part of Morocco, occurs the northern limits of the Sahara desert. Most of the Moroccan rivers flow from the Atlases to the Atlantic or Mediterranean coasts, including the Moulouya, Oued Sebou, Oum er Rbia, Tensift, and Sous.

2.3.3 Current landcover

The current landcover of the Western Mediterranean is also fairly heterogeneous, reflecting, on one side, the diversity of natural habitats resulting from the topographic and climatic diversity, and on the other side, the profound transformations of natural habitats by human activities (Blondel 2006). Cultivated and managed areas represent around 40% of the region, mainly located in the Iberian Mesetas and southwestern plains, and in northwestern Morocco (Figure 2.6b).

Tree cover classes represent roughly 24% of the study area. However, the area comprising native forests species is fairly small as most of the forested areas are represented by plantations of non-native species, such as *Eucaliptus* (*Eucalyptus* sp.) and pinewoods (*Pinus* sp.). Native forests are reduced to small fragments occurring mostly along main mountains ranges. In northern Iberia, native forests are dominated by temperate broad-leaved species, such as *Fagus sylvatica*, *Castanea sativa*, *Quercus petraea* and *Quercus robur*, while in northern and central mountains, formations of mountain conifers such as *Pinus sylvestris*, *Pinus uncinata* and *Abies alba* occur. In the south, and sporadically reaching central and eastern Iberia, main forests are dominated by typical Mediterranean species, such as *Pinus pinaster*, *Pinus pinea*, *Pinus halepensis*, *Quercus ilex*, *Quercus suber*, *Quercus canariensis* and *Quercus faginea*. Between the areas occcupied by temperate broad-leaved and Mediterranean forests, predominate sub-Mediterranean formations of *Juniperus thurifera*, *Quercus pyrenaica*, *Quercus pubescens*, *Quercus faginea* and *Pinus nigra* (Garzón et al. 2008). In Morocco, forested areas are mostly distributed along the Tangier Peninsula

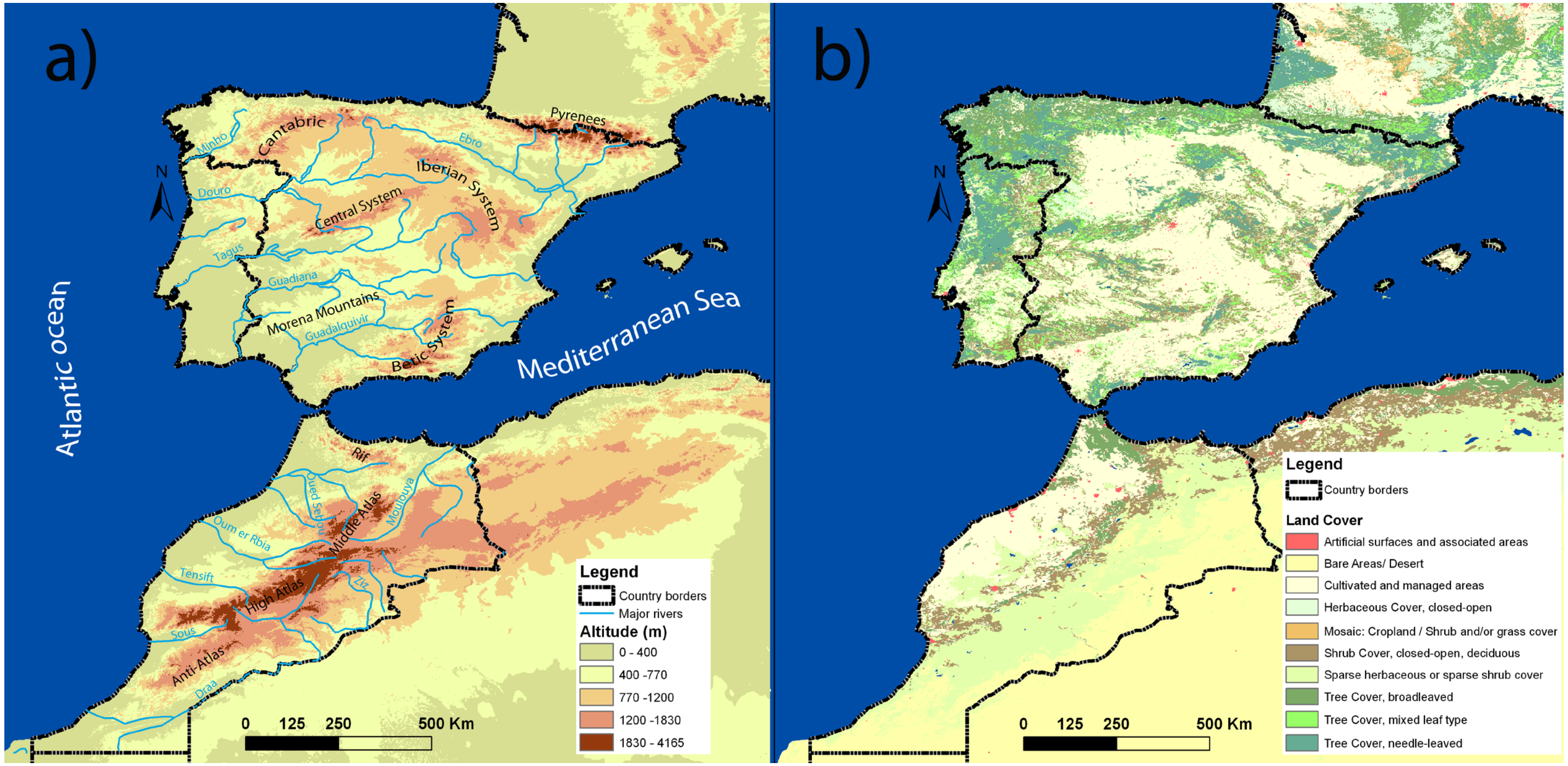

Figure 2.6 – Distribution of the mountain ranges and major rivers (a) and land cover (b) in the Western Mediteranean Region. Maps based on data from Worldclim (http://www.worldclim.org/) and Global Land Cover 2000 database (2003). Maps shown in WGS84 projection.

(south to the Strait of Gibraltar), the Rif Mountains, the Middle Atlas, the northern slopes of the Anti-Atlas and the occidental extreme of the Anti-Atlas. The species occurring in the Tangier Peninsula are similar to those occurring on the northern part of the Strait of Gibraltar, with *Quercus suber* and *Quercus canariensis* dominanting at lower altitudes. In the Rif mountains, the dominating species are *Cedrus atlantica*, *Quercus pyrenaica* and *Pinus pinaster* (Ajbilou et al. 2006). In the Atlases, particularly in the Middle Atlas, pockets of remnant *Cedrus* forests can be found. The dominant species is *Cedrus libani*, which often occurs along with *Juniperus foetidissima*.

Herbaceous plants cover about 14% of the study area, occurring particularly in southwestern Iberia and northeastern Morocco and south to the Atlas mountains. Typical Mediterranean shrubs cover southern Iberian as well as parts of the Mediterranean coasts of Iberia and Morocco. Some of the representative species include *Arbutus unedo*, *Erica arborea*, *Phillyrea* spp., *Viburnum tinus*, *Cistus* spp., *Pistacia lentiscus*, and *Myrtus communis*. The southeastern slopes of the Atlas mountains are represented by semi-desertic steppes, making a transition to the most arid areas of Morocco. Vegetation is sparse and highly seasonal, and some representative species are *Stipa tenacissima* and *Artemisia herba-alba*. High altitude spiny xerophytes are found in altitudes up to 2000 m.

About 12% of the study area is represented by bare areas, mostly occurring in southern Morocco, which constitutes the northern limit of the Sahara desert. These areas are mostly dominated by wide rocky plateaus, where vegetation is relatively rare (regs), and sandy systems (depressions or elevated sand dunes). In regs, the sparse vegetation is dominated by *Acacia ehrenbergiana* and *Acacia raddiana*. Sand systems can have vegetation comprised of tall shrubs (*Retama raetam*, *Ziziphus lotus*, *Genista saharae*, *Calligonum comosum*) and sometimes trees (*Acacia raddiana*, *Pistacia atlantica*, *Tamarix aphylla*, *Calligonum azel* and *Calligonum arich*).

2.3.4 Climate

Historical Climate

Variations in Earth's orbit with periods of 10-100 thousand years, known as the Milankovitch oscillations, have led to recurrent and rapid climatic oscillations during the past 70 MY (Jansson and Dynesius 2002). Several paleoecological studies showed that such climatic shifts drove large changes in species' geographical distributions, with consecutive contractions and expansions of species ranges, which contributed to the establishment of current patterns of species richness and endemism (Carnaval et al. 2009; Jansson 2003), by influencing evolutionary processes such as divergence, speciation and extinction (Hewitt 1996, 2000, 2004).

In the Mediterranean region, the past 2.5 MY in particular, had a decisive influence in shaping the composition and distribution of biotic communities (Blondel 2009; Blondel and Aronson 1999). Cold conditions prevailed during most part of the

Quaternary period, with ice covering most part of Northern and Central Europe, but this climatic patterns was periodically interrupted by short periods of rapid climate warming, known as interglacials. During the most severe phases of the glacial periods, almost no arboreal vegetation survived north of the mountain chains bordering the northern Mediterranean regions (such as the Alps, Pyrenees and Carpathian Mountains). Molecular evidence suggests that several European taxa contracted their range into the Mediterranean Peninsulas, where the climate was warmer and more humid (Hewitt 1996; Taberlet et al. 1998; Weiss and Ferrand 2006).

The Iberian Peninsula, in particular, was one of the most important glacial refugia in Europe for several plant and animal taxa (Gómez and Lunt 2006; Médail and Diadema 2009), although several glaciers persisted in mountain tops (Hughes and Woodward 2008), (Figure 2.7). This fact created conditions to long isolation periods of several populations. Additionally, the high topographic and climatic heterogeneity of the Iberia Peninsula and its habitat diversity, favored the occurrence of multiple glacial refugia isolated from each other, potentiating allopatric speciation. These periods were followed by post-glaciation dispersion of population towards northern latitudes and lower altitudes (Hewitt 1996). For amphibians and reptiles, in particular, phylogeographic studies indicated refugia concordance for different species in the Iberian Peninsula, mainly located at the major mountain systems (Gómez and Lunt 2006; Teixeira 2007).

In northern Africa, the impact of Quaternary climate change was less severe. Although changes on species geographical distributions are poorly documented (but see Schleich et al. 1996), there is evidence that several refugia existed for plant species, particularly in the Atlas and Rif Mountains (Médail and Diadema 2009, Cheddadi et al. 2009), which correspond to areas comprising currently higher number of amphibian and reptile endemics. However, it is possible that climate fluctuations have influenced species distributions in different ways. For example the humid climate during the glacial periods may have allowed *Podarcis* to range widely, whereas in the interglacial, range contractions into the mountains may have occurred, similar to present day conditions (Kaliontzopoulou et al. 2008).

Present Climate

The present Mediterranean climate is characterized by hot dry summers and mild wet winters, however, the climate gradient across the Mediterranean Basin is extreme. There is a gradient of aridity from west to east, and from north to south. In Western Mediterranean, the climate is mostly dictated by the proximity to the Atlantic Ocean but there are also climate heterogeneities influenced by altitudinal and inland gradients. Indeed, Iberian climate is more humid and mild along the northern and northwestern coasts, indicating direct influence of the Atlantic. Precipitation is higher in these areas, particularly in winter months. This climatic type is often referred to as Atlantic climate (Rivas-Martínez et al. 2004). In higher altitudes, along most of the Iberian and Moroccan mountain ranges, precipitation can be fairly high, winter mean temperatures are often negative and mountain peaks are snow capped throughout most of the year.

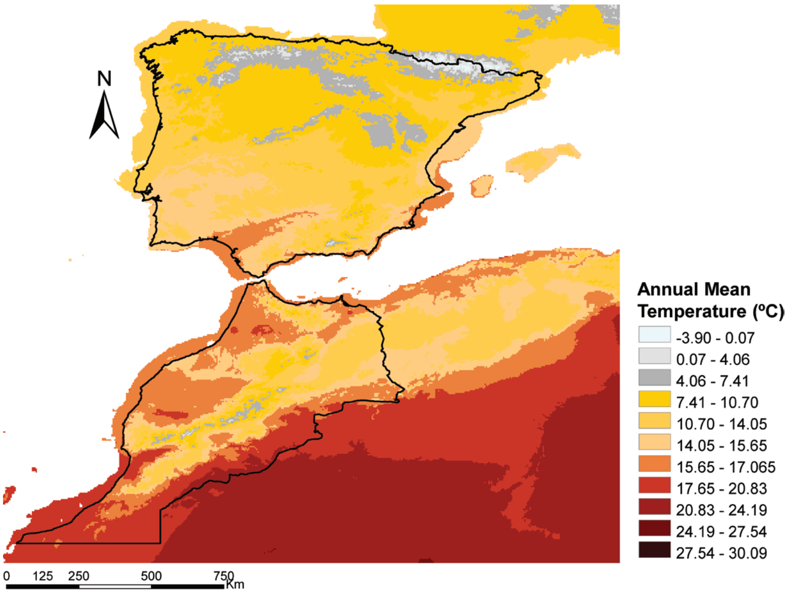

Figure 2.7 – Annual mean temperature during the Last Glacial Maximum (~21,000 years ago) in the Western Mediterranean. Values represent averages of downscaled outputs from CCSM and MIROC global climate models. Black line indicates current limits of the study area. Data source Worldclim (http://www.worldclim.org/). Map shown in WGS84 projection.

The southern, eastern and central Iberian and northern Morocco (north of the Atlas mountains) are dominated by typical Mediterranean climate, with very warm and arid summers and mild wet winters. In inland and southern areas of Morocco, the weather is very hot and dry throughout most of the year, though temperatures can drop dramatically at night, especially in winter months. The extreme south and southeast have a hotter, drier, continental climate, and the southern parts are dominated by a very dry, saharian-type climate.

Future climate projections

There is overwhelming consensus within the scientific community that we are facing a rapid global warming due to anthropogenic activities (IPCC 2007). In the Mediterranean Basin, projections of future climate indicate an increase in climatic heterogeneity. In the south, a drier climate is more probable with intensified evaporation and accentuated droughts, while in the north, it is expected that climate become more contrasted with irregular rainfall in general, wetter winters and drier summers (MIO-ECSDE 2003).

Averaged projections from three Global Circulation Models (CCCMA, HADCM3 and CSIRO), for two IPCC storylines (A2 and B2) (Nakicenovic and Swar 2000), predict a progressive decrease in precipitation and increase in temperature in the Western Mediterranean, from present until the year 2080 (Figure 2.8). Areas where a drop in total annual precipitation is expected to be higher include the Iberian and Moroccan mountain ranges, the central-southern Iberia and northern Morocco. Up to 200 mm precipitation drop per year are expected in the Pyreenees, Rif and Nevada mountains. Temperature increase is expected to be more pronounced in inland areas than coastal ones, and less pronounced in mountain ranges. In southeastern areas of Morocco, increases up to 5ºC of annual mean temperature are expected by 2080 while in the Atlantic coast it is expected an increase in temperature between 1.7 and 2.8 ºC.

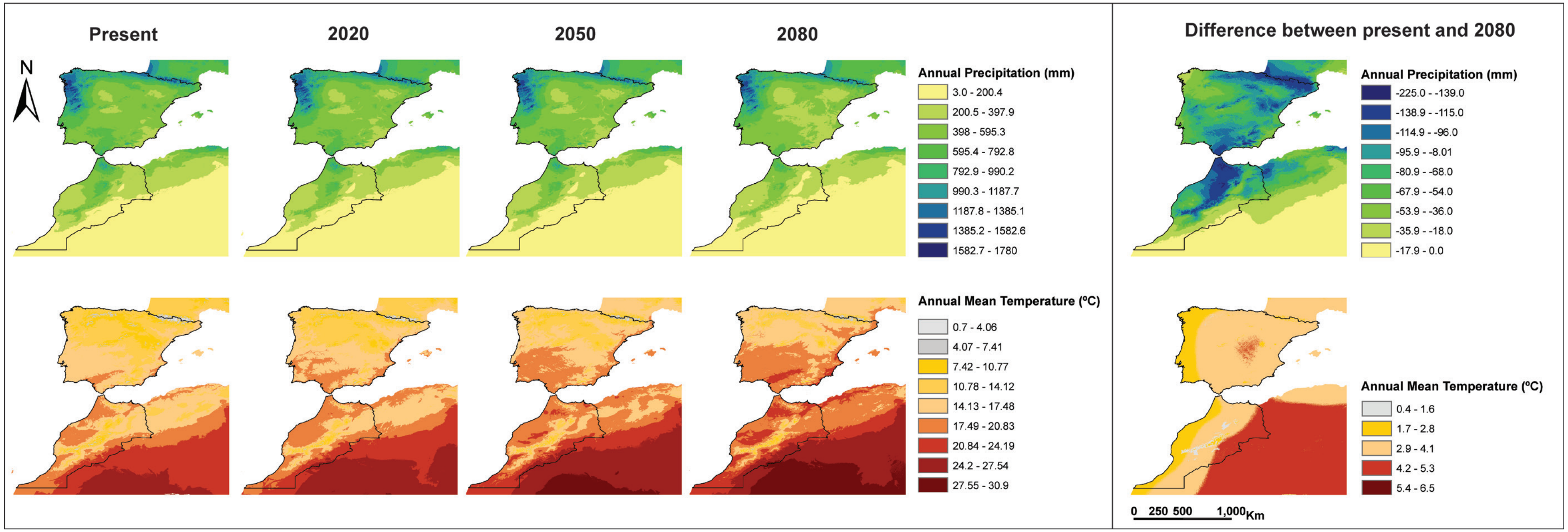

Figure 2.8 – Spatial and temporal patterns of annual precipitation and annual mean temperature in Western Mediterranean: present patterns, projections for the years 2020, 2050 and 2080, and differences between present and 2080. Projections for the future are based on averaged simulated climate data (interpolated to 30 arc seconds) of three Global Circulation models (CCCMA, HADCM3 and CSIRO) and two IPCC storylines (A2 and B2). Data source Worldclim (http://www.worldclim.org/). Maps shown in WGS84 projection.

2.4 Protected Areas Network

There are several protected areas established on the Western Mediterranean with different conservation categories, that can be divided into areas of international importance (Biosphere Reserves and Ramsar Wetlands of International Importance) and areas included in the National Protected Areas systems (with diverse designations and objectives) (Figure 2.9). In the Iberian Peninsula there are also sites incorporated in the European Natura 2000 network, including Special Protection Areas (SPAs) for birds and Special Areas of Conservation (SACs.) (Figure 2.10), but there is an extensive overlap between SPAs and SACs and between these and other Protected Areas.

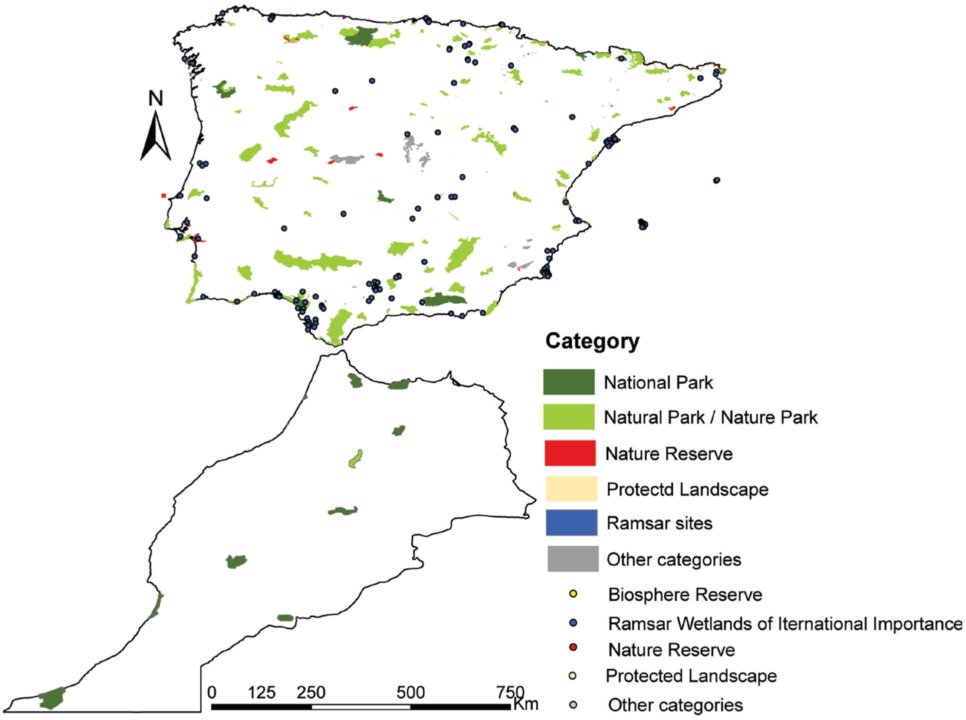

Figure 2.9 - Distribution of Protected Areas in the Western Mediterranean. Large areas are represented in polygons and smaller areas are represented by its central point. National Park includes National Parks only. Natural Park include Natural Parks and Nature Parks. Nature Reserve include Nature Reserves, Integral Nature Reserves, Biological Reserves, Partial Nature Reserves, Botanical Reserves, Fluvial Reserves, Fauna Refugia, Microreserves, Marine Reserves and Wildlife Reserves. Protected Landscapes include Protected Landscapes and Natural Landscapes; Other Designations include Regional Parks, Rural Parks, Forest Sanctuaries, Barcelona Convention Sites, Hunting Reserves, Nature Areas, Nature Areas of National Interest, Parks, Natural Monuments and Sites of Ecological and Biological Interest. Sources: Instituto da Conservação da Natureza e da Biodiversidade (Portugal), Ministerio del Medio Ambiente y Medio Rural Y Marino (Spain), Haut Commissariat aux Eaux Forêts et à la Lutte contre la Désertification (Morocco), World Database on Protected Areas IUCN and UNEP-WCMC (2010). Map shown in WGS84 projection

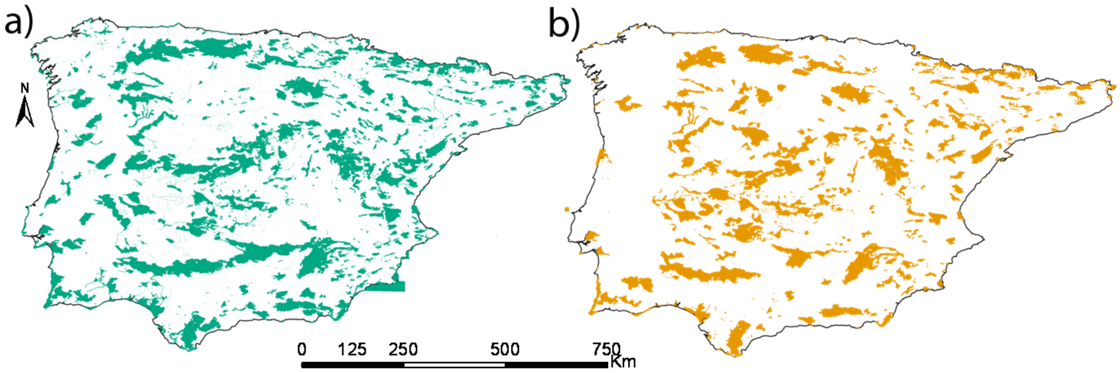

Figure 2.10 – Distribution of Natura 2000 sites in the Iberian Peninsula: a) Special Areas of Conservation; b) Special Protection Areas. Maps based on data from Instituto da Conservação da Natureza e da Biodiversidade (Portugal), Ministerio del Medio Ambiente y Medio Rural Y Marino (Spain). Maps shown in WGS84 projection.

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Photo: Vasco Flores Cruz

“There is a sufficiency in the world for man's need but not for man's greed”

Mohandas K. Gandhi

Chapter 3

Objectives and overview of the thesis

The broad objective of this thesis is to address some unresolved issues in conservation planning, by using the Western Mediterranean region as study area and the amphibian and reptile species occurring there as biological models. More specifically, the following objectives were pursued:

1. To contribute to the knowledge on the distribution of amphibians and reptiles in the Western Mediterranean:

1.1 To make field survey to complement published records of species distributions;

1.2 To analyse relations between observed distribution patterns and environmental parameters, and to predict the overall potential range of each species;

2. To evaluate which type of species distribution data performs better when used to select priority areas for conservation;

3. To develop new approaches to integrate evolutionary processes into conservation planning when molecular data are not available;

4. To forecast how future climatic changes may affect the distribution of amphibians and reptiles in the Iberian Peninsula and to discuss implications for conservation planning.

5. To develop new approaches to account for uncertainty in current and future species distributions in order to improve conservation decisions in space and time.

To accomplish these objectives, the thesis was organized into five sections, including nine chapters (Figure 3.1). **Section I** includes **chapters 1** to **3**. **Chapter 1** consists of an introduction where current knowledge and challenges of conservation planning science are contextualized. **Chapter 2** describes features and history of the study area, relevant to shape current distribution patterns of amphibians and reptiles species and to their conservation strategies. **Chapter 3**, presents the objectives and the structure of the thesis.

Section II includes **chapters 4** and **5** which address amphibian and reptile distribution data. **Chapter 4** focuses on objective 1.1, reporting on field records collected in Morocco between 2001 and 2006. Those data were used throughout the following chapters, complemented with other published sources of species distribution records. **Chapter 5** addresses objectives 1.2 and 2. Species distribution models were produced and simulation procedures were conducted to analyse the effects of using different types of distribution data on the performance of reserve selection algorithms. For that purpose, several scenarios were constructed, including varying proportions of species distribution data (observed, predicted or a mixture of both), conservation targets and costs. Results from this chapter were taken into account in subsequent ones.

Section III includes **chapter 6**, which addresses objectives 1.2 and 3. Species distribution models were produced for several species and a novel approach was proposed to surrogate two important components of genetic diversity (the neutral and the adaptive), using predicted species distributions and environmental gradients. Subsequently, it was tested how reserve selection results differed when accounting or not for evolutionary processes.

Section IV includes **chapters 7** and **8** which deal with objectives 4 and 5 respectively, while objective 1.2 is also addressed in both chapters. In this section, two relevant issues in conservation planning are analysed: dynamics and uncertainty. **Chapter 7** focus on species distribution dynamics derived from climate change. Potential range shifts of 37 endemic and nearly endemic herptiles of the Iberian Peninsula were assessed by forecasting species distributions for three different times into the future (2020, 2050 and 2080), using an ensemble of species distribution models and different combinations of species dispersal ability, emission levels and global circulation models. **Chapter 8** builds on results obtained in **chapter 7** and on predictions of the present and future distribution of remaining Iberian and reptile species, with the objective to analyse how uncertainty and dynamics in species distributions may affect decisions about resource allocation for conservation in space and time.

Section V concludes the thesis with **chapter 9**, where all results obtained are summarized, integrated and discussed, focusing on the implications for contemporary conservation planning in the western Mediterranean region and suggesting future investigation prospects.

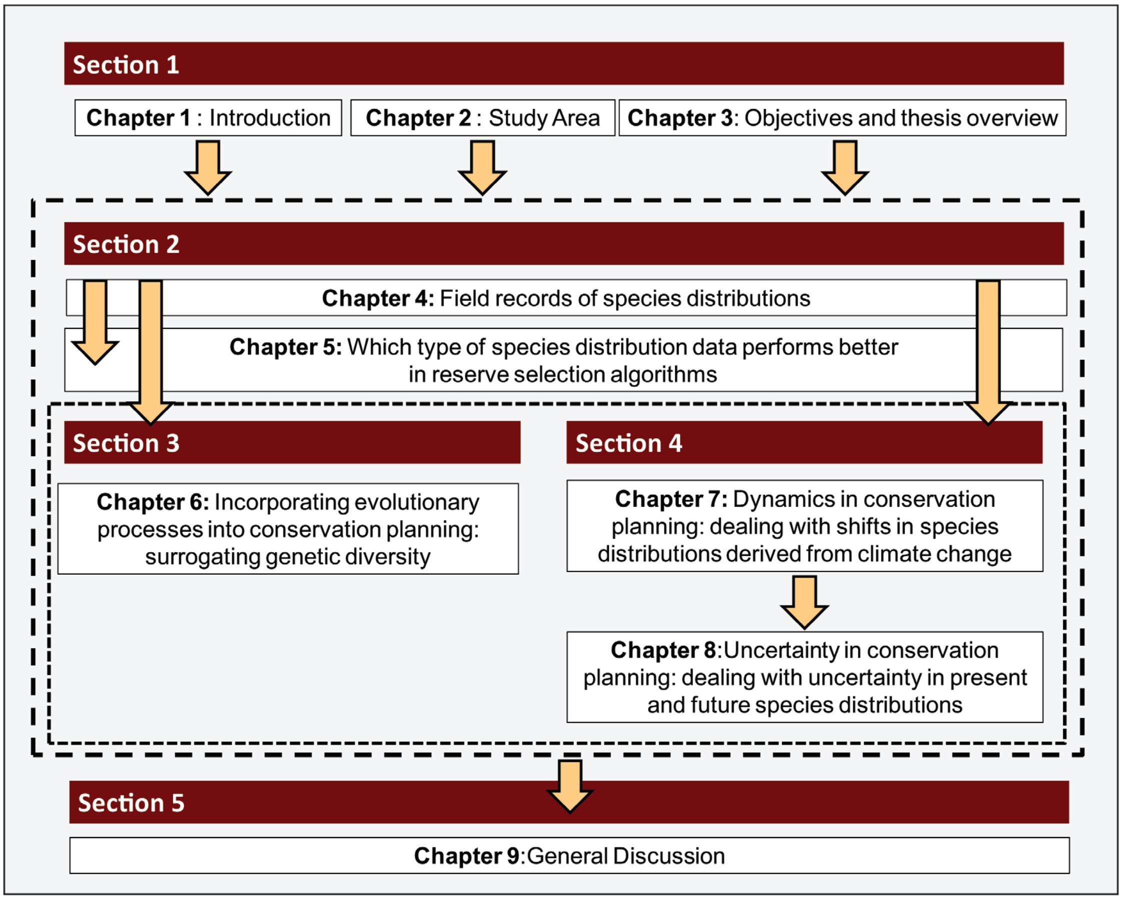

Figure 3.1 - Schematic overview of the thesis. Arrows indicate relations between sections and chapters, i.e., when outputs of one chapter are used to feed other chapters or sets of chapters. Sets of chapters are enclosed by dashed lines.

Photo: Vasco Flores Cruz

"It seems to me that we all look at Nature too much, and live with her too little."

Oscar Wilde

Chapter 4

Data on the distribution of the terrestrial herpetofauna of Morocco: records from 2001-2006

James D. Harris, Miguel A. Carretero, José C. Brito, Antigoni Kaliontzopoulou, Catarina Pinho, Ana Perera, Raquel Vasconcelos, Mafalda Barata, Diana Barbosa, Vasco Batista, Silvia B. Carvalho, Miguel M. Fonseca, Guillem Pérez-Lanuza & Catarina Rato

4.1 Abstract

Morocco is situated in the Northwest point of Africa, with an area of just over 400,000 km^2 (excluding Western Sahara). Together with Algeria and Tunisia it forms the Maghreb, a well defined geographic region within North Africa. Morocco has a great diversity of habitats, ranging from Mediterranean to Sahara, which are essentially separated by the Atlas Mountains range that traverses the country from Northeast to Southwest. Morocco has the highest diversity of herpetofauna of North Africa and of the Western Mediterranean region. Bons and Geniez (1996) accepted 104 species, with 23 endemic to Morocco, and several new taxa have been formally recognised since (e.g. Wade 2001). Additional analyses of genetic variation suggest that several widespread forms may actually be species complexes.

Here we report on the findings of six years of field work carried out in Morocco, from 2001 to 2006, totalling approximately 70 person/weeks of observations. Field trips were in most cases carried out during Spring, and a total of 427 observations of amphibian and reptile species were recorded. When a species was observed, the coordinates of the location where it was found were marked with a GPS. A total of 159 localities were sampled (Figure 4.1, Table 4.1), resulting in the observation of nine species of amphibians and 57 species of reptiles, representing more than two thirds of the known species. Specimens are classified at the species level, but subspecific comments are supplied when relevant. Since the taxonomy of several Moroccan taxa is still unresolved, we implement some of the more stable nomenclatural changes since Bons and Geniez (1996), but also discuss recently suggested alternatives.

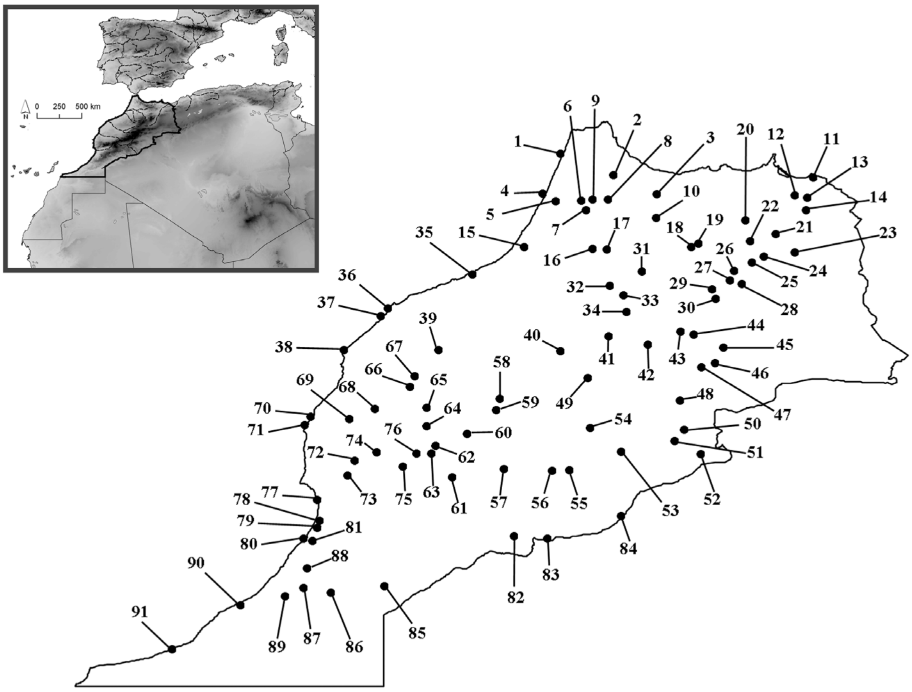

Figure 4.1 - Map of the study area and the principal localities sampled.

4.2 Amphibia

4.2.1 Urodela

Family Salamandridae

Pleurodeles waltl Michahelles 1830, localities 5 and 36.

Locality 36, El Jadida (square S11 in Bons and Geniez 1996): between the northern (main) distribution area and the southern localities were the species was observed, namely Safi [Q15] and Essaouira island [N19], for which Bons and Geniez (1996) suggested the need for confirmation. Adults were found under stones during wet weather (locality 36, reported in detail in Carretero et al. (2004), juveniles in large, shallow temporary ponds (locality 5).

4.2.2 Anura

Family Discoglossidae

Alytes obstetricans (Laurenti 1768), only found in locality 19d. Currently referred to *Alytes maurus* (Fromhage et al., 2004; Gonçalves et al., 2007). Adult specimens were found under stones on a well-grazed, steeply sloping hillside.

Table 4.1 - Localities sampled (coordinates in WGS1984; LAT D: Latitude, Degrees, LAT M: Latitude, Minutes, LONG D: Longitude, Degrees, LONG M: Longitude, Minutes). Due to the big number of localities sampled, localities that are close together are grouped together.

CODE	LOCALITY NAME	LAT D	LAT M	LONG D	LONG M
1	Assilah	35º	28.264	-6º	1.873
1a	Road Larache-Tetouan	35º	23.245	-5º	55.788
2	Chefchaouene	35º	10.023	-5º	15.145
2a	3km S of Derdara crossroad	35º	5.543	-5º	18.445
2b	Bab Taza	35º	3.98	-5º	12.08
2c	After Bab Taza	35º	3.669	-5º	6.965
3	Ketama	34º	52.694	-4º	36.652
4	Moulay Bousselhaim beach	34º	53.761	-6º	17.266
4a	1km before Moulay Bousselhaim	34º	53.27	-6º	15.5
5	Road to Moulay Bousselhaim 1	34º	46.24	-6º	5.195
5a	Road to Moulay Bousselhaim 2	34º	41.799	-6º	1.552
6	Close to Basra	34º	47.483	-5º	43.533
7	5km after Had Kourt	34º	39.059	-5º	39.628
8	Zoumi	34º	48.026	-5º	20.416
8a	Road to Zoumi	34º	46.102	-5º	30.971
8b	5km before Zoumi	34º	44.759	-5º	25.369
8c	15km before Zoumi	34º	46.102	-5º	30.971
8d	4,5km SE of Zoumi	34º	47.361	-5º	18.201
9	2km before Ouazzane	34º	47.759	-5º	33.543
9a	Close to Ouazzane	34º	37.814	-5º	32.283
10	Taounate	34º	31.797	-4º	38.085
11	Mouth of oued Moulouya; 9km W of Saida	35º	7.243	-2º	19.981
12	3 km E of Moulouya River bridge	34º	52	-2º	36
13	Road to Taforalt	34º	50	-2º	25
13a	11km S of Berkane	34º	51.435	-2º	25.525
14	10km N of El Aioun	34º	38.666	-2º	26.471
15	Foret de la Mamora	34º	6.279	-6º	33.73
15a	Kenitra (highway)	34º	12.264	-6º	33.715
16	Volubilis (Roman Ruins)	34º	4.532	-5º	33.445
17	Near Moulay Idriss	34º	3.867	-5º	21.337
18	Halouane	34º	6.791	-4º	7.283
19	Ras-El-Oued, Tazzeka	34º	9.249	-4º	0.556
19a	10km S of Taza	34º	7.829	-4º	1.751
19b	15km S of Taza - Taza Caves	34º	6.257	-4º	4.349
19c	30km S of Taza - P.N. Tazekka	34º	5.55	-4º	6.188
19d	35km S of Taza - P.N. Tazekka	34º	5.021	-4º	6.849
19e	Canyons between Sidi Abdallah and Taza	34º	11.573	-4º	11.391
20	15km S of Saka	34º	29.801	-3º	19.564

Table 4.1 (continued)

CODE	LOCALITY NAME	LAT D	LAT M	LONG D	LONG M
21	From Taourirt to Debdou	34º	18.154	-2º	53.14
22	5km S of crossroad to Missour	34º	11.629	-3º	15.13
23	60km NW of Ain Benimathar	34º	1.502	-2º	36.34
24	Gaada de Debdou	33º	57.7	-3º	2.868
24a	Gaada de Debdou 1	33º	58.476	-3º	1.876
24b	Gaada de Debdou (Plateau du Rekkam) 1	33º	47.018	-3º	2.518
25	Rchida	33º	52.472	-3º	13.644
26	Zerzaia road S329	33º	45.765	-3º	29.688
27	Fritissa	33º	37.288	-3º	32.945
28	24km E of crossroad to Ain Benimathar	33º	33.761	-3º	22.456
28a	10km E of crossroad to Ain Benimathar	33º	30.446	-3º	32.244
28b	2km E of crossroad to Ain Benimathar	33º	20.214	-3º	34.962
29	Tirnest	33º	29.268	-3º	48.658
30	Outat-Oulad-El-Haj	33º	21.198	-3º	45.63
30a	30km N of Missouri	33º	15.927	-3º	48.243
31	Midelt to Taza 1	33º	44.549	-4º	49.911
31a	Midelt to Taza 2	33º	29.666	-4º	51.754
31b	Midelt to Taza 3	33º	15.043	-4º	41.229
32	15km N of Azrou (Balcon d' Ito)	33º	32.562	-5º	19.014
32a	5km S of Azrou	33º	26.11	-5º	10.913
33	Mischliffen	33º	24.326	-5º	6.199
34	10km S of Timahdite	33º	9.313	-5º	4.096
34a	15km S of Timahdite	33º	6.788	-5º	1.652
35	N - Casablanca (highway)	33º	42.675	-7º	18.922
36	El Jadida	33º	12.725	-8º	33.058
37	Jorf Lasfar	33º	5.282	-8º	39.192
38	Moussa	32º	36.182	-9º	11.5
39	Mechra Ben Abhou; 110km NW of Marrakech	32º	36.099	-7º	48.66
40	El Ksiba	32º	34.511	-6º	2.109
40a	El Ksiba Area	32º	33.599	-6º	4.135
40b	Titt-n-Tazzart	32º	29.281	-6º	0.852
41	Kerrouchen	32º	48.106	-5º	19.386
41a	Tizi-n' Rechou	32º	47.062	-5º	13.508
42	Midelt	32º	40.972	-4º	44.568
43	Tamdafelt bridge	32º	52.471	-4º	15.916
44	25km S of Missour	32º	49.87	-4º	4.371
45	22km W of Talsinnt	32º	38.328	-3º	38.489
45a	Unnamed village 30km W of Talsinnt	32º	35.158	-3º	45.631
45b	25km W of Talsinnt	32º	34.143	-3º	42.255
45c	18km S of Talsinnt	32º	22.545	-3º	25.897
45d	25km S of Talsinnt	32º	19.321	-3º	28.777

Table 4.1 (continued)

CODE	LOCALITY NAME	LAT D	LAT M	LONG D	LONG M
46	Ait Ichchou	32°	25.13	-3°	46.232
47	10km E of Gourrama	32°	21.063	-3°	57.967
47a	Gourrama	32°	20.094	-4°	4.469
48	Ar-Rachidia (camping)	31°	51.922	-4°	17.17
48a	5km S of Source Blue de Merski	31°	50.935	-4°	15.308
48b	Aoufouss	31°	47.087	-4°	13.525
49	Lake Tisli	32°	11.564	-5°	38.054
50	Erfoud	31°	26.215	-4°	13.264
50a	5km N of Erfoud	31°	30.012	-4°	12.11
50b	10km N - Erfoud	31°	31.098	-4°	11.56
50c	15km N - Erfoud	31°	31.205	-4°	11.533
50d	12km N of Erfoud	31°	32.343	-4°	11.152
51	5km W of Rissani	31°	16.217	-4°	21.865
52	Erg Chebbi	31°	4.356	-3°	58.173
53	2km E of Alnif	31°	7.117	-5°	8.577
53a	10km E of Alnif	31°	9.609	-5°	2.237
54	Merzouga to Ouarzazate desert road 1	31°	27.708	-5°	35.661
54a	Merzouga to Ouarzazate desert road 2	31°	22.414	-5°	52.564
54b	Merzouga to Ouarzazate desert road 3	31°	6.796	-6°	24.474
54c	Merzouga to Ouarzazate desert road 4	31°	4.085	-6°	32.096
55	15km W of Tazzarine	30°	51.35	-5°	54.173
56	20km NW of Souk el Arba	30°	50.344	-6°	8.735
57	5km S of Ouarzazatte	30°	51.719	-6°	50.85
57a	10km S of Ouarzazatte	30°	49.302	-6°	46.161
58	3.5km NE of Tanannt	31°	53.201	-6°	54.85
59	Iminifri	31°	43.454	-6°	58.314
59a	After Iminifri	31°	42.428	-6°	57.376
60	Road Ouarzazatte – Marrakech	31°	22.017	-7°	23.53
61	El Azib n-Iriri (Jbel Siroua)	30°	44.818	-7°	36.557
61a	Amzdour	30°	46.617	-7°	37.229
61b	W of Tachakoucht	30°	48.337	-7°	32.627
62	Oukaimeden	31°	12.058	-7°	51.322
62a	1km S of Oukaimeden	31°	12.757	-7°	50.874
63	High Reraia river: 2km S of Sidi Chamharouch	31°	5.254	-7°	55.148
63a	High Reraia river: Sidi Chamharouch	31°	6.314	-7°	54.844
63b	Reraia river	31°	6.041	-7°	54.867
64	15km S of Marrakesh (S501 to Tahannaout)	31°	29.172	-7°	59.022
65	Marrakech-Oulad Salas	31°	45.434	-7°	58.47
65a	10km NE of Marrakesh	31°	44.335	-7°	58.698
66	Oaddour	32°	4.014	-8°	13.158
67	Oulad Branim	32°	13.496	-8°	9.89

Table 4.1 (continued)

CODE	LOCALITY NAME	LAT D	LAT M	LONG D	LONG M
68	Oulad Brahim (Oued Tensift)	31º	45.148	-8º	44.06
69	An Nzala	31º	35.43	-9º	6.283
70	Moulay Bouzertoun beach	31º	38.161	-9º	40.432
71	Essaouira	31º	30	-9º	46
71a	7km S of Essaouira	31º	27.821	-9º	45.38
72	Gran Plateau des Ida-ou-Bouzia	30º	59.567	-9º	1.8867
73	Argana	30º	46.597	-9º	7.7717
73a	13km N of Bigoudine	30º	48.713	-9º	8.044
74	Lala Aziza	31º	6.223	-8º	42.523
74a	Temporary pond by the track	31º	10.512	-8º	45.217
75	15 km S- Hazar road km 93	30º	54.028	-8º	19.888
75a	Hazar	30º	56.928	-8º	15.853
75b	Tizi-n-Test	30º	52.455	-8º	22.02
76	31km S - Asni	31º	5.413	-8º	7.765
77	Agadir, Tiznit road	30º	25	-9º	35
78	49km Tiznit	30º	6	-9º	33
79	Taroudant (Oued Massa)	29º	59.828	-9º	35.272
80	Bou Soun	29º	51.071	-9º	46.238
81	Oued Massa	29º	48.369	-9º	38.85
82	30km E of Foum Zguid	29º	52.81	-6º	42.714
82a	40km E of Foum Zguid	29º	51.042	-6º	37.318
83	Erg Mhazil - 80km E of Foum Zguid	29º	51.274	-6º	13.535
83a	112km E of Foum Zguid	29º	52.091	-6º	0.636
84	60km E of Tagounite	30º	11.096	-5º	8.796
85	60km W of Akka	29º	9.326	-8º	35.596
85a	80km SW of Akka	29º	5.1	-8º	41.391
86	3km E of Taggit	29º	3.177	-9º	22.431
86a	4km E of Taggit	29º	3.148	-9º	20.753
86b	6km E of Taggit	29º	3.362	-9º	20.093
86c	6km W of Taggit	29º	6.052	-9º	28.002
87	Tagant	29º	7.48	-9º	46.68
88	Tizi Mighert	29º	24.516	-9º	43.634
88a	Morght	29º	24	-9º	43
88b	km.49 Tiznit-Guelmine	29º	23.71	-9º	44.065
89	Guelmine	28º	59.87	-10º	3.164
90	15km E of Aoreora - Plage Blanche	28º	52.39	-10º	42.164
90a	25km S of Aoreora	28º	44.684	-10º	44.631
91	50km S of Tan-Tan Plage	28º	13.847	-11º	42.099
91a	60km S of Tan-Tan Plage	28º	11.514	-11º	49.47

Discoglossus pictus Otth 1837, localities 2a, 18, 19d, 32, 35, 47a and 61.

Currently referred to *Discoglossus scovazzi* (Fromhage et al., 2004; Zangari et al., 2006).

Locality 47a: Gourrama. Previously unreported from east of the Atlas Mountains, this extends the distribution into the drier region to the east (Figure 4.2A). Found in a variety of ponds, roadside ditches and marshy mountain meadows.

Family Bufonidae

Bufo bufo (L. 1758), localities 31b, 61, 61b, 62a and 73.

Bufo mauritanicus Schlegel 1841, localities 1, 3, 18, 19a, 19d, 24, 29, 31b, 34a, 38, 45a, 46, 50, 57, 61, 69 and 73.

Bufo viridis Laurenti 1768, localities 24, 28b, 36, 45a, 58 and 68.

Bufo viridis appears to be a species complex (Stöck et al. 2006). Some of these new localities fill gaps in the known range of this widespread species.

Bufo brongersmai Hoogmoed 1972, only found in localities 58 and 74a.

This new record connects the locations of Souss basin and south of High Atlas with the isolated observations in the Marrakech plain (Fig. 4.2B). Mature adult *Bufo* sp. were generally found under stones. Huge numbers of recent metamorphosed *B. mauritanicus* were observed in various regions of the Rif Mountains.

Family Hylidae

Hyla meridionalis Boettger 1874, localities 19d, 61, 61b and 62.

Typically found in reeds near more permanent streams and rivers. Unusual silver colored individuals were seen at Jebel Sirwah (locality 61).

Family Ranidae

Rana saharica Boulenger 1913, localities 3, 17, 19, 19a, 28b, 31b, 32, 43, 45a, 46, 47a, 61 and 73.

Proposed as a possible species complex by Bons and Geniez (1996), but analysis of mtDNA shows minimal variation across Morocco (Harris et al. 2003a). Common in a variety of water bodies throughout its range.

4.3 Reptilia

4.3.1 Chelonia

Family Testudinidae

Testudo graeca L. 1758, localities 7, 8c, 13a, 19d, 23, 24b, 32, 38, 40, 56, 59 and 65.

Locality 56: There are few citations of *T. graeca* from the East of the Atlas Mountains. Extensive anthropogenic effects make it difficult to rule out artificial introductions, although this new locality is a long way from any large human settlements (Figure 4.2C).

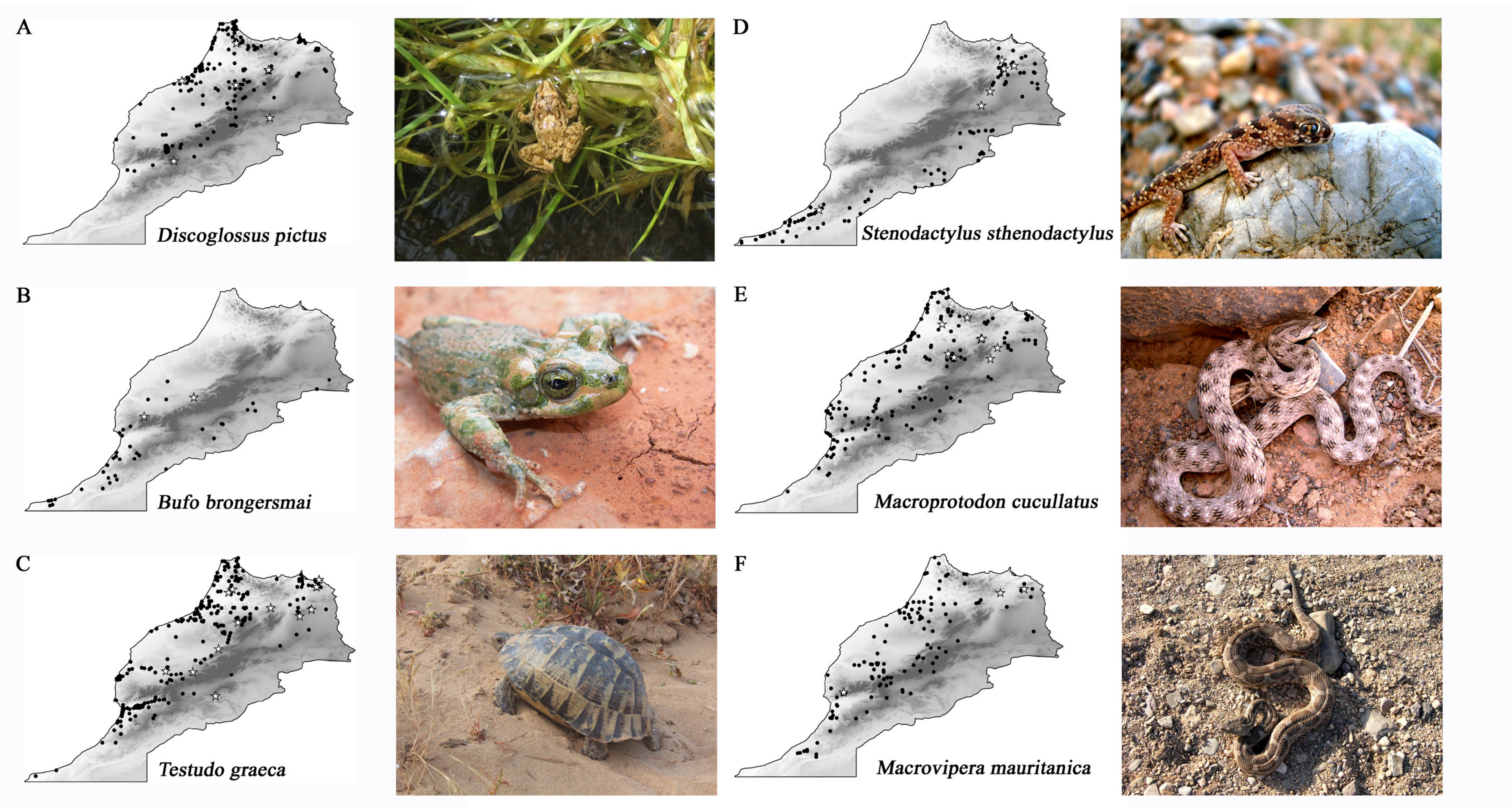

Figure 4.2 - Distribution maps of some of the species observed. Black dots represent known distributions of the species (extracted from Bons & Geniez, 1996) and stars represent new records reported in this study.

Family Bataguridae

Mauremys leprosa (Schweigger 1812), localities 1a, 8b, 8d, 35, 59 and 87.

Although most specimens were found near large mountain streams and rivers, many were clearly of a temporal nature that were likely to be dry for much of the year.

4.3.2 Sauria

Family Agamidae

Agama bibroni Dúmeril & Dúmeril 1851, localities 2a, 2b, 3, 5, 8c, 10, 13a, 18, 19d, 20, 30, 31, 32, 37, 44, 47, 47a, 54b, 59, 63b, 74, 75b, 79, 86c and 88b.

One of the most commonly seen species in Morocco, found in a wide variety of habitats but typically associated with rocks.

Trapelus mutabilis (Merrem 1820), localities 45d, 50a, 54a and 59a.

*Uromastyx acantinuru*s Bell 1825, localities 20, 44, 47, 54, 54c and 85.

Mitochondrial DNA analysis indicates all the Moroccan specimens form a clade within this species, although this includes a relatively high level of genetic variation (Harris et al. 2007). Although still quite common in the rocky desert areas, many specimens were road kills, and individuals were often observed sold in markets, indicating the dual threats to this species.

Family Anguidae

Ophisaurus koellikeri (Günther 1873).

Only found in locality 32, under stones in a broad-leaf forest. Currently referred to *Hyalosaurus koellikeri* (Macey et al., 1999).

Family Chamaeleonidae

Chamaeleo chamaeleon (L. 1758), localities 20, 54a and 91.

One specimen (locality 20) was found in a surprisingly open and arid area, walking along the ground.

Famiily Gekkonidae

Geckonia chazaliae Mocquard 1895, only found in locality 91a.

Currently referred to *Tarentola chazaliae* (Carranza et al., 2002).

Hemidactylus turcicus (L. 1758), only found in locality 11, within a ruined building.

Analysis of mtDNA sequence variation indicates *H. turcicus* is probably introduced in Morocco (Carranza and Arnold 2006).

Ptyodactylus oudrii Lataste 1880, localities 43 and 45a.

Locality 43 (Tamdafelt bridge): This record extends the distribution area of the species further north into the Moulouya river valley. All specimens were found on large boulders. In locality 43 the specimen was on the underside of a rock above an irrigation channel.

Quedenfeldtia moerens (Chabanaud 1916), localities 63, 72, 75 and 75b.

Quedenfeldtia trachyblepharus (Boettger 1874), localities 61 and 62.

Locality 61 (El Azib n-Iriri, Jbel Siroua) regarding forms: Most citations from this area are of *Quedenfeldtia* sp. only. This confirms the presence of *Q. trachyblepharus* from this area. *Quedenfeldtia* were active even when the sky was extremely overcast, and were usually found in very high densities when present.

Stenodactylus sthenodactylus (Liechtenstein 1823), localities 20, 21, 22, 30, 44 and 89.

Localities 22 and 30: these lie between the northern and southern areas of distribution, making it more continuous through the Moulouya river (Figure 4.2D). A few specimens were found under rocks, but many more by digging out the small holes beneath thorn bushes, often also occupied by *Acanthodactylus* sp.

Saurodactylus mauritanicus (Dúmeril and Bibron 1836), localities 12, 13, 13a, 14 and 23.

Saurodactylus brosseti Bons & Pasteur 1957, localities 36, 58, 64, 65, 65a, 68, 71, 72, 74, 77, 78, 81, 88a.

Saurodactylus fasciaticus Werner 1931, localities 8a, 9a and 39.

Locality 39 adds another southerly locality to the few isolated points known, and increases the range of sympatry between *S. fasciatus* and *S. brosseti*. Recent analyses suggest that *Saurodactylu*s is paraphyletic (Rato and Harris, 2008), in which case future taxonomic changes to this group are likely.

Tarentola mauritanica (L. 1758), localities 1, 2b, 3, 4, 7, 8c, 11, 17, 19, 19b, 19e, 25, 29, 31, 31b, 32, 32a, 33, 36, 39, 40, 42, 59, 61, 63b, 65, 65a, 67, 73, 75a and 76.

Tarentola mauritanica appears to be a species complex, although the two accepted subspecies in Morocco do not seem to correspond to genetic lineages (Harris et al. 2004a, b). *Tarentola mauritanica* is extremely widespread in both natural habitats but especially in buildings.

Tarentola deserti Boulenger 1891, localities 50b and 50d.

Found on clusters of large boulders. Superficially very similar to *Tarentola mauritanica*, but with a notably ochre-yellow iris.

Tropiocolotes tripolitanus Peters 1880, found only in locality 89, under rubbish in a small open area within the town of Gourrama.

Family Lacertidae

Acanthodactylus erythrurus (Schinz, 1833), localities 2b, 3, 19b, 24, 32, 32a, 33, 41, 41a, 61, 65, 65a and 72.

Acanthodactylus lineomaculatus Dúmeril & Bibron 1839, localities 4, 4a, 15, 15a, 38, 70 and 71a.

Evidence based on mtDNA do not support the distinction of this species from *A. erythrurus* (Harris et al. 2004c).

Acanthodactylus maculatus (Gray 1838), localities 14, 30a and 53a.

Acanthodactylus busacki Salvador 1982, localities 79, 81 and 90.

The morphological distinction of *A. busacki* has not always been accepted (see Harris and Arnold 2000). Mitochondrial DNA sequence variation indicates considerable variation within an "*A. pardalis* species complex", including *A. pardalis*, *A. maculatus*, *A. busacki* and *A. mechriguensis* (Fonseca et al. 2008). However, exact delimitation of species remains equivocal. Members of this species complex are extremely difficult to separate in the field. All, like the other Moroccan *Acanthodactylus* sp. are typically seen running over open areas between bushes where the animals take refuge in holes around the roots.

Acanthodactylus boskianus (Daudin 1802), localities 11, 20, 27, 28, 28a, 28b, 30, 45c, 46, 47a, 48a, 48b, 53, 55, 82, 86, 86a and 86b.

Acanthodactylus dumerili (Milne Edwards 1829), localities 50c, 50d, 82a, 83a and 84.

Acanthodactylus longipes Boulenger 1921, localities 52 and 83.

Acanthodactylus aureus Günther 1903, localities 80 and 90a.

Lacerta tangitana Lataste 1880, localities 3, 6, 18, 19a, 19d, 24, 32, 32a, 34, 34a, 40a, 40b, 45a, 45b, 61, 63a, 63b and 75. Currently referred to *Timon tangitanus* (Arnold et al. 2007), and may represent a species complex in Morocco (Paulo, 2001). While Debdou (locality 24) is within the range typically assigned to *Lacerta pater*, specimens from here are still *L. tangitana*.

Lacerta andreanszkyi Werner 1929, localities 62 and 63.

Currently referred to *Atlantolacerta andreanszkyi* (Arnold et al. 2007). Found under rocks in the open high mountain meadow of Oukaimeden, with *Podarcis hispanica* and *Scelarcis perspicillata* on the larger rocks and walls surrounding the meadow.

Mesalina guttulata (Lichtenstein 1823), localities 25, 45a, 48, 54a, 54b and 86c.

These new citations fill some gaps in the widespread distribution of this species.

Mesalina olivieri (Audouin 1829), localities 20, 24, 47 and 65a.

The specimen from the last locality (10km NE of Marrakesh) corresponds to the subspecies *M. o. simoni*. All Moroccan *Mesalina* are small, shy species found in dry open areas running between small bushes used as refugia.

Ophisops occidentalis Boulenger 1887, found only in locality 23.

Podarcis hispanica (Steindachner 1870), localities 1, 2, 2b, 3, 8, 8c, 8d, 18, 19a, 19b, 19d, 24, 32, 32a, 33, 34, 34a, 42, 61, 61a, 63b and 75.

Locality 61 (El Azib n-Iriri, Jbel Siroua): Most Moroccan and Southern Spanish populations are now referred to *Podarcis vaucheri* (Busack and Lawson 2005). Pinho et al. (2006, 2007) show that the populations from locality 61 are not related to other Moroccan populations, but rather to a Tunisian form of the *Podarcis hispanica* species complex. Generally *Podarcis* were found in areas with Mediterranean climate, and especially near water courses such as streams. However some populations, such as that from within the town of Midelt, were on walls in quite dry areas.

Psammodromus algirus (L. 1758), localities 2a, 2b, 3, 4, 7, 9a, 13a, 19, 19a, 19b, 19d, 19e, 25, 31, 32, 32a, 33, 34, 40, 41a, 45b, 59, 59a and 61.

Locality 45b (25km W of Talsinnt): Two other Mediterranean species (*P. vaucheri* and *S. perspicillata*) have isolated records from this region. This adds another Mediterranean species to this isolated group. *Scelarcis perspicillata* was confirmed at the same place, although *P. vaucheri* was not observed. The two accepted subspecies in Morocco do not appear to be genetically distinct based on analysis of mtDNA sequences (Carranza et al. 2006).

Scelarcis perspicillata (Dúmeril & Bibron 1839), localities 17, 19, 19a, 19b, 19e, 24, 31, 32, 32a, 33, 40a, 45, 59, 61, 63b and 75.

Scelarcis perspicillata has three distinct morphological forms in Morocco. Considerable mtDNA variation was reported (Harris et al. 2003b), and a 100% coincidence of morphotypes and mtDNA lineages was observed at a contact zone of two forms near Taza (Perera et al. 2007), indicating a probable species complex with forms separated by perhaps 5.5 million years (Arnold et al. 2007). However, there are only two distinct genetic lineages, and in other areas populations with similar colour morphs do not coincide with these. Specimens were found predominantly on high cliffs and large rocks, often near running water, where their flattened morphology allows them to take refuge in very narrow crevices. Occasionally also seen climbing on trees.

Family Scincidae

Chalcides colosii Lanza 1957, only found in locality 2b.

Chalcides minutus (Caputo 1993), only found in locality 24a.

Chalcides mionecton (Boettger 1874), localities 15, 15a, 68 and 89.

Chalcides ocellatus (Forsskål 1775), localities 13a, 14, 20, 22 and 24.

Chalcides polylepis Boulenger 1890, localities 19b and 36.

Chalcides pseudostriatus (Caputo 1993), only found in locality 2a.

All *Chalcides* specimens were found turning rocks. A recent extensive review suggests that future taxonomic changes for some species are likely (Carranza et al. 2008).

Eumeces algeriensis Peters 1864, localities 9a, 16, 19e, 28, 30, 36, 39, 59, 65a, 68 and 79.

Eastern localities fall within an area where the form *Eumeces (algeriensis) meridionalis* could have been expected, but all samples corresponded to *E. a. algeriensis*.

Sphenops boulengeri (Anderson 1896), only found in locality 82.

4.3.3 Amphisbaenia

Family Amphisbaenidae (currently Blanidae following Kearney and Stuart, 2004)

Blanus mettetali Bons 1963, found only in locality 40.

Blanus tingitanus Busack 1988, localities 8c, 19a and 19b.

Currently two species of *Blanus* are recognised in Morocco, *B. mettetali* and *B. tingitanus*, and one in Iberia, *B. cinereus*. Vaconcelos et al. (2006) indicate that *B. cinereus* is a species complex, and that one individual was found in Taza (locality 19). The existence of this form in North Africa needs further investigation.

Family Trogonophidae

Trogonophis wiegmanni Kaup 1830, localities 1, 9a, 19e, 23, 35, 36, 38 and 59.

Mendonça and Harris (2007) reported the two localities for *T. w. wiegmanni* in the Moulouya river valley region, that link the northern and southern populations of this form in Morocco. They indicate that three genetic lineages exist in North Africa, corresponding to the accepted subspecies in Morocco plus an additional lineage in Tunisia. All the amphisbaenians observed were found under rocks or litter.

4.3.4 Serpentes

Family Colubridae (s.l.)

Hemorrhois hippocrepis L. 1758, localities 7, 9, 9a, 17, 19b, 19c, 24a, 31a, 32, 66 and 67. As with all the following colubrid snakes, many specimens were roadkills.

Hemorrhois algirus (Jan 1863), found only in locality 54.

Coronella girondica (Daudin 1803), localities 19d, 24, 49 and 63.

Macroprotodon cucullatus (Geoffroy Saint-Hilaire 1827), localities 3, 9a, 19b, 19d, 26, 30, 32 and 33.

In a recent morphological analysis Wade (2001) recognized four species of *Macroprotodon*, with three, *M. cucullatus*, *M. mauritanicus* and *M. abubakeri* in North Africa and *M. brevis* in North Africa and the Iberian Peninsula. Assessment of mtDNA variation indicates considerable variation in North Africa and a recent colonization of the Iberian Peninsula (Carranza et al. 2004, Vasconcelos and Harris 2006). However exact delimitation of genetic units in North Africa requires further analyses (Figure 4.2E).

*Malpolon moilensis (*Reuss 1834), found only in locality 85a.

Malpolon monspessulanus (Hermann 1804), localities 1a, 2c, 8c, 17, 18, 19d, 33, 61 and 65.

Natrix maura (L. 1758), localities 3, 5a, 8d, 10, 11, 46, 59 and 61. Several specimens were caught swimming in small ponds, streams or irrigation channels. All were collected very close to such water bodies.

Psammophis schokari (Forsskål 1775), localities 20, 45, 54b and 60.

Although three colour morphs have been described for Morocco (Bons and Geniez, 1996), all three form part of the same mtDNA genetic lineage (Rato et al. 2007).

Psammophis and *Malpolon* are the only non-viperid Moroccan snakes belonging to the Subfamily Psammophiinae. Since the recognition of Atractaspididae and Elapidae make traditional Colubridae paraphyletic according to the last molecular phylogenies (Lawson et al., 2005), this well defined group probably merits Family status.

Spalerosophis dolichospilus (Werner 1923), only found in locality 47a, currently the easternmost report in Morocco.

Family Viperidae

Cerastes vipera (L. 1758), found only in locality 57a. A roadkilled specimen, without the typical horns.

Macrovipera mauritanica (Gray 1849), localities 14, 73a and 20.

Currently referred to *Daboia mauritanica* (Lenk et al., 2001). These new localities fill gaps in the range of this widespread species, particularly in the low Moulouya basin (Figure. 4.2F).

4.4 Acknowledgements

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Photo: Vasco Flores Cruz

“One thing is sure. We have to do something. We have to do the best we know how at the moment... if it doesn’t turn out right, we can modify it as we go along”

Franklin D. Roosevelt

Chapter 5

Simulating the effects of using different types of species distribution data in reserve selection

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5.1 Abstract

In a perfect world, systematic conservation planning would use complete information on the distribution of biodiversity. However, information on most species is grossly incomplete. Two main types of distribution data are frequently used in conservation planning: observed and predicted distribution data. A fundamental question that planners face is – which kind of data is better under what circumstances? We used simulation procedures to analyse the effects of using different types of distribution data on the performance of reserve selection algorithms in scenarios using different reserve selection problems, amounts of species distribution known, conservation targets and costs. To compare these scenarios we used occurrence data from 25 amphibian and 41 reptile species of the Iberian Peninsula and assumed the available data represented the whole truth. We then sampled fractions of these data and either used them as they were, or converted them to modelled predicted distributions. This enabled us to build three other types of species distribution data sets commonly used in conservation planning: "predicted", "transformed predicted" and "mixed". Our results suggest that reserve selection performance is sensitive to the type of species distribution data used and that the most cost-efficient decision depends most on the reserve selection problem and on how much we have of the species distribution data. Choosing the most appropriate type of distribution data should start by evaluating the scenario circumstances. While there is no one best approach for every scenario, we discovered that using a mixed approach usually provides an acceptable compromise between species representation and cost.

5.2 Introduction

Systematic conservation planning (Margules and Pressey 2000; Possingham et al. 2006) is now a “text book” framework developed to identify protected area systems that will efficiently meet clearly defined objectives of species representation and persistence. Ideally, this framework would use complete information on the distribution of biodiversity within the planning region. Unfortunately, we never have complete information. Two main types of distribution data are frequently used in conservation planning: observed and predicted data, both offering advantages and disadvantages (Rondinini et al. 2006). Thus, fundamental questions that planners face include: Which sort of data is better under what circumstances? When should I bother building predictive models for species?

Observed distribution data of species are often compiled from museum and herbarium records as point location data, or from distribution atlases, usually in a grid format. These data usually contain uncertainty regarding the exact location of the records and, more rarely, mistakes in species identification (Graham and Hijmans 2006). However, the largest source of error with observed distribution data occurs if we assume that species are absent where we have no records for them. False species absences are common because data compilation is generally made from multiple author sources, using biased or ad-hoc surveys. Also, even where coverage of the landscape is comprehensive, false absences occur since some species have low probabilities of detection because they are rare or secretive (de Solla et al. 2005). These data sets usually do not indicate where species were searched for but not found (Bini et al. 2006). When used for conservation planning purposes, false absences in observed distribution data can increase the cost of the reserve system because false absences mean higher apparent rarity and missed opportunities for representation of co-occurring species (Pressey et al. 1999; Rondinini et al. 2006).

To overcome the limitations of using incomplete distribution data, researchers use ecological niche-based models to predict the distributions of species. However, these models are not free of uncertainty or error because: a) the distribution data on which they are based contain errors, as discussed above; b) they cannot take into account all environmental, ecological and historical factors, and the various interactions between them, that affect species distributions; c) there might be errors in the ecogeographical variables used to create the distribution models, either through measurement errors or as a consequence of the resolution at which environmental variables are mapped; and d) different statistical modelling methods have different predictive performances (Elith et al. 2006). These errors and uncertainties usually give rise to an overestimation of species distributions due to the limitations of modelling algorithms (Segurado and Araújo 2004) and because some suitable habitat is often not occupied as a consequence of historical factors, geographical barriers or biological restrictions not captured by ecogeographical variables (Lomolino et al. 2005). These commission errors - false positives - have an adverse impact on conservation planning decisions because areas where species do not occur might be selected for conservation effort, resulting in both a waste of funds and an unrecognised failure to achieve a conservation target (Rondinini et al. 2006). In extreme cases it is conceivable that we may think we have conserved an adequate fraction of the distribution of a species when, in reality, it is absent from the conservation network entirely. Intuitively, false positives are more dangerous for conservation than false negatives (Rondinini et al. 2006).

Previous studies demonstrated that reserve selection results are sensitive to the type of species distribution data (Freitag et al. 1996; Wilson et al. 2005). However, reserve selection is a complex problem, relying on several factors that can influence the decision on which type of data to use. The interactions between these factors have not been addressed in previous studies. One of these factors is the choice of the underlying mathematical problem that we are trying to solve. Two different types of mathematical problems have been formulated in terms of reserve selection: the "minimum set", and the "maximal cover" problems (see Cabeza and Moilanen 2001; Sarkar et al. 2006 for reviews). In the "minimum set" problem, the objective is to minimize the total cost of sites such that each species is represented at or above a pre-determined target. In the "maximal cover" problem, the objective is to find a reserve system that contains the most number of species that meet their targets, subject to a limit on the total cost of selected planning units. Other factors that may influence the performance of the different types of species distribution data are the amount of the species distribution that is known when the planning process starts (Freitag and van Jaarsveld 1998; Grand et al. 2007), the level of the target (Justus et al. 2008; Warman et al. 2004), and the cost of the planning units (Balmford et al. 2003; Bode et al. 2008).

In this paper, we analyse the effects of using different types of species distribution data in reserve selection, and the sensitivity of reserve selection outcomes to the interaction of all the factors described above. The intent is to provide information to conservation planners about the pros and cons of different sorts of species distribution data in different situations and to contribute general guidelines to assist decisions about the manipulation of species distribution data before planning commences. We plan to answer these practical questions: Which sort of data is better under what circumstances? When should I bother building predictive models for species if their use is for spatial conservation planning?

5.3 Methods

5.3.1 Study region

The study region is the continental Iberian Peninsula, situated in the extreme southwest of Europe (bounded by 9º32′ to 3º20′E and 35º56′ to 43º55′N). The Iberian Peninsula is included in the Mediterranean hotspot (Myers et al. 2000) and it includes many endemic species because it was one of the major glacial refugia in Europe during the Pleistocene (Hewitt 1996). This region has also acted as a centre of diversification (Gómez and Lunt 2006) as indicated by cryptic species complexes (e.g. Pinho et al. 2007).

5.3.2 Species and distribution data

We conducted this study using the Iberian amphibians and reptiles because these groups are remarkably diverse in this region (Cox et al. 2006), with six endemic amphibian species occurring in the Iberian Peninsula plus two in the Pyrenees, and eight endemic reptile species plus two in the Pyrenees. Moreover, the observed occurrences of amphibian and reptile species are documented for the Iberian Peninsula in a comprehensive UTM grid format, which makes these taxonomic groups adequate subjects for the present study (Loureiro et al. 2008; Pleguezuelos et al. 2002).

We included in the analysis 66 species: 25 amphibians and 41 reptiles (see Appendix 5.1), defined according to the taxonomic list in Carretero et al. (2009) and Comisión de Taxonomía de la AHE (2005). However, we made three alterations to the list: (1) *Triturus marmoratus* and the recently described *T. (marmoratus) pygmaeus* were combined under *Triturus marmoratus* because distribution data for *T. (marmoratus) pygmaeus* were not available for Portugal; (2) all species from the genus *Pelodytes* were treated as one taxon, called *Pelodytes sp*., because the systematics of these populations are still uncertain; and (3) *Iberolacerta monticola*, *I. cyreni* and *I. martinezricai* were lumped as *Lacerta monticola* because these species are morphologically similar, are phylogenetic sister-taxa and have a very small range which hampered the development of accurate predictive models (Engler et al. 2004; Guisan et al. 2006; Stockwell and Peterson 2002).

Species distribution data were collected from the most recent herpetological atlases of Portugal (Loureiro et al. 2008) and Spain (Pleguezuelos et al. 2002), and referenced to the UTM grid of 10x10 km, in a total of 7687 grid cells. Each grid cell is hereafter referred to as a planning unit. We assembled these data in ArcGis 9.2 (ESRI 2006), to create a planning unit vs. species matrix where the value 1 was assigned to all planning units where each species was present, and the value 0 to all planning units where each species was absent. We used these data to build five sets of species distribution data: “real”, “observed”, “predicted”, “transformed predicted” and “mixed”. The methods in which the five distribution data sets were assembled are described next.

“Real” and “observed” data sets

We assumed that our compiled data set of species distribution data had no omission or commission errors, and represented the complete species distributions. We refer to this as the “real” data set.

We used the “create random selection” command from Hawth’s Analysis tools (Beyer 2004) to randomly delete 50%, 75% and 90% of presence records of each species from the “real” data set, obtaining three different data sets that we call: “Observed 50”, “Observed 25” and “Observed 10”, respectively. We assumed that these data sets represented the part of the species distribution that was known by the scientific community in three different scenarios. We used these “observed” data sets directly in the conservation planning process and for species distribution modelling.

"Predicted" data sets

For each of the three observed data sets (50%, 25% and 10%), we modelled the distribution of each amphibian and reptile species using a set of environmental variables. We assembled nine uncorrelated ($r^2 < 0.750$) ecogeographical variables (hereafter "variables") of two types: climate variables (temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, annual precipitation, precipitation of wettest month, precipitation of driest month and precipitation seasonality) and a topographic variable (altitude). We downloaded all variables from the WorldClim database (Hijmans et al. 2005) which is a set of global climate layers generated through interpolation of climate data from weather stations on a 30 arc-second resolution grid. We changed the resolution of all variables to a grid cell size of 10x10 km to fit the planning units, using the average value of all values inside each planning unit.

We used the software Maxent v. 3.2.1 (Phillips et al. 2006; Phillips and Dudik 2008) to predict the distribution of each species from the "observed" data sets. Maxent uses a maximum entropy method to estimate the distributions of species with the constraint that the expected value of each variable (or its transform and/or interactions) should match its empirical average, i.e. the average value for a set of sample points taken from the target species distribution. We used Maxent because this method seems to perform better than other modelling methods for predicting species distributions (Elith et al. 2006). We used the default "auto features" option, the recommended default values for the convergence threshold (10^{-5}), the maximum number of iterations (500) and with the regularization value set to 1. We set the random test percentage to 20% to every species with more than 5 occurrences and for the others we did not reserve data for testing. We used the logistic output, which assigns a probability of occurrence of each species to each cell in the study region.

With the Maxent results, we built a species vs. planning unit matrix similar to the "observed" ones, but using probabilities of occurrence instead of data on "observed" occurrences. In this way we obtained three new data sets: "Predicted 50", "Predicted 25" and "Predicted 10". We evaluated the agreement between each model output and the "real" dataset by plotting a Receiver-Operating Characteristic Curve (ROC) (Zweig and Campbell 1993) and calculating the area under the curve (AUC) (see Appendix 5.1).

"Transformed predicted" data sets

For each of the three "predicted" data sets (50%, 25% and 10%), we transformed the Maxent output probabilities to a predicted absence/presence (0/1) matrix. For this purpose, we found a threshold probability for each species to balance commission and omission errors. Thus, we used the widely adopted method of choosing a threshold at the point on the ROC curve where the sum of the sensitivity and specificity is maximized and calculated an individual threshold for each model (Liu et al. 2005). Then, for each species, we transformed the probability value in each planning unit to 0 if it was lower than the threshold and to 1 if it was equal to or higher than the threshold. In this way we obtained three new data sets: “Transformed Predicted 50”, “Transformed Predicted 25” and “Transformed Predicted 10”.

“Mixed” data sets

Because statistical models for some species are relatively unreliable, we also created a “mixed” data set that was a combination of “observed” and “transformed predicted” data sets. Commission (false positive) errors generated by uncertainty in species distribution models have consequences for conservation planning because areas where species do not occur might be mistakenly selected for conservation purposes. This error is more likely when dealing with restricted-range and threatened species. The typically low number of occurrence records of these species leads to predictive distribution models with low accuracy (Guisan et al. 2007; Stockwell and Peterson 2002) and consequently false presences are common. Too many false presences could dramatically compromise conservation outcomes for restricted range and threatened species by directing conservation toward areas where they are absent (Purvis et al. 2000). For these reasons, we used two criteria to select species that would be represented by “observed” data: a) distribution range less than 5% of the study area (measured in the “real” data set); and/or b) conservation status Endangered or Critically Endangered in at least one of the countries of the Iberian Peninsula. For all the species that did not fulfil at least one of these criteria, we used the data from the “transformed predicted” data sets.

5.3.3 Reserve selection

We used two different approaches to select optimal sets of planning units necessary to achieve species conservation targets: “the minimum set” and the “maximal cover” approaches. In both we evaluated the performance of each of the 13 data sets described above in four different target scenarios and two cost scenarios in a total of eight combined cost-target scenarios.

A common way to set species targets in conservation planning is to use a proportion of species distributions, usually 10% (Tear et al. 2005). Thus, in three of our target scenarios we set targets as a fixed proportion of “real” species occurrences. We used the 10% target because this is often used, and two additional scenarios with lower proportion (5% and 1%), in order to analyse the sensitivity of our results to different target amounts. We refer to these scenarios as T10, T5 and T1, respectively. We also set another target scenario where we attributed different target proportions to different species according to their conservation status, geographic range and biological status (see Appendix 5.2 for details). We refer to this scenario as Tdif. For each target scenario, the number of occurrences targeted for the conservation of each species was therefore equal for all the data sets, regardless of the number of occurrence records actually present in the data sets. In this way the reserve selection algorithms were trying the achieve the same number of occurrences for a given species when using data sets derived from different subsets of the “real” data (50, 25 and 10%). For “observed”, “transformed predicted” and “mixed” data sets, we had allocated species to planning units as simple presences so application of targets was straightforward. For the “predicted” data sets, we summed the probabilities to generate an expected number of occurrences and applied percentage targets to this number.

The two cost scenarios were set in a manner that, in one of them, all PUs had the same cost (Uniform cost scenario9, and, in the other, costs differed in different PUs (Log normal cost scenario). In the Uniform cost scenario we set the cost to 10 000 units in all PUs, since this is approximately the area of each PU (in ha). In the Log-normal cost scenario, we attributed a random cost to each PU using a Log-normal distribution with a mean of 10 000 units and a standard deviation of 2 500.

The Minimum Set approach

We used the 13 species distribution data sets as input data in the Marxan software v1.8.10 (Ball and Possingham 2000) with the eight combinations of cost and target. Marxan software delivers decision support for reserve system design by using a simulated annealing algorithm to choose a set of planning units that meets a suite of biodiversity targets for the lowest possible total cost.

For each run, we used the following recommended Marxan parameters (Ball et al. 2009): algorithm - simulated annealing; number of runs - 100; penalty cost for not achieving the target - 10 000; iterations per simulation - 1 000 000; temperature decreases per simulation - 10 000; initial temperature and cooling factor - adaptive. This approach produced 104 Marxan analyses each of which identified potential conservation areas across the study region based on different combinations of species distribution data (13), targets (4), and costs (2).

Reserve Selection Performance

For each of the Marxan simulations we chose the best of the 100 solutions, i.e., the one that achieved all the targets at lowest cost. For each of these best solutions we analyzed the performance in terms of species representation, cost and cost-efficiency.

Species Representation

To evaluate the performance of each method of assembling distribution data when used for reserve selection purposes, we compared how the selected planning units represented the “real” distribution of each species, or in other words, how many occurrences of the “real” distribution of each species were covered by the Marxan best solution in every one of the 104 simulations. We called this measure the real species representation (R). We then calculated a biodiversity performance metric (BP), as the number of species that achieved targets (this metric values range from 0 to 65). We compared biodiversity performances across the 104 reserve solutions, incorporating types of distribution data, amounts of distribution data known, different targets and costs.

Cost

For each scenario we calculated the cost of the best Marxan solution as the sum of the costs of all planning units selected in the best solution.

Cost-efficiency

For each scenario, we derived a cost-efficiency metric to evaluate the relationship between biodiversity performance and cost:
CE= 1000000 BP/ Cost

The maximal cover approach

We used the 13 data sets as input data in the Zonation software v 2.00 (Moilanen 2007; Moilanen et al. 2005; Moilanen et al. 2009), using the eight combinations of cost and target described above. Zonation uses a gradient-like iterative heuristic, which gives a solution very close to globally optimal (van Teeffelen and Moilanen 2008) to produce a sequence of cell removal throughout the planning region. This output allows us to calculate how much of the "real" distribution of each species is covered in the solution for different maximum costs. We used the target-based planning removal rule because we wanted to find the best solution in which the maximum number of species met conservation targets. The target-based planning uses a particular benefit function in which species representations will approach the species-specific targets from above by keeping the highest number of species above targets as long as possible (Moilanen 2007). At some point, the representation of one or more of the species falls below target. From that point on, the algorithm assumes that the remaining distribution of that species has no value for the reserve network. Thus removing cells where only this species occurs does not increase the loss of biological value from the network.

In the species file we set all species weights to 1 and the targets of each species were set to the same percentages of occurrences as in the minimum set scenarios (T1, T5, T10 and Tdif). We used the same two cost layers, one for each cost scenario (Uniform and LogNormal). We set the warp factor to 1, excluded the reserve network aggregation and allowed planning units to be removed from anywhere in the region.

Reserve selection performance

To evaluate the performance of each type of data set using Zonation we identified the set of planning units with the highest ranks in which the sum of all the PU costs was under a given budget. We set six budgets based on a percentage (0.1, 0.5, 1.0, 2.5, 5.0 and 7.5) of the cost of the whole system for each cost scenario. For each solution under each budget, we evaluated how many occurrences of the "real" distribution of each species were covered and attributed the value of 1 if target was achieved and the value 0 if it was not. We then calculated BP as the number of species that reached their targets.

5.4. Results

5.4.1 The minimum set approach

Our results do not show evidence that one type of data set alone can achieve better performance in every situation. In most scenarios, the type of data set that achieved higher biodiversity performance metric (BP) scores were the “observed”, followed by the “mixed”, the “predicted” and the “transformed predicted” (Figure 5.1). In some scenarios, the “observed” and the “mixed” data sets achieved a similar biodiversity performance to the “real” data set. This result was consistent, regardless of the target and the cost scenarios. However, reserve systems driven by “observed” data were much more expensive solutions than the ones found by the other types of data sets, and was more evident in scenarios where we knew less of the distribution of species (Figure 5.2).

Cost efficiency analysis (Figure 5.3) revealed that, in most scenarios, the “mixed” data sets generated the highest cost-efficiency. However, these results seemed to be sensitive to the amount of species distribution known. For example the solution derived by the “transformed predicted” data sets had higher cost efficiency when we knew 10% of the species distribution. In contrast, “observed” data sets were the ones that generated the least cost-efficient reserve systems in many scenarios, particularly when we knew a small percentage of the species distributions.

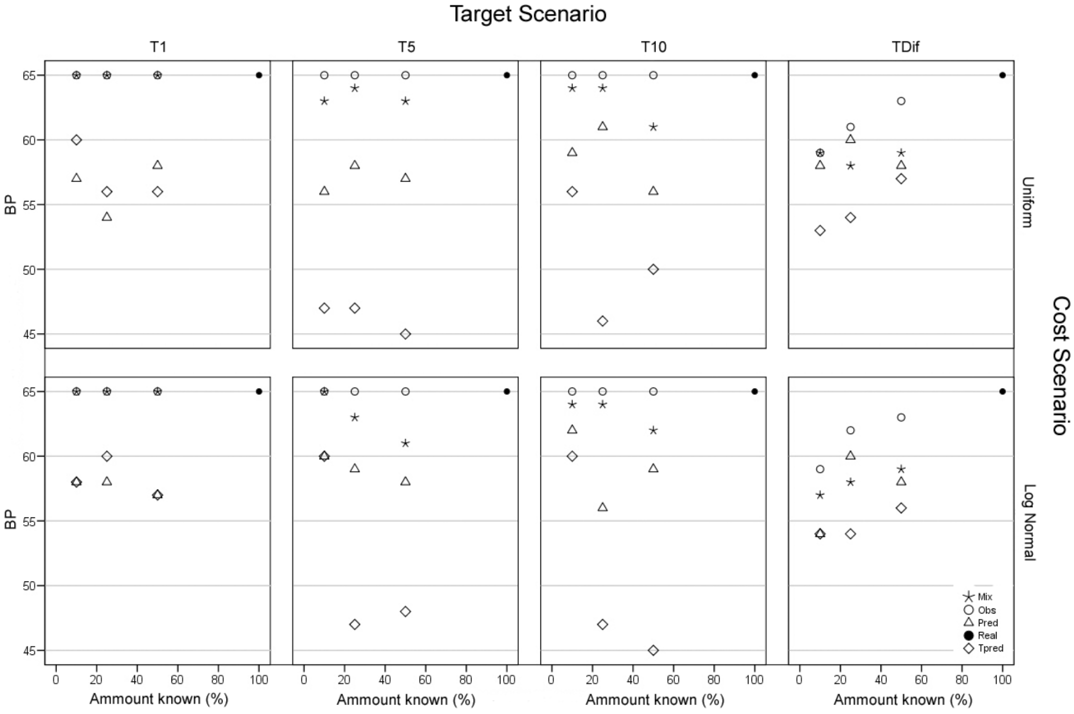


Figure 5.1 - Biodiversity performance (BP), i.e. number of species achieving conservation target, obtained by each type of distribution data set in different scenarios of percentage of distribution data known (10%, 25% and 50%), representation targets (T1, T5, T10 and Tdif) and costs (uniform and log-normal). Mix – “mixed”; Obs – “observed”; Pred – “predicted”; Real – “real”; Tpred – “transformed predicted”.

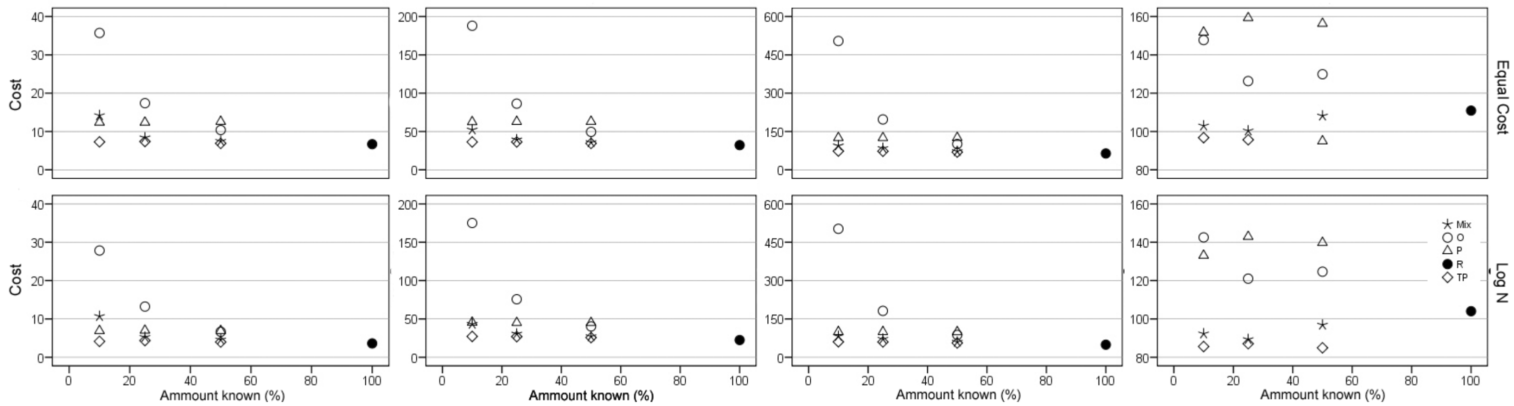
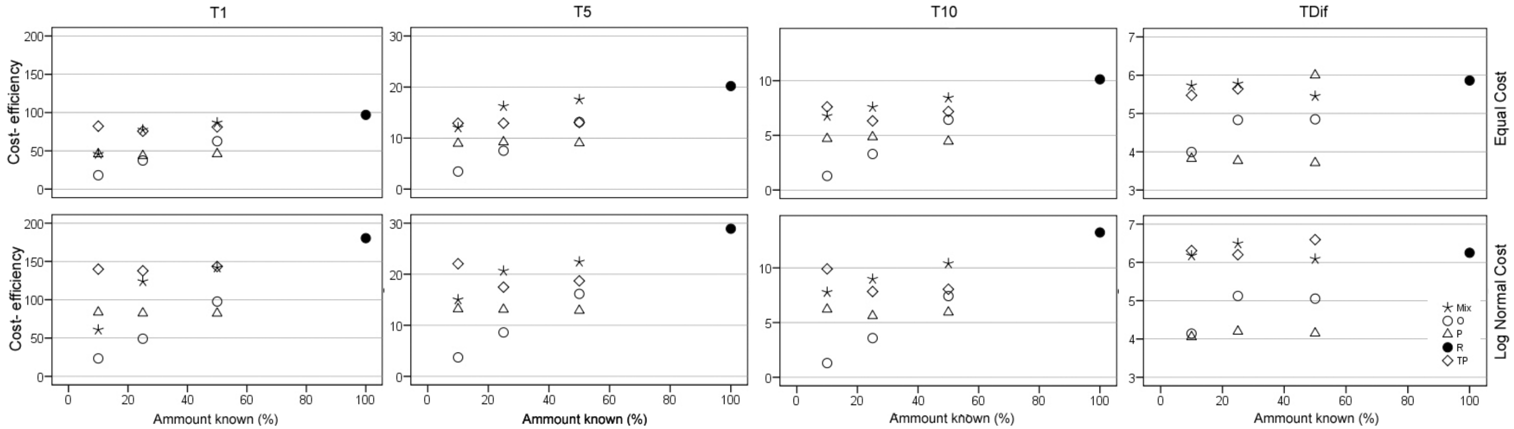


Figure 5.2 - Total cost of all selected planning units, obtained by each type of distribution data set in different scenarios of percentage of distribution data known (10%, 25% and50%), representation targets (T1, T5, T10 and Tdif) and costs (uniform andlog-normal). Mix – "mixed"; Obs – "observed"; Pred – "predicted"; Real – "real"; Tp–"transformed predicted".



gure 5.3 Cost-efficiency i.e., number of species achieving targets by unit cost, obtained by each type of distribution data set in different scenarios of percentage of distribution data known (10%, 25% and 50%), representation targets (T1, T5, T10 and Tdif) and costs (uniform and log-normal). Mix – "mixed"; Obs – "observed"; Pred – "predicted"; Real – "real"; Tpr– "transformed predicted".

Overall, scores achieved using the “observed” data sets, both for representation, cost and cost efficiency seem to be more sensitive to the amount of species distribution known than when we use other data sets. Results of the different target scenarios suggest that the rank of the performance of each type of data set is more sensitive to the method of setting targets (equal proportions vs. different proportions) than to different amounts targeted (1% vs. 5% vs. 10%). Finally, the cost scenario did not seem to have a major influence in the performance rank of the different types of data sets.

5.4.2 The maximum cover approach

Similar to the minimum set approach, in the maximum cover scenarios we did not find evidence that one type of species distribution data alone performed better than the others in every scenario. We also found that the best type of data set seems to be dependent on the cost threshold available for a given scenario. Biodiversity performance tends to increase for higher cost values until all species achieve targets (Figures 5.4 and 5.5). In a low target scenario (T1), all types of data sets are able to achieve all species targets at low costs. For higher target scenarios (T5 and T10), higher cost values are required to achieve targets for all species and differences in biodiversity performance achieved with different costs are more distinct.

In general, “observed” and “mixed” data sets achieved higher biodiversity performances in many scenarios, particularly for lower cost values, lower targets and where we knew a larger fraction of species distributions. This was true both in the uniform cost scenario (Figure 5.4) and the Log-normal cost scenario (Figure 5.5). However, if one just compares the costs thresholds where at least one of the data sets achieved targets for all species (BP = 65), “predicted” and “transformed predicted” data sets are the ones that achieved better biodiversity performance in some of the uniform and Log-normal cost scenarios, respectively, and particularly where there are high targets and we know little about species distributions. The cost scenario influences the biodiversity performances achieved by the “predicted” and the “transformed predicted” data sets most.

5.5. Discussion

Within a conservation planning framework, conservation practitioners need to decide which type of species distribution data to use, when faced with incomplete knowledge. Our results suggest that for our particular data set no single type of species distribution data is better in every conservation planning situation. Different types of data sets have different sensitivities to different factors, and thus the decision process should start by analyzing the circumstances in which the planning process is being conducted. Our results show that the factors that most influence the best choice are the type of mathematical reserve selection problem to be addressed and how much we know about the distribution of the conservation features. Conservation plans derived from “observed” data are much more sensitive to how much we know about species distributions than conservation

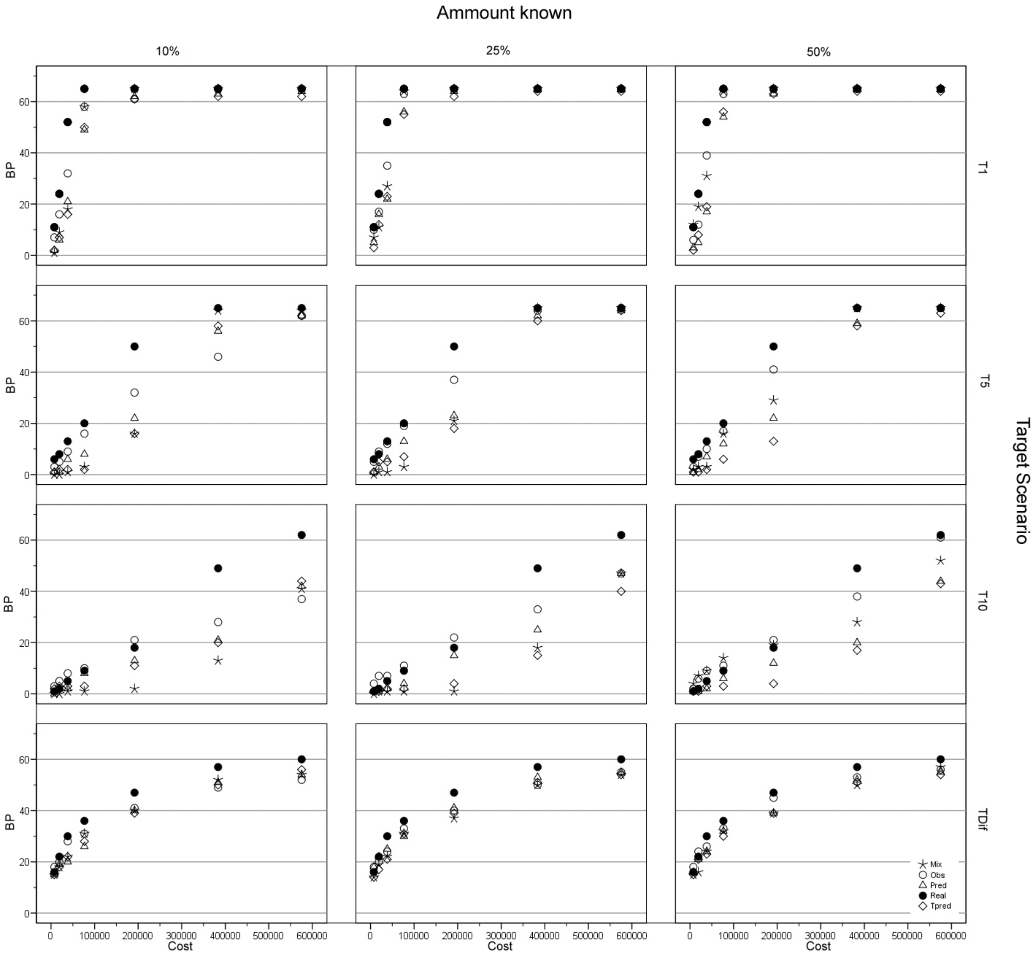


Figure 5.4 Biodiversity performance (BP), i.e. number of species achieving conservation target, obtained, using the maximal cover approach, by each type of distribution data set in different scenarios of percentage of distribution data known (10%, 25% and 50%), representation targets (T1, T5, T10 and Tdif) and cost thresholds in the uniform cost scenario. Mix – "mixed"; Obs – "observed"; Pred – "predicted"; Real – "real"; Tpred – "transformed predicted".

plans derived using the other types of distribution data sets. This is particularly important when we use a minimum set approach. With this approach, conservation plans using "observed" data met the most conservation targets because we assumed that "observed" data had no commission errors, and thus no chance of selecting reserves where species do not exist. When we used data derived from species distribution models, there was the chance that sites with false presences will be selected to conserve species and consequently conservation objectives may not be met during implementation. However, reserve systems driven by "observed" data were also much more expensive solutions than the ones found by the other types of distribution data and the cost was much higher when targets were a fixed proportion of the real data. This is because the minimum set approach applies an algorithm that forces the achievement of all targets. When only a fraction of a species distributions is known, the overlap between species distributions is less, fewer

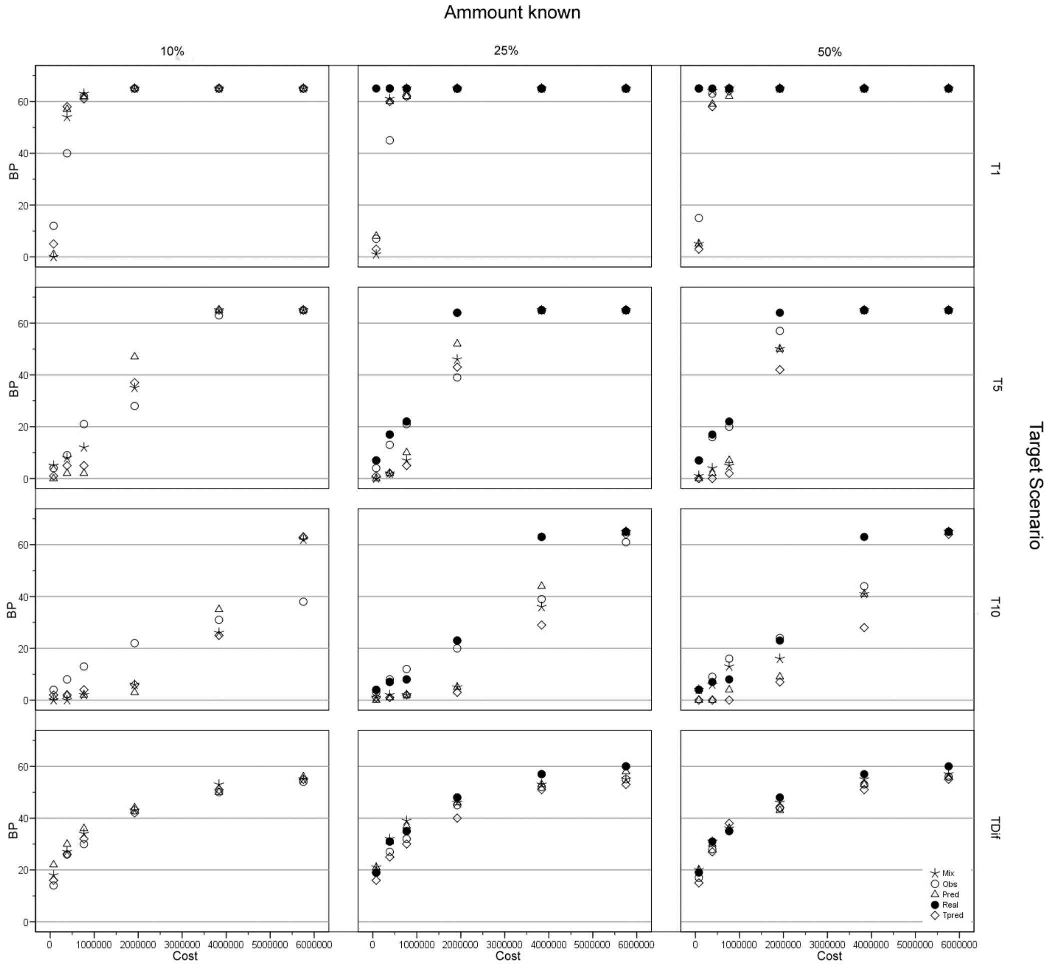


Figure 5.5 - Biodiversity performance (BP) obtained, using the maximal cover approach, by each type of distribution data set in different scenarios of percentage of distribution data known (10%, 25% and 50%), representation targets (T1, T5, T10 and Tdif) and cost thresholds in the log-normal cost scenario. Mix – ‘‘mixed”; Obs – ‘‘observed”; Pred – “predicted”; Real – ‘‘real”; Tpred – ‘‘transformed predicted”.

species co-occur in planning units, and the number of selected planning units (and cost) increases. These results are consistent with those found by Grand et al. (2007) and Pressey et al. (1999). The sensitivity of conservation plans derived from “observed” data to the amount of species distribution known was less obvious when we used the maximum cover approach because, in this case, we were not forcing the algorithm to achieve all targets and, for a given cost, there is a possibility of covering, by chance, localities where species do occur but are not known.

“Predicted” data sets produced conservation plans with generally higher biodiversity performances than those generated using the “transformed predicted” data, but at a higher cost. This may have occurred because, in the predicted data sets, the probabilities of occurrence are low in a considerable proportion of the area and this may lead to larger areas being selected to achieve targets. An alternative method for using the “predicted” data sets would be to use an algorithm that favours planning units with higher probabilities (Game et al. 2008) instead of meeting a target by summing probabilities within different planning units. In both the minimum set and the maximum cover approaches, including variable land costs did not have a major influence on which data set generated the best conservation plans.

We recognize that our methodology has limitations and that a few of the assumptions made in this theoretical study need to be tested more broadly. One limitation is that we conducted this study in one region only and with one set of species. It plausible that the size of the region and relationships between the distributions of the species will affect the performance of reserve selection (Warman et al. 2004). The assumption that the "real" data set had no omission or commission errors may cause a bias in our ability to evaluate the performance of the data sets derived by the species distributions models ("predicted", "transformed predicted" and "mixed"). It is possible that the use of these sorts of data yield a better performance than we found here because it is likely that areas where models predict species occurrences are in fact true presences. Additionally, it is also possible that the "observed" data set contains false presences. We chose not to introduce false positives because they are generally much rarer than false absences and in our particular data set we were very confident about the small number of false presences. This was because both the Portuguese and the Spanish atlases of amphibians and reptiles were produced recently (2008 and 2002, respectively) and the methodology used in both of them included field work, which confirmed a large proportion of the oldest records. Furthermore, uncertain records were reanalyzed and the most uncertain ones were removed from the database based on expert knowledge. However, we are aware that false presences can be an important source of error in some data sets. If we had simulated false presences in our "real" data, the biodiversity performance and cost-efficiency scores achieved by the different data sets could be slightly different. Thus, an interesting avenue of research would be to test the combined effects of different rates of both false presences and false absences in the "observed" data.

Knowing that complete and accurate distribution data are impossible to obtain in the real world we were able to simulate how the degree of data incompleteness influences the effectiveness of reserve selection by assuming that our data represented the truth. An alternative method to carry out this analysis would be to use virtual species but, in this case, we would be losing plausible statistical relationships between species and environmental variables, which will also create a bias in the outcomes of the predictive distribution models.

One further limitation is that we used only one sample of the "real" data set to produce each of the "observed" subsamples (obs50, obs25 and obs10). Using replicates of the randomizations may have produced more robust outcomes, although we do not believe that it would have produced fundamentally different results. The modelling technique for creating species distributions might also influence the results, since different modelling techniques perform differently with respect to commission and omission errors with different data (Segurado & Araújo 2004). Nonetheless, at present, Maxent is considered one of the most robust modelling techniques (Elith et al. 2006), even with small data sets (Hernandez et al. 2006; Pearson et al. 2007). This robustness was largely confirmed when we analysed the agreement between model outputs and the "real" data set. In general, our models had a good performance, with about half of them having AUC values higher than 0.9, and only 3% having poor performance (AUC values under 0.7) when we used half of the real data. The AUC values were only slightly lower for most species when we used smaller proportions of the "real" data to build the models. The better the models are, the better they are expected to perform in reserve selection. Thus, additional criteria for using "observed" data in the "mixed" data set for particular species could be the use of "observed" data where model performance is low (low AUC). However we did not do so because most of the species whose models did not perform well were widespread, which is a common case (Guisan et al. 2007).

Another consideration is that there are a number of ways to select a threshold to convert "predicted" to "transformed predicted" data, all with different consequences (Liu et al. 2005). The consequences of how we chose the threshold has been discussed elsewhere (Wilson et al. 2005) and goes beyond the scope of the present work. The size chosen for the planning units is another factor known to influence reserve selection solutions (Pressey and Logan 1998; Warman et al. 2004). Smaller planning units are thought to deliver more cost-efficient reserve networks but some authors argue that groups of selected planning units should be large enough to support ecological processes (Pressey et al. 2003). In the present work by using a planning unit size equal to the grid size used in the models, we assured that we were comparing results under the most efficient reserve solution possible regarding our base data. However, it remains to be determined if our results would be different if we had used different sized planning units.

We used two different reserve selection algorithms. In the minimum set approach, we used a simulated annealing algorithm, which delivers many sub-optimal solutions to the problem (Possingham et al. 2000). In the maximum cover approach, we used a gradient-like iterative heuristic. The reason we used different algorithms is because Marxan software is designed to solve the minimum set problem and Zonation is best suited to solving the maximum cover problem by using a target-based analysis.

Finally, we emphasize that species representation is only one of the two objectives of conservation planning and, ultimately, conservation planning should aim for species persistence (Araújo and Williams 2000; Araújo et al. 2002; Cabeza and Moilanen 2001; Cowling et al. 1999; Pressey et al. 2007; Pressey et al. 2003). Moving from habitat models to persistence presents many challenges. Extinction risk is a complex metric, dependent on habitat suitability but also on population processes not captured by habitat models (Nicholson et al. 2006; Purvis et al. 2000; Tyre et al. 2001), and also in the possible shift in species distributions driven by climate change or habitat fragmentation. Exactly which sort of data and reserve selection algorithm is best remains an open problem which is almost impossible to test empirically.

5.6 Conclusion

Our results shed light on how conservation practitioners should decide which type of species distribution data to use in different spatial conservation prioritisation decisions. We recommend that the decision process should start by evaluating how much we know about the distribution of the conservation features. Clues can be found by identifying the well-sampled grid cells in the study area (see Hortal et al. 2007) or by building species distribution models and comparing the estimated and observed distribution ranges.

We can conclude that when there is very good unbiased distributional data, the "observed" distribution data is best for achieving representation goals in conservation planning. However, information on probabilities of occurrence allow planners to discern between occupied sites of different quality, which may be useful for achieving persistence goals (Araújo and Williams 2000). When species distributions are incomplete, the normal case, is not always clear which distribution data is best.

If we formulate our conservation planning problem as a minimum set problem and if knowledge of species distributions is poor, our solutions will be costly. Where there are poor data we recommended that planners choose one of two options. The first option would be to use a "mixed" type of data set. Mixed data sets can achieve good cost-efficiency and have the advantage of reducing the risk of failing to protect vulnerable and rare species, while achieving all established targets. The second option would be to use the "observed" or the "mixed" data sets in a maximum cover approach if our distributional knowledge is poor, but not very poor, or the "transformed predicted" if it is extremely poor. However, using "transformed predicted" data requires care for several reasons. First, this approach does not guarantee that the plan will cover all species adequately, and the species that do meet their targets may be the ones of least conservation concern. Second, we recognize that our results are influenced by the particular correlation patterns of species in our study area. Since a considerable number of our species are widespread in the study area, the correlation between species distributions was high, and the chance of placing a reserve where several species co-occur was also high. Thus, we believe that a fruitful avenue of research would be to repeat our analyses with data with different distributional relationships between species. A third option could be to invest in further data sampling, an option to which cost-efficiency was not evaluated in the present work. However, Grantham et al. (2008) found that investing in additional data might not be the most cost-efficient approach to conservation when implementation is gradual and accompanied by ongoing habitat loss.

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Appendix 5.1

Table S.5.1.1 - Amphibian species list, number of Planning Units (N) where each species is known to occur within the Iberian Peninsula and agreement between each Maxent model and the "real" dataset (AUC), when running it with 50, 25 and 10% of N, respectively. * indicates endemic species.

Family	**Species**	**N**	**AUC 50%**	**AUC 25%**	**AUC 10%**
Alytidae	*Alytes cisternasii* Boscá, 1879 *	1032	0.91	0.90	0.88
	Alytes dickhilleni Arntzen & García-París, 1995*	132	0.98	0.98	0.95
	Alytes obstetricans (Laurenti, 1768)	2130	0.87	0.85	0.85
	Discoglossus galganoi Capula, Nascetti, Lanza, Bullini & Crespo, 1985 *	1182	0.83	0.82	0.80
	Discoglossus jeanneae Busack, 1986 *	520	0.87	0.86	0.79
Bufonidae	*Bufo bufo* (Linnaeus, 1758)	4002	0.72	0.70	0.69
	Bufo calamita Laurenti, 1768	3456	0.70	0.69	0.65
Hylidae	*Hyla arborea* (Linnaeus, 1758)	1378	0.81	0.79	0.76
	Hyla meridionalis (Boettger, 1874)	1074	0.92	0.91	0.90
Pelobatidae	*Pelobates cultripes* (Cuvier, 1829)	1844	0.77	0.75	0.72
	Pelodytes punctatus (Daudin, 1802) / *P. Ibericus* Sánchez-Herráiz, Barbadillo, Machordom & Sanchiz, 2000	1520	0.80	0.79	0.75
Ranidae	*Pelophylax perezi* (Seoane, 1885)	5080	0.76	0.71	0.65
	Rana dalmatina Fitzinger in Bonaparte, 1838	32	0.99	0.98	0.97
	Rana iberica Boulenger, 1879 *	836	0.97	0.97	0.96
	Rana pyrenaica Serra-Cobo, 1993 *	24	0.99	0.99	0.99
	Rana temporaria Linnaeus, 1758	546	0.98	0.97	0.95
Salamandridae	*Calotriton asper* (Dugès), 1852 *	200	0.99	0.99	0.99
	Chioglossa lusitanica Bocage, 1864 *	392	0.98	0.98	0.98
	Lissotriton boscai (Lataste, 1879) *	1448	0.91	0.90	0.89
	Lissotriton helveticus (Razoumowsky, 1789)	676	0.95	0.95	0.94
	Mesotriton alpestris (Laurenti, 1768)	128	0.98	0.97	0.96
	Pleurodeles waltl Michahelles, 1830	1608	0.86	0.85	0.84
	Salamandra salamandra (Linnaeus, 1758)	2164	0.86	0.85	0.84
	Triturus marmoratus (Latreille, 1800) T. Pygmaeus Wolterstorff, 1905	2208	0.79	0.79	0.74
AVERAGE			0.88	0.87	0.85
MAXIMUM			0.99	0.99	0.99
MINIMUM			0.70	0.69	0.65

Table S.5.1.2 - Reptile species list, number of Planning Units (N) where each species is known to occur within the Iberian Peninsula and agreement between each Maxent model and the "real" dataset (AUC), when running it with 50, 25 and 10% of N, respectively. * indicates endemic species.

Family	**Species**	**N**	**AUC 50%**	**AUC 25%**	**AUC 10%**
Anguidae	*Anguis fragilis* Linnaeus, 1758	1218	0.92	0.90	0.91
Bataguridae	*Mauremys leprosa* (Schweigger, 1812)	1930	0.85	0.85	0.84
Blanidae	*Blanus cinereus* (Vandelli, 1797) *	1616	0.87	0.86	0.85
Chamaeleonidae	*Chamaeleo chamaeleon* (Linnaeus, 1758)	122	0.98	0.98	0.98
Colubridae	*Coronella austriaca* Laurenti, 1768	598	0.90	0.89	0.87
	Coronella girondica (Daudin, 1803)	1716	0.71	0.69	0.64
	Hemorrhois hippocrepis (Linnaeus, 1758)	1348	0.87	0.86	0.84
	Hierophis viridiflavus (Lacépède, 1789)	96	0.99	0.99	0.98
	Macroprotodon brevis (Günther, 1862)	584	0.89	0.88	0.86
	Malpolon monspessulanus (Hermann, 1804)	3312	0.74	0.73	0.69
	Natrix maura (Linnaeus, 1758)	3672	0.71	0.69	0.64
	Natrix natrix (Linnaeus, 1758)	1950	0.71	0.70	0.67
	Rhinechis scalaris (Schinz, 1822)	2924	0.72	0.71	0.69
	Zamenis longissima (Laurenti, 1768)	134	0.98	0.98	0.96
Emydidae	*Emys orbicularis* (Linnaeus, 1758)	528	0.79	0.76	0.72
Gekkonidae	*Hemidactylus turcicus* (Linnaeus, 1758)	594	0.93	0.92	0.89
	Tarentola mauritanica (Linnaeus, 1758)	2248	0.85	0.83	0.82
Lacertidae	*Acanthodactylus erythrurus* (Schinz, 1833)	792	0.83	0.82	0.80
	Algyroides marchi Valverde, 1958 *	30	0.97	0.97	0.88
	Iberolacerta aranica (Arribas, 1993)*	6	0.99	1.00	0.99
	Iberolacerta aurelioi (Arribas, 1994)*	8	0.84	0.85	0.99
	Iberolacerta bonnali Lantz,1937*	24	1.00	1.00	1.00
	Lacerta agilis Linnaeus, 1758	10	0.98	0.99	0.99
	Lacerta bilineata (Daudin, 1802)	450	0.98	0.98	0.97
	Lacerta monticola Boulenger, 1905*	144	0.97	0.97	0.97
	Lacerta schreiberi Bedriaga, 1878*	922	0.94	0.93	0.92
	Podarcis bocagei (Seoane, 1884)*	468	0.98	0.98	0.97
	Podarcis carbonelli Pérez Mellado, 1981*	88	0.98	0.96	0.96
	Podarcis hispanica (Steindachner, 1870)	3886	0.69	0.67	0.63
	Podarcis muralis (Laurenti, 1768)	642	0.98	0.97	0.97

Table S.5.1.B.2 (continued)

Family	Species	N	AUC 50%	AUC 25%	AUC 10%
	Psammodromus algirus (Linnaeus, 1758)	3678	0.79	0.77	0.74
	Psammodromus hispanicus Fitzinger, 1826	1476	0.76	0.74	0.71
	Timon lepida (Daudin, 1802)	4120	0.69	0.66	0.66
	Zootoca vivipara (Jacquin, 1787)	226	0.98	0.98	0.98
Scincidae	*Chalcides bedriagai* (Boscá, 1880)*	776	0.80	0.78	0.76
	Chalcides striatus (Cuvier, 1829)	1448	0.76	0.75	0.73
Testudinidae	*Testudo graeca* Linnaeus, 1758	32	0.99	0.97	0.94
	Testudo hermanni Gmelin, 1789	8	0.96	0.59	0.50
Viperidae	*Vipera aspis* (Linnaeus, 1758)	322	0.98	0.98	0.98
	Vipera latastei Boscá, 1878	1018	0.79	0.78	0.74
	Vipera seoanei Lataste, 1879*	434	0.97	0.97	0.97
AVERAGE			0.88	0.86	0.84
MAXIMUM			1.00	1.00	1.00
MINIMUM			0.69	0.59	0.50

Appendix 5.2

Description of the method used to assign species targets according to Tdif scenario

Species were ranked according their conservation priority and vulnerability. Three sets of variables were evaluated for each species: Conservation status (CS), Biological status (BS) and Geographic range (GR). These variables were combined in an index ranging from zero to 100. The main assumption of this method is that 100% target are likely required for highly endangered species, whereas 0% is probably sufficient for non endangered widespread species, because they are likely to persist even if any conservation effort is implemented.

Following this principle, species were ranked according to an index which comprised conservation status, biological features and distribution ranges as a mean to determinate the percentage of species distribution that should be considered under protected areas according to equation S.5.2.2. A geometric transformation was made in order that most vulnerable species tended to have conservation targets of 100% of its distribution and less vulnerable species tended to have 0% targets.

$$Rank_i = \frac{\left(\frac{CS_i + BS_i + GR_i}{3}\right)^5}{\max\left[\left(\frac{CS + BS + GR}{3}\right)^5\right]} \times 100 \qquad \text{equation S.5.2.1}$$

, where *i* is the species.

Conservation Status

Conservation status value of each species was calculated based on a three categorical variables model: Portuguese Red Book Status (PTRB), Spanish Red Book Status (ESRB) and European Conservation Status (EC). The first two variables refer to IUCN categories in each country red book (Pleguezuelos et al., 2002; Cabral et al., 2005), while EC refers to species classification according to European Habitats Directive (92/43/EEC). A conservation score was assigned to each category of each variable (table **S.5.2.1**).

Conservation Status of each species was calculated according to S.5.2.2, for species occurring both in Portugal and Spain, and according to equation S.5.2.3, for species occurring only in Spain.

$$CS_i = \frac{\frac{PTRB_i + ESRB_i}{2} + EC_i}{3} \qquad \text{equation S.5.2.2}$$

, where *i i*s the species.

$$CS_i = \frac{ESRB_i + EC_i}{2}$$ equation S.5.2.3

, where *i i*s the species.

Biological Status

Biological startus value of each species was calculated base on an index with four categorical variables: Annual fecundity (AF), Age of female sexual maturity (AFSM), Trophic specialization (TS) and Mean Individual Biomass (MIB). Annual Fecundity refers to the mean number of eggs or young produced per year by adult females. Age of Sexual Maturity refers to minimum age of female reproduction. Trophic Specialization refers to species position on trophic chain and Mean Individual Biomass refers to mean biomass of males and females. To each category a conservation score was assigned according to table S.5.2.1. All biologic data was collected from Salvador (1998) and García-París et al. (2004). Biological Status (BS) of each species was calculated according to equation S.5.2.4.

$$BS_i = \frac{AF + AFSM + TS + MIB}{4}$$ equation S.5.2.4

, where *i i*s the species.

Geographic Range

Geographic range value of each species was calculated based on an index with two variables: Global distribution (GD) and Iberian distribution (ID). These variables reflect the rarity degree of the species at global and Iberian scales. To each category it was assigned a conservation score according to table 1. The Geografic Range (GR) value of each species was calculated according to equation S.5.2.5.

$$GR_i = \frac{GD_i + ID_i}{2}$$ equation S.5.2.4

, where *i i*s the species.

Thus, he final targets assigned to each species according to Tdif method, ranging from 0 to 100, are showed in table S.5.2.2.

Table S.5.2.1 - Method to determine species targets: sets, variables, categories and scores.

Set	Variable	Category	Score
Conservation Status (CS)	Portuguese Red Book Status (PTRB)	Critically endangered (CR)	100
		Endangered (EN)	75
		Vulnerable (VU)	50
		Near threat (NT)	25
		Least Concern (LC)	0
		Data deficient (DD)	0
		Not evaluated (NE)	0
	Spanish Red Book Status (ESRB)	Critically endangered (CR)	100
		Endangered (EN)	75
		Vulnerable (VU)	50
		Near threat (NT)	25
		Least Concern (LC)	0
		Data deficient (DD)	0
		Not evaluated (NE)	0
	European Conservation Status (EC)	Priority species	100
		Species included in Annex II and IV	75
		Species included in annex II	50
		Species included in annex IV	25
		Species not included in any annex	0
Biological Status (BS)	Annual fecundity (AF)	< 5 eggs or youngs	100
		≤ 5 a ≤10 eggs or youngs	80
		<10 a ≤ 15 eggs or youngs	60
		<15 a ≤ 100 eggs or youngs	40
		<100 a ≤ 1000 eggs or youngs	20
		> 1000 eggs or youngs	0
	Age of female sexual maturity (AFSM)	> 5.0 years	100
		3.5 – 5.0 years	80
		1.5 – 3.5 years	60
		1.0 – 1.5 years	40
		0.2 – 1.0 years	20
		< 0.2 years	0
	Trophic specialization (TS)	Omnivores	0
		Secondary consumers	100
	Mean Individual Biomass (MIB)	> 500 g	100
		100 – 500 g	80
		30 – 100 g	60
		15 – 30 g	40
		10 – 15 g	20
		< 10 g	0

Table S.5.2.1 (continued)

Set	Variable	Category	Score
Geographic range (GR)	Global Distribution (GD)	Iberian and/ or Pyrenean endemism	100
		Species with 2/3 of its distribution in the Iberian Peninsula	75
		Species from West Paleartic (includes North Africa and middle East)	25
		Common species	0
	Iberian Distribution (ID)	Distribution range < 1.5% of Iberian Peninsula	100
		Distribution range between 1.5 and 5.5% of Iberian Peninsula	75
		Distribution range between 5.5 and 10.0% of Iberian Peninsula	50
		Distribution range between 10.0 and 25.0% of Iberian Peninsula	25
		Distribution range >25.0% of Iberian Peninsula	0

Table S.5.2.2 - Targets assigned to each species according to the Tdif method.

Amphibian species	Tdif	Reptile species	Tdif
Chioglossa lusitanica	27.09	*Acanthodactylus erythrurus*	0.62
Euproctus asper	14.34	*Algyroides marchi*	27.09
Pleurodeles waltl	0.07	*Anguis fragilis*	0.08
Salamandra salamandra	0.08	*Blanus cinereus*	3.31
Mesotriton alpestris	0.57	*Coronella austriaca*	7.63
Lissotriton boscai	0.57	*Coronella girondica*	0.67
Lissotriton helveticus	0.04	*Hemorrhois hippocrepis*	5.67
Triturus marmoratus/ T. pygmaeus	0.08	*Hierophis viridiflavus*	7.63
Alytes cisternasii	1.70	*Chalcides bedriagai*	11.55
Alytes dickhilleni	0.57	*Chalcides striatus*	2.32
Alytes obstetricans	0.01	*Chamaeleo chamaeleon*	3.50
Discoglossus galganoi	9.65	*Zamenis longissima*	7.63
Discoglossus jeanneae	4.60	*Rhinechis scalaris*	4.13
Discoglossus pictus	1.39	*Emys orbicularis*	16.95
Pelobates cultripes	0.32	*Hemidactylus turcicus*	0.67
Pelodytes punctatus/ P. ibericus	0.00	*Lacerta agilis*	4.13
Bufo bufo	0.00	*Lacerta aranica*	74.38
Bufo calamita	0.01	*Lacerta aurelioi*	54.31
Hyla arborea	0.12	*Lacerta bilineata*	0.35
Hyla meridionalis	0.73	*Lacerta bonnali*	100.00
Rana dalmatina	6.27	*Lacerta lepida*	0.49
Rana iberica	4.60	*Lacerta monticola*	37.49
Rana perezi	0.16	*Lacerta schreiberi*	16.26
Rana pyrenaica	15.60	*Lacerta vivipara*	0.91
Rana temporaria	0.04	*Macroprotodon brevis*	2.47
		Malpolon monspessulanus	0.91
		Mauremys leprosa	10.56
		Natrix maura	0.49
		Natrix natrix	0.67
		Podarcis bocagei	1.59
		Podarcis carbonelli	6.27
		Podarcis hispanica	0.35
		Podarcis muralis	0.02
		Psammodromus algirus	0.06
		Psammodromus hispanicus	0.32
		Tarentola mauritanica	0.91
		Testudo graeca	50.87
		Testudo hermanni	44.52
		Vipera aspis	4.60
		Vipera latastei	13.75
		Vipera seoanei	59.81

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Photo: Vasco Flores Cruz

"Biology is the science. Evolution is the concept that makes biology unique"

Jared Diamond

Chapter 6

Incorporating evolutionary processes into conservation planning using species distribution data:

a case study with the Western Mediterranean herpetofauna

Sílvia B. Carvalho, José C. Brito, Eduardo J. Crespo & Hugh P. Possingham

6.1 Abstract

Aim: To incorporate evolutionary processes into conservation planning using current patterns of species distributions and environmental gradients as surrogates for genetic diversity.

Location: Western Mediterranean basin.

Methods: Distributions of 154 herpetological species were predicted using maximum entropy models, and groups of significantly co-occurring species (biotic elements) were identified. Environmental gradients were characterized for the complete area and for the area covered by each biotic element, by performing a Principal Component Analysis on the data matrix composed of nine environmental variables and categorising and combining the first two axes. In order to identify priority conservation areas, biotic elements and environmental categories were used as surrogates for the neutral and adaptive components of genetic diversity, respectively. Priority areas for conservation were identified under three scenarios: a) setting targets for species only; b) setting targets for species and for each environmental category of the overall area; and c) setting targets for each species and for each environmental category within each biotic element.

Results: Nine biotic elements were identified, four for the amphibians and five for the reptiles. Priority areas identified in the three scenarios were similar in terms of amount of area selected, but exhibited low spatial agreement.

Main Conclusions: Prioritisation exercises that integrate surrogates for evolutionary processes can deliver spatial priorities that are quite different to classical spatial prioritisations where only species representation is accounted. While new methods are

emerging to incorporate molecular data in spatial conservation prioritisation there is unlikely to be enough data for enough taxa for this to be practically useful in the near future. Here we develop an approach using surrogates for both the neutral and adaptive components of genetic diversity that may enhance biodiversity persistence when molecular data is not available or is not geographically comprehensive.

6.1 Introduction

In the current global biodiversity crisis (Pimm and Raven, 2000), prioritising conservation areas that maximise species representation and enable persistence by maintaining key ecological and evolutionary processes has been a major goal of conservation biology (e.g. Brooks et al. 1992; Desmet et al. 2002; Margules and Pressey 2000; Moritz 2002; Rouget et al. 2003). However, conservation planning has tended to focus more on biodiversity pattern (representation) than on the evolutionary processes that generate and maintain biodiversity (Pressey et al. 2007). In order to maximise the probability of species persistence, conservation practitioners should incorporate knowledge on evolutionary processes and the distribution of genetic diversity in conservation planning (Crandall et al. 2000; Moritz 2002; Neel 2008).

Several methodologies have been suggested to incorporate evolutionary history and processes in conservation planning. For example, phylogenetic diversity (PD) (Faith 1992; Vane-Wright et al. 1991) is a biodiversity index that measures the length of evolutionary pathways that connect a given set of taxa. By using appropriate algorithms (e.g. Rodrigues and Gaston 2002; Steel 2005), it is possible to choose a subset of taxa that maximizes representation of evolutionary distinctiveness. In general, in a balanced phylogenetic tree, PD diversity would be higher if one selects a set of taxa from branches separated by the main splits in the tree, i.e. by selecting sample taxa of the main phylogenetic lineages (Avise 1992; Rodrigues and Gaston 2002). These main lineages are probably the result of extensive historical isolation periods, such as vicariance events, derived from allopatric speciation (Avise 1992). While this approach would maximize the representation objective of conservation planning, by including maximum genetic diversity, it has been criticised on the grounds that it disregards areas of recent diversification, where adaptive genetic variation is highest, driving phenotypes or ecological traits, and therefore influencing retention of individual fitness and population viability (Smith et al. 2000, 2005). Consequently, it has been recognized that both the neutral and adaptive components of genetic diversity need to be preserved while targeting conservation of evolutionary processes (Brooks et al. 1992; Moritz 2002).

One of the challenges of integrating evolutionary processes in conservation planning derives from conservation planning being a spatially explicit process, which makes it necessary to spatially identify the neutral and adaptive components of genetic diversity. Previous studies have made progress to circumvent such challenge. For example, some authors (e.g. Moritz and Faith 1998; Smith et al. 2000) used comparative phylogeography to identify sets of species sharing a common vicariance history, and subsequently used Venn diagrams to identify areas representing multiple range restricted unique lineages. Another approach identified areas with higher concentrations of lineage breaks to spatially reveal endemism at the sub-specific level (Rissler et al. 2006). In parallel, the adaptive component of genetic diversity has been addressed by identifying areas where recently diverged endemic species co-occur, as a proxy for rapid diversification areas or evolutionary hotspots (Davis et al. 2007; Vandergast et al. 2008). One important consideration about these studies is that they focused on a limited number of taxa, to which molecular data was available. However, molecular data is still lacking or is very incomplete for most taxa and available information is often collected using different molecular markers and statistical methods, which hinders integration into consensual phylogenies for multiple taxa. Therefore, using spatial surrogates for evolutionary processes is likely to be essential in conservation planning in the near future.

One of the possible surrogates for the neutral component of genetic diversity is community structure. Comparative phylogeography studies show that species with similar ranges often tend to be genealogically structured in similar ways (Avise 2000, 2009). The explanation for this finding is that the emergence of geographic barriers can lead to vicariance and subsequent allopatric speciation of several taxa (Hickerson et al. 2010). Consequently, deeply separated phylogroups are often confined to biogeographical regions as identified from current species assemblages (Avise 2000; Crisci et al. 2003). In other words, the vicariance model predicts that the ranges of the species originating by the same vicariant events, will be, on average, more similar to each other (Hausdorf 2002). A classic example where genetic surveys have provided strong evidence for phylogeographic concordance is represented by the Mediterranean Peninsulas which constituted Pleistocene refugia for many taxa (Hewitt 2000; Taberlet et al. 1998; Weiss and Ferrand 2006). Thus, in areas where vicariance events played an important role in structuring biotas, the identification of groups of species with significantly co-occurring ranges may be a surrogate for the neutral component of genetic diversity.

Regarding the adaptive component of genetic diversity, some studies use ecological and climatic gradients as surrogates (e.g. Cowling et al. 2003; Rouget et al. 2003). The rationale for using these surrogates is that ecology plays a major role in speciation and adaptive radiation in many natural populations (Smith et al. 2005) because environmental gradients facilitate genetic differentiation and character displacement (Doebeli and Dieckmann 2003). Thus, adaptive speciation is expected to be greatest along steep environmental transitions, such as ecotones (Budd and Pandolfi 2010; Smith et al. 2001), which often coincide with areas of high beta diversity, where different species assemblages co-occur (Spector 2002). However, crossroads constitute marginal areas of species distributions, where overall genetic diversity within species populations is generally lower (see Emerson and Gillespie 2008 for a comprehensive review). Thus, the recommended conservation strategy is to protect contiguous habitats of sufficient area across major environmental gradients within the overall species assemblages, including core areas and crossroads (Araújo 2002; Moritz 2002; Smith and Grether 2008).

In this study we aim to incorporate evolutionary processes into conservation planning strategies using current patterns of species distributions and environmental gradients as surrogates. To do so, we identify groups of significantly co-occurring species – biotic elements (as surrogates for the neutral component of genetic diversity), characterize environmental gradients within such groups (as surrogates for the adaptive component), and use a reserve selection algorithm to identify priority areas for conservation. We compare the results with the ones obtained without incorporating evolutionary processes.

The study focuses on the herptiles of the Western Mediterranean region, because multiple historical events are claimed to have promoted vicariance events through changes in its climate and physical environment (Busack 1986; Busack and Lawson 2008; Hewitt 1996; Le Houérou 1997). Additionally, the phylogeography of several herptiles in this region have been studied using molecular tools, which allows making assumptions whether groups of significantly co-occurring species originated by vicariance.

6.2 Methods

6.2.1 Study Region

The study region is located at the western part of the Mediterranean Basin (bounded by 13º9’W to 3º20’E and 27º38’’ to 43º49’N) and includes the continental territories of Portugal, Spain and Morocco (see Appendix 6.1).

6.2.2 Species and environmental data sources

A total of 154 herpetological species are described as occurring in the study area (Appendix 6.2), of which 136 occur on only one side of the Strait of Gibraltar and 18 occur on both sides of the strait. Forty five species are endemic to the study region.

Species distribution data were collected from the atlases of Portugal (Loureiro et al. 2008), Spain (Pleguezuelos et al. 2002) and Morocco (Bons and Geniez 1996), other scientific publications (Carretero et al. 2004; Crochet et al. 2004b; Escoriza and Ortiz 2004; Fahd et al. 2005; Fahd and Pleguezuelos 2001; Guzmán et al. 2007; Martinez-Medina 2001) and fieldwork (Harris et al. 2008). The study area was divided into 12730 cells using a 10x10 km grid. Species distribution data were assembled in a geographical information system.

Climatic variables, such as temperature seasonality (TSEAS), maximum temperature of warmest month (TMAX), minimum temperature of coldest month (TMIN), temperature annual range (TAN), annual precipitation (PAN), precipitation of wettest month (PWET), precipitation of driest month (PDRY) and precipitation seasonality (PSEAS), and altitude (ALT) were downloaded from the Worldclim database (Hijmans et al. 2005). The resolution of all variables was converted to a grid cell size of 10x10 km to match with the species distribution data, using the average value inside each grid cell.

6.2.3 Species distribution modelling and patterns of species richness

Species distribution data from the study region may contain several biases. For example, the Iberian Peninsula was much more surveyed than Morocco, and within Iberia, protected areas and easily accessible regions have more data. Because of this sampling bias, and because the type of input data can influence the identification of significantly co-occurring species (Moline and Linder 2006), we used a maximum entropy modelling approach with software MAXENT (Phillips et al. 2006) to predict the distribution of each species in non-surveyed areas. This modelling technique requires only presence data as input, but consistently performed well in comparison to other methods (Elith et al. 2006).

To build the models, we selected nine variables (highest Pearson's R was 0.75) known to be related to the distribution of amphibians and reptiles (e.g. Rodriguez et al. 2005; Soares and Brito 2007; Whittaker et al. 2007): TSEAS, TMAX, TMIN, TAN, PAN, PWET, PDRY, PSEAS, and ALT.

Given that the Iberian Peninsula was considerably more sampled than Morocco, we reduced the number of occurrences in the Iberian Peninsula for species occurring on both sides of the Strait of Gibraltar, in order to avoid sampling bias. A minimum convex polygon was drawn around each species' occurrence in Morocco to calculate the occurrence density for each species. Then, presence data in the Iberian Peninsula was randomly selected to match the density in Morocco.

To run Maxent, we used the default "auto features" option, the recommended values for the convergence threshold (10^{-5}) and the maximum number of iterations (500). We set the random test percentage to 20% and the regularization value to 1. We used logistic output, which assigns a probability of occurrence of each species to each cell in the study region (Phillips and Dudík 2008). We ran the models 10 times for each species to avoid bias resulting from randomly splitting the data into training and testing and selecting background points. The final model for each species was an average of the 10 models, a method considered to increase significantly the accuracy of species distribution models (Marmion et al. 2009).

We evaluated the accuracy of each model by plotting a Receiver-Operating Characteristic curve (Zweig and Campbell 1993) and calculating the area under the curve (AUC). We reclassified MAXENT outputs (relative probability of each species occurrence in each grid cell) to zero (species absence) or one (species occurrence) by determining a species-specific threshold. The threshold was calculated according to the 10 percentile method, i.e. the threshold value corresponds to the model probability where 90% of the occurrence records with the highest model probabilities are considered as presences.

To avoid over-prediction, for all species that only occur at one side of the Strait, we converted the probability of occurrence to zero at the side where they are not known to occur. Distributions of species with less than 20 occurrence records were not modelled and only observed records were used in subsequent analysis.

After predicting the potential distribution of each species, we intersected the individual species maps to derive maps of potential species richness for amphibians, reptiles and total species.

6.2.4 Biotic elements

We identified significantly co-occurring species groups of amphibians and reptiles in the Western Mediterranean region by using the biotic elements methodology proposed by (Hausdorf 2002). Biotic elements are defined as groups of species whose ranges are significantly more similar to each other than to those of taxa of other groups. It is recognized that such groups probably have similar ecological traits and are also likely to share a common biogeographic history (Hausdorf 2002; Morrone 2001).

The biotic elements methodology is implemented in the program package prabclus v 2.1.2 (Hennig and Hausdorf 2008), which is an add-on package for the software R (R Development Core Team 2008). We first tested if there is a significant non-random congruence of species ranges using the function *prabtest*. This function applies an algorithm which tests if the observed degree of clustering of ranges can be explained by the varying number of taxa per cell and the spatial autocorrelation of the occurrences of a taxon alone (Hausdorf and Hennig 2003). Clustering of ranges means that dissimilarities between ranges of the same cluster are small, whereas the distances between ranges of different clusters are large. We used the statistic T (Hausdorf and Hennig 2003) to test if the distances between ranges of the same biotic element are significantly smaller than the distances between ranges of different biotic elements. The value of this statistics ranges from 0 to 1 and it is expected to be smaller for clustered data than for homogeneous data.

If there was a significant clustering, we determined species biotic elements by using the function *prabclust*. This function calculates a distance matrix using one of five available methods and then produces a Multidimensional Scaling (MDS) from the distances. Subsequently, it uses a model-based Gaussian clustering with “noise” approach to define the clusters. Support to determine the meaningful number of clusters is provided by the Bayesian Information Criteria. The prabclust function also integrates an initial estimation of noise, allowing identifying species whose ranges cannot be assigned to any biotic element. To calculate the distance matrix, we used the Kulczynski index because it is the most appropriate for data sets characterized by large differences in species ranges (Hennig and Hausdorf 2004; Moline and Linder 2006). The number of nearest neighbours to determine the initial noise estimation was set to one for the amphibians and to four for the reptiles, in order to be proportional to the number of species in each dataset (as suggested by Hennig, personal com).

6.2.5 Environmental gradients within biotic elements

To identify environmental gradients within each biotic element and the overall study area, we performed a Principal Component Analysis on the data matrix composed of the nine environmental variables used to build the species distributions models and the grid cells covered by the overall distribution of the species attributed to each biotic element. This way, we decreased the variability of the nine variables to two principal components (PC), explaining a relatively high proportion of total environmental variability. Each component was then classified into four categories, according to quartiles of each axis. Subsequently, each grid cell was classified according to the combination of the categories obtained in PC1 and PC2, resulting in 16 categories for each biotic element. The classification codes were composed of two digits, which coded PC1 and PC2's categories respectively. For example, code "12" stands for the combination of category one on the first axis and category two on the second axis of the PCA.

6.2.6 Priority areas for conservation

In order to indentify priority areas for conservation we used software Marxan (Ball and Possingham 2000; Ball et al. 2009). Marxan uses a simulated annealing algorithm to configure areas that minimize the sum of the cell's costs while ensuring that targets set for each conservation feature are met. We identified priority areas for conservation under three scenarios: setting targets for species only (Scenario Sp); setting targets for species and for each environmental category of the overall area (Scenario SpEnv); and setting targets for each species and for each environmental category within each biotic element (Scenario SpEnvBE). In each scenario we aimed to represent 10% of the area covered by each species and/or environmental category while minimizing the total area needed to achieve those targets. Scenario SpEnvBE aims to assure that representation of species distributions within biotic elements is distributed across the environmental variability of each biotic element, and thus targets both the neutral and adaptive components of genetic diversity.

In each scenario, we run a preliminary sensitivity analysis in order to determine the minimum species penalty factor (spf) that would assure that all targets were met. We set this value as five for scenarios Sp and SpEnv and as 10 for scenario SpEnvBE. We also conducted a sensitivity analysis in order to identify a boundary length modifier (BLM) value that would retrieve solutions with a reasonable level of compactness. We set BML to five in all scenarios after visual inspection of results obtained with BLM ranging from one to 10. Iterations per simulation were set to 10 000 000, temperature decreases per simulation to 10 000 and the initial temperature and cooling factor to adaptive.

Because Marxan retrieves near optimal solutions, we run it 100 times for each scenario and identified the best out of the 100 solutions as the one achieving lowest score for the Marxan objective function. We also identified the number of times that each cell was selected out of the 100 runs, hereafter called selection frequency as it is a measure of how frequently a cell is amongst the 100 good solutions the Marxan algorithm found.

We analysed congruence between solutions by calculating the Pearson correlation coefficient between selection frequencies obtained with each pair of scenarios. We also evaluated agreement between the best solutions found in each scenario. To do so, we classified each grid cell in one of two categories (selected/not selected) and calculated

Cohen's kappa coefficient of agreement (k) between pairs of scenarios, using package "psy" in software R (R Development Core Team 2008). If pairs of scenarios are in complete agreement then k value equals one. If k value is less than 1, it means less than perfect agreement between pairs of scenarios. If k is negative, it indicates that the pair of scenarios agrees less than would be expected by chance.

6.3 Results

6.3.1 Predicted species richness

The AUC values obtained in 123 individual-species models ranged between 0.72 and 1.00 (Appendix 6.2). Predicted species richness was unevenly distributed in the study area (Figure 6.1). Higher total richness (amphibians plus reptiles) was predicted for south-western and north-western Iberia, the Iberian Central System and the Morena Mountains in the Iberian Peninsula. In Morocco, higher total richness was predicted for the Rif and Atlas Mountains and along the Atlantic coast. The correlation between predicted amphibian and reptile richness was low (Pearson R=0.074, p< 0.01) indicating that distribution patterns of richness differs among taxonomic groups: Iberia was richer in amphibians and Morocco was richer in reptiles.

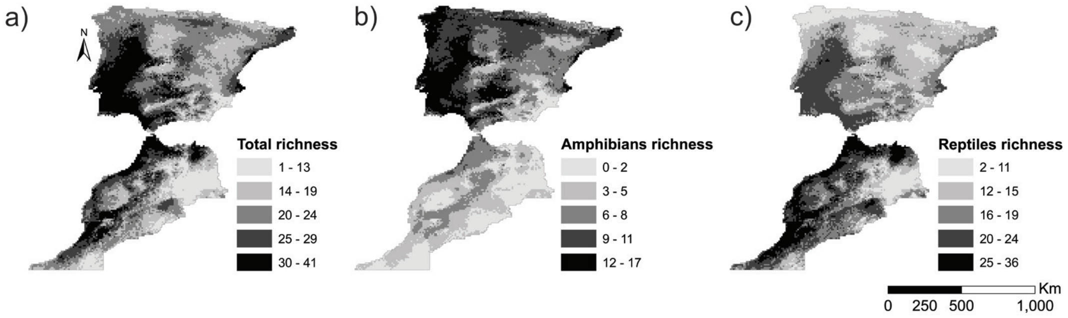

Figure 6.1 Species richness calculated from the predicted distribution model of each individual species for (a) total amphibians and reptiles, (b) amphibians-only, and (c) reptiles-only. In each map, species richness is classified in five classes and natural breaks were selected in order to maximise the difference between the classes. Maps shown in WGS 84 projection.

6.3.2 Biotic elements

We found that distribution areas of amphibians and reptiles were significantly clustered. The statistic T was significantly smaller than expected under the null model for amphibians (p = 0.001, based on 500 simulations) and for reptiles (p= 0.008, based on 250 simulations).

We determined four biotic elements for amphibians (clusters A1 to A4) and five for reptiles (clusters R1 to R5), and a noise component for each taxonomic group (Figure 6.2). Although clustering was significant, a relatively high proportion of amphibians (53%) and a smaller fraction (7%) of reptiles were not assigned to any biotic element.

The amphibian biotic elements (Figure 6.3a; Appendix 6.3) included one element comprising species that occur strictly in Morocco (cluster A1) and three elements comprising species that only occur in the Iberian Peninsula (clusters A2, A3 and A4). The Iberian biotic elements overlapped to some extent, particularly A2 and A4. However, the core areas of A2 were mainly located in western Iberia while the core areas of A4 were mainly in south-western and central Iberia.

The reptile biotic elements included three groups comprising species distributed at both sides of the Strait of Gibraltar (R1, R2 and R5) and two groups exclusively in Morocco (clusters R3 and R4) (Figure 6.3b; Appendix 6.3). Cluster R1 was largely represented by widespread species, including most of the species with Iberian-Moroccan range. Cluster R2 comprised mostly species distributed along the high altitude Iberian mountains and also Rif in Morocco. A considerable amount of spatial overlap occured between clusters R3 and R5, but cluster R3 had its core area in high altitudes, including the Rif and the Atlas Mountains and the Moroccan Atlantic coastal strip, while cluster R5 included predominantly lower altitude species along Atlantic and Mediterranean coastal areas. Cluster R4 was characterised by species occurring mainly in south-eastern Morocco.

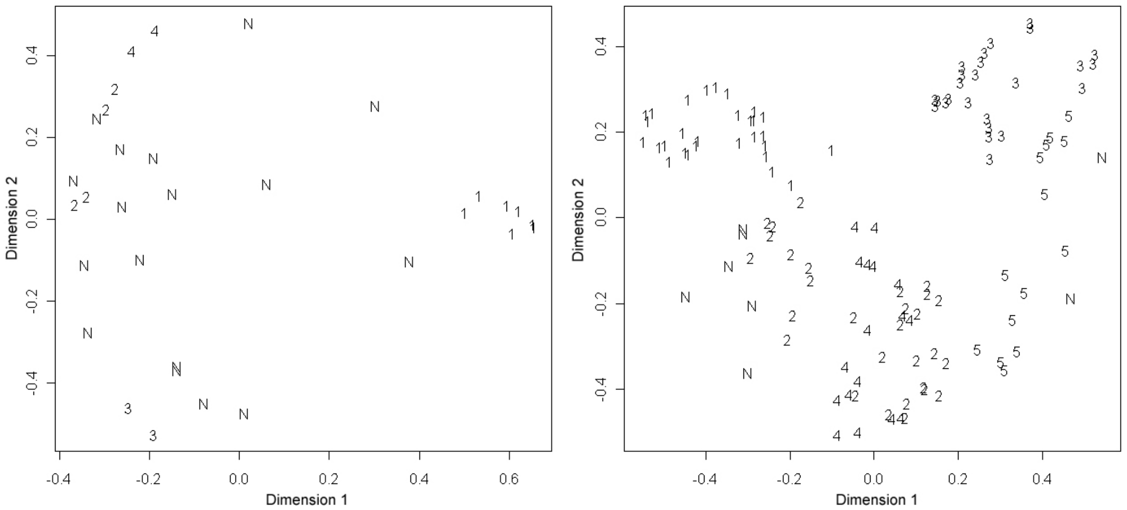

Figure 6.2 Multidimensional scaling of the distribution data of (a) amphibians – four dimensions used, only first two dimensions shown. Four biotic elements were identified (1-4) plus a noise component (N); and (b) reptiles –three dimensions, used, only first two dimensions shown. Five biotic elements were identified (1-5) plus a noise component (N).

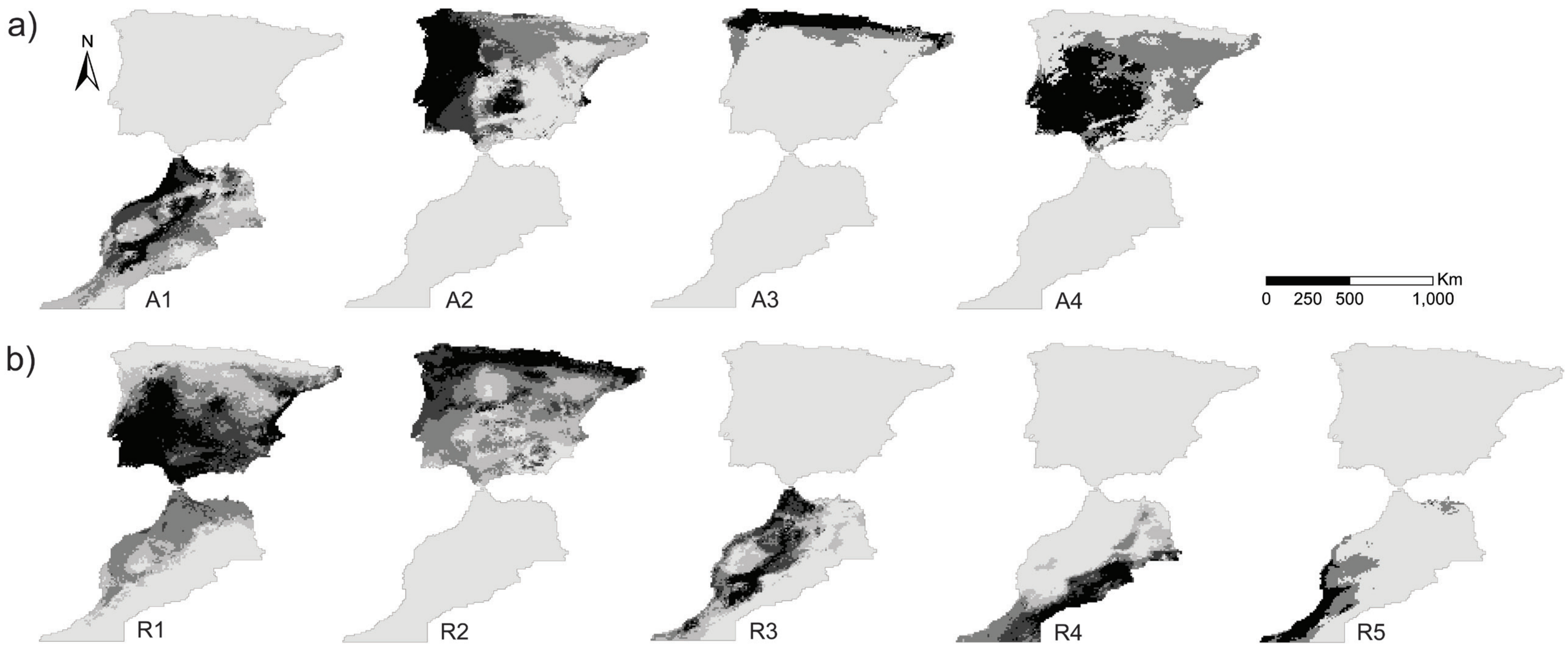

Figure 6.3 – Geographic distribution of species richness within each of four amphibian (a) and five reptile (b) biotic elements. Species richness is represented in a grey scale, with darker colour indicating higher species richness and the lighter colour indicating absence of species. In each biotic element, species richness is classified in five classes and natural breaks were selected in order to maximise the difference between the classes. Maps shown in WGS 84 projection.

6.3.3 Environmental gradients within biotic elements

The environmental variability within each biotic element and of the total area was reduced to 16 environmental categories (Figure 6.4). The total variance explained by the two axes was higher than 75% in all cases (Appendix 6.4).

6.3.4 Priority areas for conservation

The cells identified as priority for conservation differed among scenarios, both with respect to the best solution and to the selection frequency map (Figure 6.5).

Cells with higher selection frequency identified when targeting only species (scenario Sp) were mainly located along the Tagus river valley, mountains of Peneda-Gerês, Cantabrian, eastern Pyrenees, Guadarrama, Betic system, and the western section of the Central Mountain System, in the Iberian Peninsula, and along the Moulouya, Ziz, Drâa and Souss river valleys, in particular sections of the Atlases and Rif Mountains and other scattered transition areas in Morocco. Spatial patterns of selection frequency found when targeting species and overall environmental gradients (scenario SpEnv), were relatively similar to those found with scenario Sp, but cells around the Tagus river valley and the south-western section of the High and the Anti-Atlas mountains obtained lower selection frequency values, while a section of the Guadiana river valley (east to Merida) and Guadarrama mountains obtained higher selection frequency values. Spatial patterns of selection frequency obtained when targeting species and environmental variability within biotic elements (scenario SpEnvBE), were considerable different from those found with Sp and SpEnv (highest Pearson correlation coefficient was 0.51, table 6.1). Cells with high selection frequency scores were located along coastal northern Portugal, the Esla river valley, northern Iberian System, Rif Mountains and several other smaller regions. Lower selection frequency scores are mainly located along the Tagus river valley, northeast of the Iberia, the Moulouya river valley and the western sections of the Atlases Mountains.

The best solutions found were surprisingly dissimilar between scenarios (figure 4) (the maximum Cohen's Kappa coefficient is 0.07, table 6.1), although the number of grid cells selected was fairly similar (1134 grid cells in SP, 1188 in SpEnv and 1288 in SpEnvBE).

	Sp	**SpEnv**	**SpEnvBE**
Sp	1	0.07	0.05
SpEnv	0.73	1	0.06
SpEnvBE	0.47	0.51	1

Table 6.1 - Cohen's kappa coefficients for the pairs of best solutions (upper matrix) and Pearson correlation coefficient for pairs of selection frequency solutions (lower matrix).

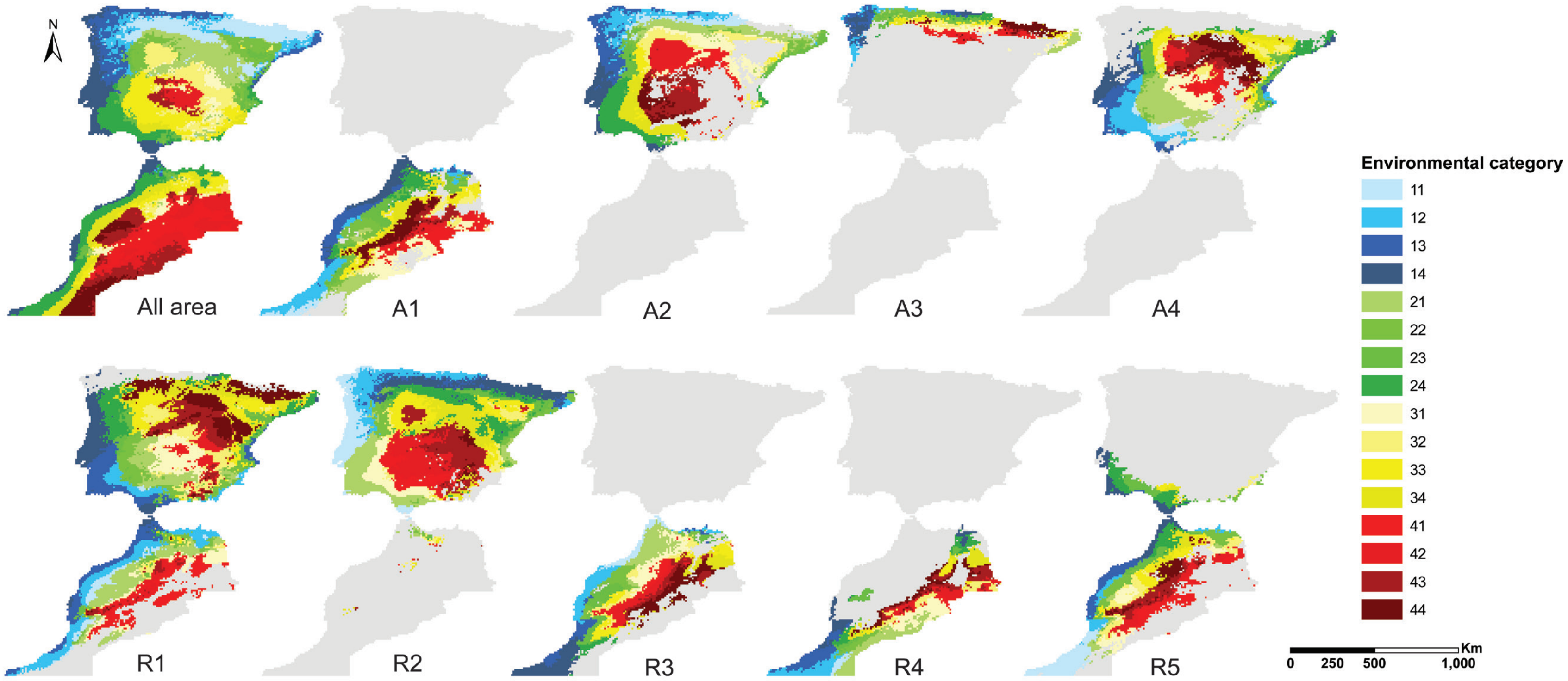

Figure 6.4 – Geographic distribution of the environmental categories within the overall study area (All area) and within the area covered by each biotic element (A1 to A4 and R1 to R5). The first and second digits of the colour code corresponds to the classification obtained with the first and second axes of the Principal Component Analysis, respectively, after being classified in four categories according to their quartiles. Maps shown in WGS 84 projection.

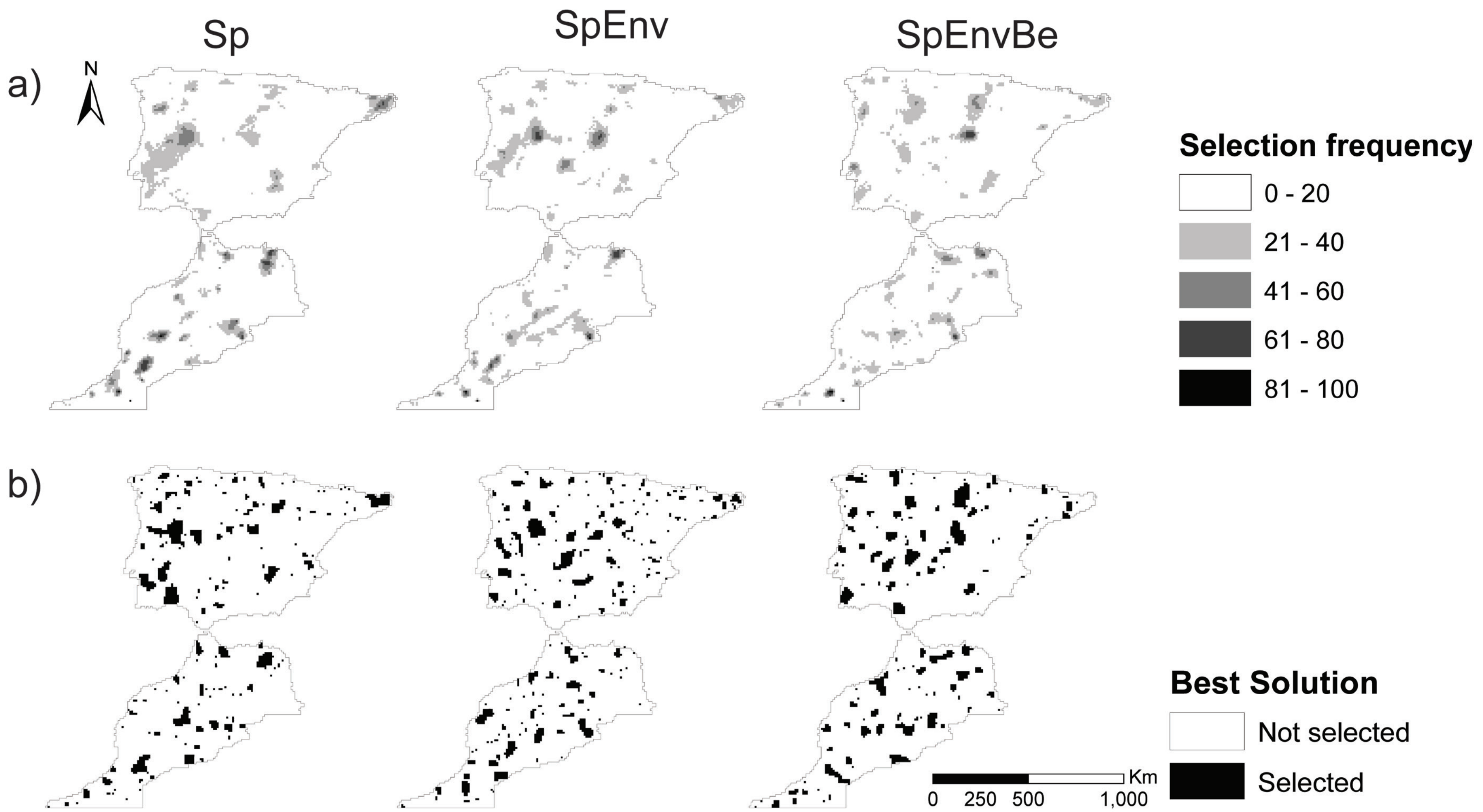

Figure 6.5 – Spatial distribution of a) selection frequency values, and b) best solution, identified in each Marxan scenarios: Sp - setting targets for species only; SpEnv - setting targets for species and for each environmental category of the overall area; and SpEnvBE - setting targets for each species and for each environmental category identified within each biotic element. Maps shown in WGS 84 projection.

6.4 Discussion

This study demonstrates how we can use species distribution and environmental data to account for evolutionary processes in conservation planning. Despite earlier recommendations to explicitly address these processes in conservation strategies (Brooks et al. 1992; Crandall et al. 2000; Moritz 2002), they are generally disregarded (but see e.g. Desmet et al. 2002; Klein et al. 2009; Rouget et al. 2003), probably due to difficulties in identifying spatial surrogates for evolutionary processes.

In the present study, we identified biotic elements and environmental gradients as surrogates for the neutral and the adaptive components of genetic variability, respectively. Our results showed that spatial prioritisation exercises that explicitly integrate such surrogates retrieve fairly different solutions from the planning in which we only account for species representation. The most important question here is, how effective are these surrogates?

The usefulness of biotic elements as surrogates for neutral genetic diversity is limited, because biotic elements can also originate due to post-vicariance dispersal or by other speciation modes (Hausdorf and Hennig 2004). Thus, caution is needed interpreting our results and it would be useful to integrate them with other biogeographical knowledge. There is evidence in our results that vicariance was not the only process underlying current distribution patterns because: a) the range of different biotic elements overlaps extensively and b) a large numbers of amphibian species could not be assigned to any biotic element. Still, the biotic elements found in the present study are fairly consistent with the most important vicariance events believed to have determined genetic patterns in some of the species (see Appendix 6.5 for interpretation of biotic elements). Thus, current species distributions are probably derived from an interplay of vicariance and dispersal events and biotic elements are a relatively good surrogate for the neutral component of genetic diversity.

Cladistic methods based on current species distributions, such as biotic elements or parsimony analysis of endemicity, have been criticized for creating misleading interpretations about historical events influencing current species ranges (e.g. Garzón-Orduña et al. 2007; Szumik and Goloboff 2004). However, in the case of biotic elements, its usefulness goes beyond the identification of groups of species with common biogeographic histories. Determining areas of significantly co-occurring species is relevant from the ecological point of view because it allows recognition of groups of species that share similar niches and respond similarly to ecological disturbances (Azeria et al. 2009; Marquet et al. 2004). Additionally, it allows identification of the core area for the niche of such species, and transitional areas. Such identification is important because environmental characteristics enhancing the probability of persistence, as well as the type and degree of disturbances, differ between biotic elements and thus management and conservation strategies should also differ. For example, species identified under A3 probably have a strong dependence on water, since their range is restricted to areas of high precipitation, while species identified under R4 are probably adapted to xeric conditions. By targeting populations along environmental gradients within biotic elements, we ensure that the overall ecological variability of each niche is preserved, which enhances the probability of persistence under ecological disturbances such as climate change (Pyke and Fischer 2005). Additionally, targeting ecological gradients among biotic elements forces the Marxan algorithm to choose grid cells that incorporate both: 1) core areas where populations' densities are generally higher and more stable and thus more resistant to stochastic threats; and 2) crossroads where the genetic differentiation and the adaptation potential are usually higher.

Despite the evidence that environmental gradients facilitate genetic differentiation (Doebeli and Dieckmann 2003), particularly differentiation of fitness-related traits (Smith et al. 2005), further explicit molecular, morphological and behavioural studies would be required to test such assumptions for all the species targeted in this study and to fully understand spatial patterns of genetic diversity. However, there is evidence that ecological gradients may have influenced speciation. For example, the *Iberolacerta* genus probably diverged from *Podarcis* due to ecological segregation derived from competition, with *Iberolacerta* adapting to high altitudes and *Podarcis* to the lowlands (Crochet et al. 2004a). There is also evidence that recent lineages of the *Podarcis* species complex may have originated from ecological speciation (Carretero 2008). Other correlative evidence of genetic and morphological variation with ecological gradients have been reported for many species, mainly justified by postglacial dispersion towards environmental gradients after climate amelioration (e.g. Alexandrino et al. 2007)

One of the most important challenges in conservation planning for evolutionary process is setting representation targets with ecological meaning. Without explicit molecular data, there is a big challenge to determine how many populations of a species are required to adequately capture within-species diversity (Neel and Cummings 2003). In this study we applied the widely used approach of targeting 10% of each feature distribution. Yet, this method does not specify how many populations (or landscape patches) are necessary for delivering adequate conservation, and does not assure that all populations marked for conservation are viable. The question of how much is enough is central in conservation planning but remains largely unresolved (Tear et al. 2005).

A second important issue concerns connectivity between conservation sites. Connectivity facilitates range shifts, gene flow and recolonisation after local extinction (Neel 2008). However, connecting naturally isolated populations could also result in outbreeding, which may not be desirable from a conservation perspective. Additionally, it has been recently argued that quantifying benefits of connectivity is plagued with uncertainty (for example, uncertainties in species dispersal abilities) and that connectivity can be improved by targeting other metrics such as habitat area and quality (Hodgson et al. 2009). Planning for connectivity is probably superfluous in our case because amphibians and reptiles have low vagility and the total study area is relatively large.

We recognize that this study could be improved by incorporating other prioritisation criteria, such as threats, other ecological processes and socio-economic features. However, our goal was not to identify priority areas to be implemented on the ground, but instead to demonstrate that it is possible to integrate evolutionary criteria into conservation planning, and that those criteria can deeply influence the selection of the priority sites.

Given the urgent need to make conservation decisions (Grantham et al. 2009), approaches such as the one demonstrated in this study are useful because they enhance the probability of capturing evolutionary processes when molecular data are unavailable or not geographically comprehensive. However, we note that such approaches do not constitute an alternative to studies incorporating molecular data. Recently, there have been several attempts to incorporate evolutionary processes at the sub-specific level using molecular data. The neutral component has been addressed, for example, by delimitating evolutionarily significant units (Moritz 2002), measuring evolutionary distinctiveness (Faith et al. 2004; Forest et al. 2007; Posadas et al. 2001), or identifying Pleistocene refugia (Carnaval et al., 2009). The adaptive component has been addressed by identifying areas of rapid diversification or evolutionary hotspots (Davis et al. 2007; Vandergast et al. 2008) or modelling relationships between environmental heterogeneity and genetic and phenotypic variation (Thomassen et al. 2010). However, a comprehensive methodology of how to spatially optimize conservation areas using molecular data for multiple species remains an open challenge (but see Diniz-Filho and Telles 2006; Rissler et al. 2006), particular in what refers to taxonomically complex groups of organisms, generally characterized by the presence of uniparental lineages and reticulate evolution (Ennos et al. 2005).

The Western Mediterranean is the ideal region to extend spatial conservation prioritisation methodologies incorporating molecular data because, particularly for herptiles, there is already an extensive set of available molecular data at the sub-specific level and an interesting evolutionary history dominated by successive cycles of fragmentation, expansion and subsequent admixture of populations. Consequently, in this region we can find multiple examples of species with exceptionally divergent lineages (e.g. Alexandrino et al. 2007), species complexes with incipient speciation (e.g. Perera et al. 2007; Pinho et al. 2007). The challenge is to integrate this dispersed and disparate data, collected in a multitude of geographical scales and using distinct molecular markers, and to find coherent spatial patterns of evolutionary processes that could be useful for conservation planning.

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Appendix 6.1

Map and description of the study area

The study region has relatively high climatic, topographic and habitat diversity, including three distinct climatic types (Atlantic, Mediterranean and Saharan), an altitude range from 0 to 4000 meters, and habitat diversity ranging from Euro-Siberian forests to sand dune deserts. This heterogeneity allows the coexistence of species with diverse biogeographic affinities such as Palearctic, Western-European, Mediterranean and Saharo-Sindian (Sindaco and Jeremcenko 2008), resulting in high herpetological species richness: 32 amphibian and 122 reptile species.

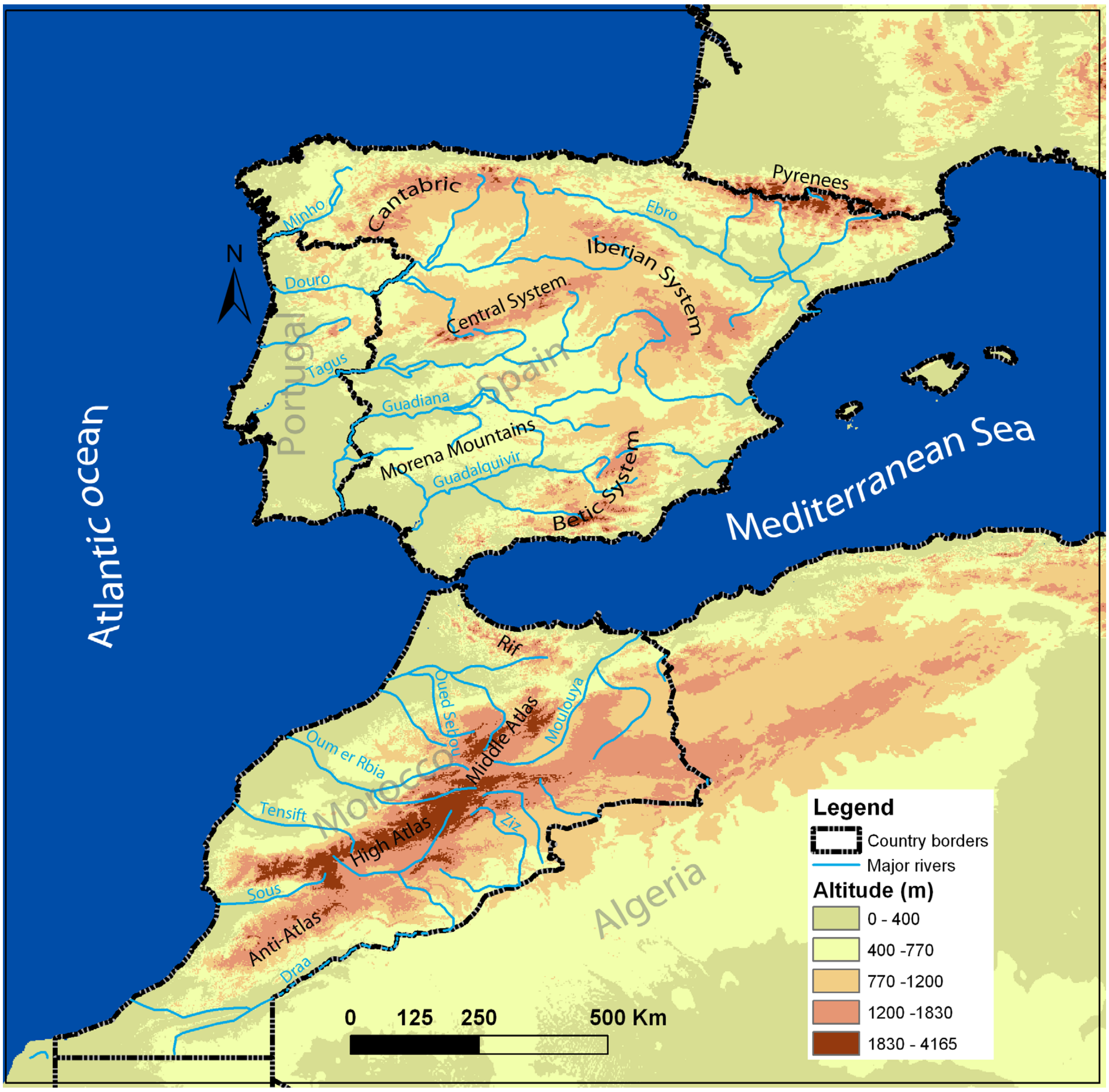

Figure S.6.1.1 – Map of the study areas illustrating elevation and main rivers. Map shown in WGS84 projection.

Appendix 6.2

Species list, and maxent outputs

Table S.6.2.1 - Species list, number of occurrences of each amphibian species (N), area under the curve (AUC) obtained in each Maxent model using the test data, threshold use to convert model probabilities (THR), and contribution of each variable to the model: ALT- altitude; PAN – annual precipitation; PDRY - precipitation of driest month; PSEAS - precipitation seasonality; PWET - precipitation of wettest month; TAN - temperature annual range TMAX - maximum temperature of warmest month; TMIN - minimum temperature of coldest month; TSEAS - temperature seasonality. * - species not modelled due to low occurrence records.

Species	N	AUC	THR	ALT	PAN	PDRY	PSEAS	PWET	TAN	TMAX	TMIN	TSEAS
Alytes cisternasii Boscá, 1879	1290	0.91	0.37	9.34	32.58	30.41	10.81	0.92	8.76	2.59	2.17	2.42
Alytes dickhilleni Arntzen & García-París, 1995	164	0.99	0.39	12.13	3.32	15.95	6.35	11.86	35.69	9.93	1.62	3.15
Alytes obstetricans (Laurenti, 1768)	2662	0.85	0.40	0.18	0.45	73.42	0.97	0.46	15.70	7.92	0.25	0.66
Alytes maurus Pasteur & Bons, 1962 *	19	-	-	-	-	-	-	-	-	-	-	-
Bufo mauritanicus Schlegel, 1841	377	0.88	0.36	13.34	5.87	41.32	20.81	4.57	3.32	2.33	4.59	3.85
Bufo viridis Laurenti, 1768	158	0.92	0.29	17.21	6.39	20.84	27.22	4.64	7.31	5.79	3.99	6.61
Bufo brongersmai Hoogmoed, 1972	38	0.96	0.34	1.89	46.14	32.81	2.75	3.19	0.09	1.87	0.81	10.46
Bufo bufo (Linnaeus, 1758)	5050	0.74	0.40	0.47	54.81	14.76	1.33	0.18	21.97	3.94	0.37	2.18
Bufo calamita Laurenti, 1768	4317	0.75	0.41	1.91	37.73	13.67	8.40	2.00	29.55	2.81	0.63	3.32
Calotriton asper (Dugès), 1852	247	0.99	0.38	1.04	1.55	52.51	30.11	0.59	5.97	2.71	0.17	5.35
Chioglossa lusitanica Bocage, 1864	490	0.97	0.36	0.30	44.74	12.33	1.51	30.24	2.98	0.53	0.63	6.73
Discoglossus scovazzi Camerano, 1878	152	0.94	0.26	12.05	14.33	5.68	37.85	10.58	1.83	9.93	3.88	3.88
Discoglossus galganoi Capula, Nascetti, Lanza, Bullini & Crespo, 1985	1476	0.87	0.34	2.94	35.99	3.71	24.40	7.81	11.18	1.82	1.11	11.05
Discoglossus jeanneae Busack, 1986	650	0.89	0.33	6.63	38.96	3.99	10.91	9.41	14.51	2.96	0.57	12.07
Hyla arborea (Linnaeus, 1758)	1722	0.85	0.37	2.78	35.81	11.70	9.33	1.08	13.48	15.03	6.59	4.21
Hyla meridionalis (Boettger, 1874)	1466	0.88	0.28	8.68	34.31	16.60	0.32	17.33	5.38	3.93	10.42	3.02

Table S.6.2.1 (continued)

Species	**N**	**AUC**	**THR**	**ALT**	**PAN**	**PDRY**	**PSEAS**	**PWET**	**TAN**	**TMAX**	**TMIN**	**TSEAS**
Lissotriton boscai (Lataste, 1879)	1810	0.89	0.31	1.72	37.10	1.52	35.38	10.01	10.02	1.77	0.32	2.15
Lissotriton helveticus (Razoumowsky, 1789)	843	0.95	0.34	1.50	8.57	65.16	5.23	0.25	3.26	6.29	0.05	9.69
Mesotriton alpestris (Laurenti, 1768)	159	0.99	0.40	0.30	3.72	40.89	14.66	6.43	0.18	13.54	0.15	20.13
Pelobates varaldii Pasteur & Bons, 1959	33	0.99	0.25	7.43	7.66	48.41	2.06	32.89	0.26	0.00	0.16	1.12
Pelobates cultripes (Cuvier, 1829)	2303	0.82	0.38	6.11	45.24	8.31	5.84	0.23	17.74	8.57	3.15	4.80
Pelodytes punctatus (Daudin, 1802) / *P. ibericus* Sánchez-Herráiz, Barbadillo, Machordom & Sanchiz, 2000	1897	0.83	0.35	2.11	47.95	6.76	3.76	11.66	22.48	2.82	0.52	1.94
Pelophylax perezi (Seoane, 1885)	6347	0.72	0.44	2.46	42.43	11.98	9.69	0.22	30.10	1.77	0.35	0.99
Pleurodeles waltl Michahelles, 1830	2044	0.86	0.36	6.46	42.82	29.57	2.77	0.59	11.69	2.12	1.78	2.20
Rana saharica Boulenger, 1913	391	0.88	0.35	11.79	5.34	50.90	8.27	5.12	9.08	3.28	3.28	2.94
Rana dalmatina Fitzinger in Bonaparte, 1838	37	1.00	0.35	4.27	1.05	67.48	10.55	0.00	0.08	0.05	14.16	2.37
Rana iberica Boulenger, 1879	1044	0.95	0.25	0.21	39.67	21.04	13.47	15.65	4.01	4.73	0.19	1.03
Rana pyrenaica Serra-Cobo, 1993	29	1.00	0.29	0.22	0.00	27.53	68.55	0.02	0.13	0.70	0.94	1.91
Rana temporaria Linnaeus, 1758	681	0.96	0.43	0.16	24.99	61.10	3.34	0.41	2.26	1.08	0.14	6.52
Salamandra algira Bedriaga, 1883	25	0.94	0.14	13.86	0.30	28.90	8.12	46.25	1.42	0.82	0.30	0.02
Salamandra salamandra (Linnaeus, 1758)	2703	0.84	0.33	0.66	58.84	5.91	3.44	12.44	14.67	1.94	0.15	1.96
Triturus marmoratus (Latreille, 1800) *T. pygmaeus* Wolterstorff, 1905	2757	0.82	0.37	3.59	56.55	7.82	7.52	1.13	19.79	2.25	0.33	1.02
Average	**1356**	**0.90**	**0.34**	**4.96**	**26.30**	**26.87**	**12.77**	**8.00**	**10.48**	**4.06**	**2.06**	**4.51**

Table S.6.2.2 - Species list, number of occurrences of each amphibian species (N), area under the curve (AUC) obtained in each Maxent model using the test data, threshold use to convert model probabilities (THR), and contribution of each variable to the model: ALT- altitude; PAN – annual precipitation; PDRY - precipitation of driest month; PSEAS - precipitation seasonality; PWET - precipitation of wettest month; TAN - temperature annual range TMAX - maximum temperature of warmest month; TMIN - minimum temperature of coldest month; TSEAS - temperature seasonality. * - species not modelled due to low occurrence records.

Species	**N**	**AUC**	**Thr**	**ALT**	**PAN**	**PDRY**	**PSEAS**	**PWET**	**TAN**	**TMAX**	**TMIN**	**TSEAS**
Acanthodactylus lineomaculatus Duméril & Bibron, 1839	67	0.98	0.26	17.14	16.85	52.45	2.66	0.70	1.92	0.09	0.15	8.05
Acanthodactylus aureus Günther, 1903	52	0.99	0.31	2.40	4.18	34.31	1.12	0.39	1.44	0.04	9.24	46.88
Acanthodactylus boskianus (Daudin, 1802)	182	0.94	0.35	1.21	81.54	1.48	2.83	2.24	4.51	4.14	0.56	1.51
Acanthodactylus busacki Salvador, 1982	64	0.98	0.23	3.40	9.23	54.79	1.69	4.16	0.66	0.00	0.62	25.44
Acanthodactylus dumerilii Salvador, 1982	43	0.99	0.23	0.03	4.93	0.36	0.76	41.59	4.55	12.36	0.24	35.19
Acanthodactylus longipes Boulenger, 1918*	11	-	-	-	-	-	-	-	-	-	-	-
Acanthodactylus maculatus (Gray, 1838)	82	0.94	0.30	2.20	55.48	12.58	14.48	1.58	0.53	4.09	2.63	6.41
Acanthodactylus erythrurus (Schinz, 1833)	1202	0.83	0.33	4.32	19.59	30.84	2.45	8.27	0.46	24.81	3.92	5.33
Agama impalearis Boettger, 1874	651	0.88	0.32	12.68	21.47	39.15	14.29	3.42	0.29	2.72	1.21	4.77
Algyroides marchi Valverde, 1958	35	0.99	0.18	16.21	0.01	22.20	11.62	6.20	31.63	1.97	0.42	9.74
Anguis fragilis Linnaeus, 1758	1522	0.91	0.36	0.48	31.13	35.63	0.80	0.12	6.19	24.45	0.31	0.89
Bitis arietans (Merrem, 1820)	20	0.98	0.21	5.47	21.62	36.93	3.66	6.80	0.10	0.10	0.00	25.31
Blanus mettetali Bons, 1963	34	0.95	0.35	5.72	0.97	38.60	26.53	20.93	1.28	0.00	0.86	5.11
Blanus tingitanus Busack, 1988	46	0.96	0.07	2.33	0.54	41.83	1.33	53.07	0.24	0.12	0.53	0.01
Blanus cinereus (Vandelli, 1797)	2017	0.85	0.37	2.22	26.86	40.75	4.68	0.77	18.82	2.88	0.69	2.33
Cerastes cerastes (Linnaeus, 1758)	50	0.96	0.32	0.77	66.48	2.80	2.27	1.25	21.44	3.62	0.40	0.97
Cerastes vipera (Linnaeus, 1758)	26	0.99	0.40	0.73	71.45	1.52	0.68	2.63	0.17	5.11	11.61	6.10
Chalcides colosii Lanza, 1957	44	0.97	0.15	6.00	1.12	32.41	14.32	40.88	0.66	1.98	0.18	2.44
Chalcides ebneri Werner, 1931*	3	-	-	-	-	-	-	-	-	-	-	-
Chalcides lanzai Pasteur, 1967*	13	-	-	-	-	-	-	-	-	-	-	-
Chalcides manueli Hediger, 1935*	7	-	-	-	-	-	-	-	-	-	-	-

Table S.6.2.2 (continued)

Species	N	AUC	Thr	ALT	PAN	PDRY	PSEAS	PWET	TAN	TMAX	TMIN	TSEAS
Chalcides mauritanicus (Duméril & Bibron, 1839)*	4	-	-	-	-	-	-	-	-	-	-	-
Chalcides minutus Caputo, 1993	20	0.94	0.17	0.73	41.91	34.76	2.87	0.20	0.00	5.09	1.61	12.82
Chalcides mionecton (Boettger, 1873)	92	0.97	0.20	1.61	13.97	55.77	1.21	0.88	0.51	0.01	0.10	25.94
Chalcides montanus Werner, 1931*	12	-	-	-	-	-	-	-	-	-	-	-
Chalcides ocellatus (Forskål, 1775)	117	0.96	0.30	0.69	54.33	4.33	21.79	1.23	1.62	7.15	3.23	5.62
Chalcides parallelus Caputo & Mellado, 1992*	11	-	-	-	-	-	-	-	-	-	-	-
Chalcides polylepis Boulenger, 1896	100	0.94	0.38	4.01	4.51	20.10	32.62	11.37	9.23	1.38	0.40	16.38
Chalcides pseudostriatus Caputo, 1993	50	0.95	0.33	5.15	0.87	13.66	40.44	31.93	7.05	0.00	0.81	0.09
Chalcides bedriagai (Boscá, 1880)	967	0.86	0.33	2.72	18.51	22.96	6.01	10.26	26.38	6.24	1.64	5.28
Chalcides striatus (Cuvier, 1829)	1809	0.82	0.31	0.53	59.18	9.88	4.48	0.90	14.20	7.03	2.63	1.18
Chamaeleo chamaeleon (Linnaeus, 1758)	299	0.91	0.24	12.29	1.93	30.71	23.21	4.65	1.50	13.34	8.84	3.53
Coronella austriaca Laurenti, 1768	745	0.92	0.27	1.68	5.84	48.58	1.54	0.39	2.11	38.31	0.12	1.42
Coronella girondica (Daudin, 1803)	2246	0.78	0.35	1.12	46.09	10.44	2.78	2.75	5.10	25.64	0.89	5.19
Daboia mauritanica (Duméril & Bibron, 1848)	126	0.92	0.33	11.36	2.27	22.45	38.32	14.24	0.85	4.51	2.50	3.51
Dasypeltis scabra (Linnaeus, 1758)*	10	-	-	-	-	-	-	-	-	-	-	-
Echis leucogaster Roman, 1972*	1	-	-	-	-	-	-	-	-	-	-	-
Emys orbicularis (Linnaeus, 1758)	682	0.86	0.33	16.15	40.89	3.45	2.21	1.03	7.73	15.61	3.86	9.07
Eryx jaculus (Linnaeus, 1758)*	4	-	-	-	-	-	-	-	-	-	-	-
Eumeces algeriensis Peters, 1864	177	0.94	0.30	2.05	28.35	39.90	19.80	2.56	0.36	0.33	0.82	5.84
Hemidactylus turcicus (Linnaeus, 1758)	754	0.92	0.32	3.03	21.23	11.14	1.51	4.77	8.38	14.67	32.52	2.74
Hemorrhois algirus (Jan, 1863)	39	0.96	0.29	0.94	81.24	4.79	2.79	2.09	3.72	3.01	0.00	1.42
Hemorrhois hippocrepis (Linnaeus, 1758)	1985	0.82	0.33	5.89	8.29	29.49	3.58	24.58	10.86	3.23	12.01	2.08
Hierophis viridiflavus (Lacépède, 1789)	120	0.99	0.32	1.57	1.88	65.73	14.44	0.46	7.45	1.81	1.57	5.08
Hyalosaurus koellikeri (Günther, 1873)	44	0.93	0.23	20.69	1.53	5.22	34.91	19.53	2.31	0.21	12.60	3.01
Iberolacerta aranica (Arribas, 1993)*	5	-	-	-	-	-	-	-	-	-	-	-

Table S.6.2.2 (continued)

Species	N	AUC	Thr	ALT	PAN	PDRY	PSEAS	PWET	TAN	TMAX	TMIN	TSEAS
Iberolacerta aurelioi (Arribas, 1994)*	7	-	-	-	-	-	-	-	-	-	-	-
Iberolacerta bonnali Lantz,1937	29	1.00	0.24	0.41	2.33	23.12	71.84	0.09	0.00	0.84	0.31	1.05
Iberolacerta cyreni (Müller & Hellmich, 1937)	51	0.99	0.32	38.42	0.90	32.04	10.48	1.20	15.48	0.65	0.46	0.38
Iberolacerta martinezricai (Arribas, 1996)	3	0.99	0.64	5.52	0.32	23.12	0.00	0.00	16.48	23.13	8.14	23.28
Lacerta andreanszkyi Werner, 1929	22	0.99	0.13	84.88	1.38	2.08	6.47	0.92	0.52	0.02	3.56	0.16
Lacerta agilis Linnaeus, 1758 *	11	-	-	-	-	-	-	-	-	-	-	-
Lacerta bilineata (Daudin, 1802)	562	0.97	0.39	0.28	3.90	53.86	34.61	0.18	1.20	0.48	0.51	4.96
Lacerta monticola Boulenger, 1905	179	0.99	0.42	0.34	23.55	6.86	16.94	20.67	1.87	25.29	1.59	2.88
Lacerta pater Lataste, 1880 *	7	-	-	-	-	-	-	-	-	-	-	-
Lacerta schreiberi Bedriaga, 1878	1152	0.93	0.29	0.42	50.92	8.87	9.47	9.56	1.78	16.52	0.34	2.12
Lacerta tangitanus (Boulenger, 1887)	231	0.94	0.20	29.41	2.80	13.65	25.95	16.37	6.42	2.49	1.41	1.49
Lamprophis fuliginosus (Boie, 1827)*	9	-	-	-	-	-	-	-	-	-	-	-
Leptotyphlops macrorhynchus (Jan, 1862)*	9	-	-	-	-	-	-	-	-	-	-	-
Lytorhynchus diadema (Duméril, Bibron & Duméril, 1854)	23	0.96	0.18	0.95	61.90	6.99	2.35	1.24	0.53	0.13	16.92	9.00
Macroprotodon abubakeri Wade, 2001*	17	-	-	-	-	-	-	-	-	-	-	-
Macroprotodon cucullatus (Geoffroy Saint-Hilaire, 1827)*	7	-	-	-	-	-	-	-	-	-	-	-
Macroprotodon brevis (Günther, 1862)	873	0.87	0.30	5.04	20.58	33.88	11.64	14.95	4.46	7.00	1.16	1.29
Malpolon moilensis (Reuss, 1834)	42	0.96	0.32	2.76	77.36	9.50	3.89	1.97	1.73	2.34	0.37	0.08
Malpolon insignitus (Geoffroy Saint-Hilaire, 1827)	263	0.91	0.34	7.86	3.99	35.26	25.20	9.44	2.01	2.05	3.47	10.71
Malpolon monspessulanus (Hermann, 1804)	4470	0.73	0.41	4.25	37.93	8.80	2.85	2.70	28.40	10.15	1.28	3.63
Mauremys leprosa (Schweigger, 1812)	2654	0.81	0.31	12.18	33.78	21.76	2.03	2.87	5.55	8.85	10.73	2.25
Mesalina pasteuri (Bons, 1960)*	3	-	-	-	-	-	-	-	-	-	-	-
Mesalina rubropunctata (Lichtenstein, 1823)*	9	-	-	-	-	-	-	-	-	-	-	-
Mesalina simoni (Boettger, 1881)	41	0.96	0.26	0.41	29.51	36.84	12.05	9.28	1.44	2.33	0.64	7.50
Mesalina guttulata (Lichtenstein, 1823)	75	0.95	0.30	10.07	63.24	8.30	0.05	2.72	9.73	1.93	0.15	3.78

Table S.6.2.2 (continued)

Species	N	AUC	Thr	ALT	PAN	PDRY	PSEAS	PWET	TAN	TMAX	TMIN	TSEAS
Mesalina olivieri (Audouin, 1829)	114	0.94	0.35	11.04	33.72	6.31	13.96	20.90	0.65	6.05	6.24	1.12
Naja haje (Linnaeus, 1758)	49	0.97	0.24	3.24	24.32	46.99	0.90	8.79	0.03	0.17	0.13	15.43
Natrix maura (Linnaeus, 1758)	4860	0.72	0.42	2.14	55.92	6.24	4.62	3.73	21.08	2.82	0.63	2.81
Natrix natrix (Linnaeus, 1758)	2370	0.79	0.35	2.03	48.73	10.20	3.42	0.25	13.83	19.04	0.61	1.89
Ophisops occidentalis Boulenger, 1887*	9	-	-	-	-	-	-	-	-	-	-	-
Podarcis vaucheri (Boulenger, 1905)	224	0.96	0.20	33.41	10.49	7.74	22.45	11.55	2.75	7.54	1.80	2.27
Podarcis bocagei (Seoane, 1884)	584	0.97	0.30	0.12	37.27	22.74	16.64	11.82	0.22	8.51	0.49	2.20
Podarcis carbonelli Pérez Mellado, 1981	110	0.99	0.37	4.96	5.93	17.82	13.81	25.08	3.12	23.99	0.29	4.99
Podarcis hispanica (Steindachner, 1870)	4856	0.73	0.42	1.76	38.03	20.38	5.63	0.40	28.83	2.94	0.25	1.78
Podarcis muralis (Laurenti, 1768)	801	0.96	0.34	0.11	3.15	48.07	28.50	0.65	3.33	14.79	0.07	1.33
Psammodromus blanci (Lataste, 1880)*	7	-	-	-	-	-	-	-	-	-	-	-
Psammodromus microdactylus (Boettger, 1881)*	15	-	-	-	-	-	-	-	-	-	-	-
Psammodromus algirus (Linnaeus, 1758)	4909	0.74	0.41	2.27	51.93	11.53	1.78	2.30	14.87	10.97	1.87	2.48
Psammodromus hispanicus Fitzinger, 1826	1844	0.81	0.40	2.31	27.02	17.22	3.37	1.96	21.44	21.35	1.31	4.01
Psammophis schokari (Forskål, 1775)	199	0.90	0.30	4.52	33.38	38.75	6.09	2.61	2.17	3.58	4.14	4.77
Ptyodactylus oudrii Lataste, 1880	94	0.96	0.28	14.89	45.62	5.84	0.97	0.73	24.85	2.74	0.17	4.18
Quedenfeldtia moerens (Chabanaud, 1916)	72	0.97	0.26	34.19	1.08	15.48	24.29	3.46	0.46	8.81	5.04	7.19
Quedenfeldtia trachyblepharus (Boettger, 1873)	20	0.98	0.16	74.07	0.01	2.02	16.04	2.88	2.08	0.00	2.20	0.69
Rhinechis scalaris (Schinz, 1822)	3653	0.77	0.42	3.49	39.44	12.08	4.46	0.60	25.08	10.29	0.77	3.79
Saurodactylus brosseti Bons & Pasteur, 1957	205	0.96	0.30	1.77	24.00	15.90	30.85	8.87	0.62	1.26	0.48	16.24
Saurodactylus fasciatus Werner, 1931	32	0.98	0.19	6.34	0.00	44.40	0.08	34.57	8.46	5.23	0.00	0.92
Saurodactylus mauritanicus (Duméril & Bibron, 1836)	31	0.98	0.24	7.72	16.13	36.12	8.07	3.12	0.22	2.64	5.11	20.86
Scincus albifasciatus Boulenger, 1890*	14	-	-	-	-	-	-	-	-	-	-	-
Spalerosophis dolichospilus (Werner, 1923)	37	0.94	0.28	1.95	86.63	3.09	3.17	2.66	0.31	0.00	0.06	2.13
Spalerosophis cliffordi Schmidt, 1939*	5	-	-	-	-	-	-	-	-	-	-	-

Table S.6.2.2 (continued)

Species	N	AUC	Thr	ALT	PAN	PDRY	PSEAS	PWET	TAN	TMAX	TMIN	TSEAS
Sphenops boulengeri (Anderson, 1892)	27	0.98	0.29	0.97	78.00	0.14	0.06	2.20	1.20	15.47	0.00	1.95
Sphenops sphenopsiformis (Duméril, 1856)	35	0.99	0.33	3.80	6.12	39.92	3.53	0.22	1.64	0.00	8.82	35.94
Stenodactylus petrii Anderson, 1896*	11	-	-	-	-	-	-	-	-	-	-	-
Stenodactylus sthenodactylus Lichtenstein, 1823	92	0.94	0.31	1.17	77.75	6.77	6.39	2.08	3.75	0.39	0.83	0.86
Tarentola annularis (Geoffroy Saint-Hilaire, 1827)*	1	-	-	-	-	-	-	-	-	-	-	-
Tarentola boehmei Joger, 1984	38	0.97	0.34	4.61	46.88	36.68	3.02	6.27	0.73	0.07	1.69	0.04
Tarentola deserti Lataste, 1891	28	0.99	0.34	0.00	7.58	13.19	3.53	47.97	4.18	0.17	0.06	23.32
Tarentola ephippiata O'Shaughnessy, 1875*	2	-	-	-	-	-	-	-	-	-	-	-
Tarentola chazaliae (Mocquard, 1895)	51	0.99	0.35	2.13	8.59	21.66	0.71	0.68	0.69	0.00	49.55	16.01
Tarentola mauritanica (Linnaeus, 1758)	3228	0.77	0.35	2.67	14.66	4.16	1.06	26.93	10.37	18.79	15.91	5.45
Scelaris perspicillata (Duméril & Bibron, 1839)	89	0.94	0.16	43.96	9.02	2.12	24.77	0.35	10.90	2.21	1.21	5.46
Telescopus guidimakaensis (Chabanaud, 1916)*	3	-	-	-	-	-	-	-	-	-	-	-
Testudo graeca Linnaeus, 1758	280	0.93	0.34	2.37	8.97	41.62	11.21	9.87	2.47	2.09	2.43	18.97
Testudo hermanni Gmelin, 1789 *	9	-	-	-	-	-	-	-	-	-	-	-
Timon lepida (Daudin, 1802)	5149	0.73	0.43	1.80	41.12	13.30	9.27	0.61	28.52	2.62	0.54	2.23
Trapelus mutabilis (Merrem, 1820)	88	0.95	0.18	0.35	68.44	6.48	2.40	13.56	1.98	0.94	0.00	5.84
Trogonophis wiegmanni Kaup, 1830	137	0.94	0.35	6.63	13.48	38.38	10.02	10.75	2.08	3.21	10.12	5.32
Tropiocolotes tripolitanus Peters, 1880	74	0.95	0.37	0.48	93.85	1.05	2.37	1.13	0.30	0.16	0.17	0.49
Uromastyx acanthinura Bell, 1825	214	0.95	0.33	1.44	72.18	1.55	4.26	1.73	5.20	10.00	0.95	2.70
Varanus griseus (Daudin, 1803)	38	0.98	0.28	0.78	57.65	0.23	1.37	15.11	5.17	11.42	0.80	7.46
Vipera monticola Saint Girons, 1954	27	0.98	0.26	80.60	2.08	0.73	9.30	0.75	0.70	0.06	5.78	0.00
Vipera aspis (Linnaeus, 1758)	402	0.98	0.38	0.40	0.85	43.80	46.49	0.10	0.86	0.62	0.52	6.37
Vipera latastei Boscá, 1878	1298	0.84	0.32	8.55	36.13	12.56	4.81	7.87	15.30	6.89	4.50	3.38
Vipera seoanei Lataste, 1879	541	0.97	0.41	0.15	25.75	23.82	7.00	12.53	0.87	22.55	0.13	7.21
Zamenis longissima (Laurenti, 1768)	165	0.99	0.31	1.88	1.51	50.86	21.66	5.63	4.14	1.60	3.26	9.46
Zootoca vivipara (Jacquin, 1787)	281	0.98	0.36	0.12	9.44	52.99	5.91	0.80	1.09	16.75	0.16	12.75
Average	**531**	**0.93**	**0.31**	**8.22**	**27.65**	**22.15**	**10.70**	**8.01**	**6.29**	**6.62**	**3.37**	**7.00**

Appendix 6.3

List of amphibian and reptile species assigned to each biotic element

Table S.6.3.1 – List of amphibian species assigned to each biotic element

Species	**Biotic elment**
Alytes dickhilleni	N
Alytes obstetricans	N
Bufo brongersmai	N
Bufo bufo	N
Bufo calamita	N
Calotriton asper	N
Chioglossa lusitanica	N
Discoglossus jeanneae	N
Hyla meridionalis	N
Mesotriton alpestris	N
Pelodytes punctatus	N
Pelophylax perezi	N
Pleurodeles waltl	N
Rana dalmatina	N
Rana iberica	N
Rana pyrenaica	N
Salamandra salamandra	N
Alytes maurus	A1
Bufo mauritanicus	A1
Bufo viridis	A1
Discoglossus scovazzi	A1
Pelobates varaldii	A1
Rana saharica	A1
Salamandra algira	A1
Discoglossus galganoi	A2
Hyla arborea	A2
Lissotriton boscai	A2
Triturus marmoratus / T. pygmaeus	A2
Lissotriton helveticus	A3
Rana temporaria	A3
Alytes cisternasii	A4
Pelobates cultripes	A4

Table S.6.3.2 – List of reptile species assigned to each biotic element

Species	Biotic element
Acanthodactylus maculatus	N
Agama impalearis	N
Chalcides ocellatus	N
Coronella girondica	N
Mesalina olivieri	N
Naja haje	N
Psammodromus algirus	N
Psammophis schokari	N
Acanthodactylus erythrurus	R1
Blanus cinereus	R1
Chalcides bedriagai	R1
Emys orbicularis	R1
Hemidactylus turcicus	R1
Hemorrhois hippocrepis	R1
Macroprotodon brevis	R1
Malpolon monspessulanus	R1
Mauremys leprosa	R1
Natrix maura	R1
Psammodromus hispanicus	R1
Rhinechis scalaris	R1
Tarentola mauritanica	R1
Vipera latastei	R1
Algyroides marchi	R2
Anguis fragilis	R2
Chalcides striatus	R2
Coronella austriaca	R2
Hierophis viridiflavus	R2
Iberolacerta aranica	R2
Iberolacerta aurelioi	R2
Iberolacerta bonnali	R2
Iberolacerta cyreni	R2
Iberolacerta martinezricai	R2
Lacerta agilis	R2
Lacerta bilineata	R2
Lacerta monticola	R2
Lacerta schreiberi	R2
Natrix natrix	R2
Podarcis bocagei	R2
Podarcis carbonelli	R2
Podarcis hispanica	R2
Podarcis muralis	R2
Testudo hermanni	R2
Timon lepida	R2
Vipera aspis	R2

Table S.6.3.2 (continued)

Species	Biotic element
Vipera seoanei	R2
Zamenis longissima	R2
Zootoca vivipara	R2
Acanthodactylus aureus	R3
Acanthodactylus busacki	R3
Acanthodactylus lineomaculatus	R3
Bitis arietans	R3
Blanus mettetali	R3
Blanus tingitanus	R3
Chalcides colosii	R3
Chalcides ebneri	R3
Chalcides lanzai	R3
Chalcides manueli	R3
Chalcides montanus	R3
Chalcides polylepis	R3
Chalcides pseudostriatus	R3
Dasypeltis scabra	R3
Hyalosaurus koellikeri	R3
Lacerta andreanszkyi	R3
Lamprophis fuliginosus	R3
Macroprotodon cucullatus	R3
Podarcis vaucheri	R3
Psammodromus microdactylus	R3
Quedenfeldtia moerens	R3
Quedenfeldtia trachyblepharus	R3
Saurodactylus brosseti	R3
Saurodactylus fasciatus	R3
Scelaris perspicillata	R3
Sphenops sphenopsiformis	R3
Tarentola chazaliae	R3
Timon tangitanus	R3
Vipera monticola	R3
Acanthodactylus boskianus	R4
Acanthodactylus dumerilii	R4
Acanthodactylus longipes	R4
Cerastes cerastes	R4
Cerastes vipera	R4
Echis leucogaster	R4
Hemorrhois algirus	R4
Leptotyphlops macrorhynchus	R4
Lytorhynchus diadema	R4
Malpolon moilensis	R4
Mesalina pasteuri	R4
Mesalina rubropunctata	R4
Mesalina guttulata	R4
Ptyodactylus oudrii	R4
Scincus albifasciatus	R4
Spalerosophis dolichospilus	R4
Spalerosophis cliffordi	R4
Sphenops boulengeri	R4

Table S.6.3.2 (continued)

Species	**Biotic element**
Stenodactylus petrii	R4
Stenodactylus sthenodactylus	R4
Tarentola annularis	R4
Tarentola boehmei	R4
Tarentola deserti	R4
Tarentola ephippiata	R4
Telescopus guidimakaensis	R4
Trapelus mutabilis	R4
Tropiocolotes tripolitanus	R4
Uromastyx acanthinura	R4
Varanus griseus	R4
Chalcides mauritanicus	R5
Chalcides minutus	R5
Chalcides mionecton	R5
Chalcides parallelus	R5
Chamaeleo chamaeleon	R5
Daboia mauritanica	R5
Eryx jaculus	R5
Eumeces algeriensis	R5
Lacerta pater	R5
Macroprotodon abubakeri	R5
Malpolon insignitus	R5
Mesalina simoni	R5
Ophisops occidentalis	R5
Psammodromus blanci	R5
Saurodactylus mauritanicus	R5
Testudo graeca	R5
Trogonophis wiegmanni	R5

Appendix 6.4

Results of the Principal Components Analysis

Table S.6.4.1 – Percentage of variance explained (% var.) within the first and second axis of the Principal Components Analysis within each biotic element (A1 to A4 and R1 to R5) and the overall study area (SA), and the weight of each variable in each axis.

	Axis	% var.	ALT	PANN	PDRY	PSEAS	PWET	TANN	TMAX	TMIN	TSEAS
A1	1	53.32	0.40	0.04	0.35	-0.38	-0.05	0.41	0.23	-0.42	0.41
	2	26.06	0.16	0.60	0.23	-0.02	0.57	-0.16	-0.40	-0.18	-0.16
A2	1	47.75	0.17	-0.42	-0.22	-0.03	-0.42	0.46	0.35	-0.21	0.45
	2	37.39	-0.44	-0.08	-0.45	0.49	0.03	-0.03	0.35	0.47	-0.08
A3	1	53.18	0.34	-0.25	0.21	-0.40	-0.34	0.40	-0.01	-0.40	0.42
	2	33.42	0.33	0.45	0.45	-0.06	0.31	-0.16	-0.55	-0.23	-0.10
A4	1	51.72	0.37	-0.30	0.25	-0.38	-0.37	0.33	-0.02	-0.43	0.37
	2	30.36	0.17	0.24	0.46	-0.29	0.18	-0.37	-0.58	-0.16	-0.29
R1	1	39.16	0.44	0.03	0.24	-0.38	-0.09	0.38	0.01	-0.51	0.43
	2	37.50	0.02	0.45	0.43	-0.23	0.39	-0.34	-0.49	-0.09	-0.23
R2	1	47.36	0.02	-0.43	-0.32	0.07	-0.41	0.44	0.41	-0.07	0.42
	2	37.26	0.47	-0.01	0.37	-0.47	-0.13	0.15	-0.25	-0.52	0.21
R3	1	58.39	0.38	0.16	0.35	-0.37	0.07	0.41	0.23	-0.41	0.41
	2	21.15	0.14	-0.66	0.10	-0.15	-0.71	0.01	-0.03	-0.04	-0.01
R4	1	54.55	0.40	0.19	0.33	-0.37	0.06	0.38	0.25	-0.43	0.40
	2	31.48	0.12	0.51	0.20	-0.16	0.53	-0.29	-0.47	-0.07	-0.26
R5	1	55.04	0.39	0.10	0.34	-0.36	0.02	0.42	0.24	-0.42	0.42
	2	22.10	-0.07	0.68	0.09	0.01	0.69	-0.10	-0.18	-0.01	-0.02
SA	1	45.67	0.11	-0.42	-0.35	0.18	-0.4	0.42	0.45	-0.03	0.34
	2	35.35	-0.46	-0.13	-0.32	0.43	-0.03	-0.25	0.09	0.54	-0.34

Appendix 6.5

Comparison between biotic elements identified and phylogeographic patterns

The Strait of Gibraltar is claimed to be a geographic barrier for amphibians and reptiles, and to have promoted vicariance of many species (Busack 1986; Busack and Lawson 2008; De Jong 1998). Consequently, according to the vicariance models, we would expect biotic elements to be mainly identified at one side of the Strait of Gibraltar only. Such pattern was verified in our results: all biotic elements except R1, R2 and R3 comprised species occurring at only one side of the Strait. However, we also identified assemblages with species (mostly reptiles) occurring in both sides of the Strait, which denotes that dispersal may have also occurred across the geographical barrier. This assumption is also consistent with molecular studies indicating that some species dispersed in different historical periods from Iberia to Morocco and vice-versa. Species that may have dispersed from Morocco to Iberia include *Acanthodactylus erythrurus* (Fonseca et al. 2009), *Blanus cinereus* (Albert et al. 2007), *Malpolon monspessulanus*, *Hemorrhois hippocrepis* (Carranza et al. 2006a), *Macroprotodon brevis* (Carranza et al. 2004b), *Chamaeleo chamaeleon* (Paulo et al. 2002a) and *Testudo graeca* (Alvarez et al. 2000), and from Iberia to Morocco, *Psammodromus algirus* (Carranza et al. 2006b), *Mauremys leprosa* (Fritz et al. 2006), *Podarcis hispanica* (Pinho et al. 2006) and *Vipera latastei* (Brito et al. 2008). The majority of these species probably dispersed during periods when there was a terrestrial land bridge between Africa and the Iberian Peninsula, which occurred after the formation of the Betic Strait at end of the Tortonian (7.2-7.6 MY ago) (Duggen et al. 2003; Krijgsman et al. 2000), during the formation of the Rif belt (6.7 – 6 MY ago) (Krijgsman et al. 2000) and during the Messianic Salinity Crisis (6.7 – 6 MY ago) (Hsü et al. 1977; Krijgsman et al. 1999). However, trans-marine dispersal (Carranza et al. 2006b) and anthropogenic introductions (Carranza and Arnold 2003; Paulo et al. 2002b) were also reported.

Within the Iberian Peninsula, we identified three assemblages for amphibians and two for reptiles, although one of the reptile groups contained a significant number of species also present in Morocco. It is often assumed that climate oscillations during the Quaternary induced range contractions in many species into refugia which triggered vicariance events (Hewitt 2004; Wronski and Hausdorf 2008). Consequently, it is expected that species originating in the same refugia may have currently similar ranges. However, contrary to this expectation, assemblage patterns found in the Iberian Peninsula were not easily justified based only on putative localities suggested for Pleistocene refugia (see Gómez and Lunt 2006; Teixeira 2007). In fact, there was no clear overlap between these and the core areas of assemblages. This lack of congruence might be explained by other vicariance events that are known to have occurred in Iberia and by post-vicariance dispersal. Indeed, species included in the same assemblage were frequently involved in common vicariance events. For example, three historical events have influenced vicariance of many species including the northwest and northern coast assemblages (A2, A3 and R2): 1) the uplift of the Pyrenean Mountains is claimed to have caused vicariance events for major lineages of *Discoglossus* (e.g. Fromhage et al. 2004), *Triturus* and *Calotriton* (Carranza and Amat 2005), and *Podarcis* (Carretero 2008); 2) the Tortonian and the Messianic Salinity crises, characterised by global aridity (Krijgsman et al. 2000) triggered range fragmentation of many taxa included in R2, such as *Iberolacerta* (Carranza et al. 2004a), *Podarcis* (Pinho et al. 2006), *Lacerta* (Paulo et al. 2001) and *Coronella austriaca* (Santos et al. 2008), and the subsequent dispersal of these species towards higher altitudes and latitudes, where climate was more humid; 3) dispersal from refugia after climate amelioration is assumed to have occurred for many species with refugia in western and central Iberia (northwest mountains, Montemuro, Buçaco and Caramulo mountains, Central mountain system mountains and Southwest Mountains; Gómez and Lunt 2006) with an predominant direction from south to north (Teixeira 2007). Species with such dispersal patterns include *Lissotriton boscai* (A3) (Martínez-Solano et al. 2006), *Lissotriton helveticus*, *Lacerta schreiberi* (Paulo et al. 2001), *Podarcis bocagei, P. carbonelli* and *P. hispanica* (R2) (Pinho et al. 2007). Thus, northwards range expansion of these species may explain the current range concordance. For south-western assemblages (A4 and R1), the land bridges formed during the Tortonian and the MSC between the Iberian Peninsula and Morocco, and trans-marine dispersals, are related to the dispersion of many African taxa into this area, as already described above. Thus, these events seem to be more relevant in shaping current species assemblages than Pleistocene glaciations.

Within Morocco, our results are partially consistent with the major historical events usually claimed to have caused vicariance within Moroccan taxa: 1) almost all species known as having radiated due to the opening of the Strait of Gibraltar were grouped in R3 (e.g. *Timon tangitanus, Chalcides pseudostriatus*, *Blanus tingitanus*, *Podarcis vaucheri*, *Acanthodactylus lineomaculatus*) although they clustered together with most of Moroccan mountain endemics (Appendix 6.3), which probably originated by distinct vicariance events. Indeed, the origin of the high number of Moroccan mountain endemics is not completely clear, but the recent estimated time of divergence of many species, and the fact that most of them have an allopatric distributions, suggests that they probably originated under climate oscillation events (Carranza et al. 2000); 2) the Atlas Mountains separated coastal (R1, and R5) from desert (R4) assemblages, which is consistent with the theory that the formation of this mountain range caused vicariance events (Brown et al. 2002; Fritz et al. 2006); and 3) species occurring in desert areas also form a distinct assemblage, which concurs with the hypothesis that the climatic fluctuations during the past 10 MY produced repeated changes in habitat, from heavily vegetated land to desert and vice versa, promoting rapid changes in distribution and speciation by vicariance (Douady et al. 2003). That would have been the cause of divergence for example between different *Chalcides* (Carranza et al. 2008) and *Acanthodactylus* clades (Fonseca et al. 2008, 2009), and the radiation of desert forms within *Tarentola* (Carranza et al. 2002), *Sphenops*, *Scincus* (Carranza et al. 2008), and *Mesalina* (Kaplia et al. 2008).

From the previous paragraphs, we substantiate that the non-random distribution of species is derived from both vicariance and dispersal events. Indeed, dispersal events probably accounted for the great number of amphibian species being classified in the noise component. Many of the amphibians were classified in the noise component probably due to complex dispersal routes that resulted in present dissimilar species distributions, which mask previous vicariant events. The difficulty in finding strong biogeographical patterns for the amphibians in the Iberian Peninsula has been reported before (Busack and Jaksic 1982; Vargas et al. 1997), although it was attributed to a hypothesised low ecological specialization of the group (Busack and Jaksic 1982). However, Sillero et al. (2009) revealed that both specialist and generalist amphibian species occur in this area, which refutes that hypothesis.

For reptiles, we were able to classify almost all species in significant clusters and to relate them to a few important vicariance events. However, we also found that species within the same genera tended to be classified within the same biotic element, which contradicts the vicariance hypothesis. In fact, species of genera *Iberolacerta*, *Lacerta* and *Podarcis* were predominantly classified in R2, of genera Blanus in R3, and *Acanthodactylus*, *Mesalina*, *Spalerosophis*, *Stenodactylus* and T*arentola* in R4. This fact suggests that either distinct speciation mechanisms other than vicariance are related to species divergence or that post-vicariance dispersal occurred. Nevertheless, molecular studies available to support any of these assumptions are scarce (but see e.g. Fritz et al. 2006).

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Photo: Vasco Flores Cruz

"It is not the strongest of the species that survive, nor the most intelligent, but the one most responsive to change"

Charles Darwin

Chapter 7

From climate change predictions to actions:

conserving vulnerable animal groups in hotspots at a regional scale

Sílvia B. Carvalho, José C. Brito, Eduardo J. Crespo & Hugh P. Possingham

7.1 Abstract

Current climate change is a major threat to biodiversity. Species unable to adapt or move will face local or global extinction and this is more likely to happen to species with narrow climatic and habitat requirements and limited dispersal abilities, such as amphibians and reptiles. Biodiversity losses are likely to be greatest in global biodiversity hotspots where climate change is fast, such as the Iberian Peninsula. Here we assess the impact of climate change on 37 endemic and nearly endemic herptiles of the Iberian Peninsula by predicting species distributions for three different times into the future (2020, 2050 and 2080) using an ensemble of bioclimatic models and different combinations of species dispersal ability, emission levels and global circulation models. Our results show that species with Atlantic affinities that occur mainly in the North-western Iberian Peninsula have severely reduced future distributions. Up to 13 species may lose their entire potential distribution by 2080. Furthermore, our analysis indicates that the most critical period for the majority of these species will be the next decade. While there is considerable variability between the scenarios, we believe that our results provide a robust relative evaluation of climate change impacts among different species. Future evaluation of the vulnerability of individual species to climate change should account for their adaptive capacity to climate change, including factors such as physiological climate tolerance, geographical range size, local abundance, life cycle, behavioural and phenological adaptability, evolutionary potential and dispersal ability.

7.2 Introduction

Anthropogenic driven climate change is evident and for the next two decades a warming of at least 0.2°C per decade is projected (IPCC 2007) with associated changes in precipitation patterns. Throughout the history of Earth, climate has changed and species have coped and adapted to these changes, but current climate change is threatening biodiversity because it is fast compared to most past changes (Thomas et al. 2004). Current climate warming was considered the second most important threat to terrestrial biodiversity, only exceeded by land-use change (Sala et al. 2000).

Climate change have been reported to affect many aspects of populations: physiology, distribution, phenology, behaviour and propensity for local extinction (Hughes 2000; McCarty 2002; Parmesan 2006; Root et al. 2003; Walther et al. 2002). Species may be able to adapt to climatic changes via ecological (Root et al. 2005) or evolutionary processes (Bradshaw and Holzapfel 2006; Skelly et al. 2007). However, species unable to achieve a sufficient level of adaptation will likely face local or global extinction and this is more likely to happen to species with restricted climate and habitat requirements, limited dispersal abilities and ectothermal physiology (Massot et al. 2008; Walther et al. 2002; Thomas et al. 2004).

Amphibians and reptiles are considered one of the most vulnerable taxonomic groups to climate change (Araújo et al. 2006; Carey and Alexander 2003; Gibbons et al. 2000; Wake 2007). Climate warming is projected to induce a) changes in abundance; b) fragmentation of suitable habitats; c) changes in the timing of life-cycle events, such as hibernation, aestivation and breeding (Blaustein et al. 2001; Chadwick et al. 2006) and d) the spread of agents of infectious diseases such as the chytridiomycete fungus (Bosch et al. 2007; Pounds et al. 2006; Wake 2007). The interaction of these impacts causes disruptions in population and metapopulations dynamics, which ultimately may lead to changes in distributions.

The impact of global warming on biodiversity is likely to be more severe in regions rich in endemic species that are also predicted to be affected by dramatic climatic changes. The Mediterranean Basin is a particularly susceptible region: it is a biodiversity hotspot holding many endemic species (Médail and Quézel 1999; Mittermeier et al. 2005; Myers et al. 2000) and climate predictions for this region include a substantial rise in temperature and a drastic drop in rainfall, contributing to desertification (MIO-ECSDE 2003). The synergistic effect of climate change with other threats to biodiversity makes this region one of the most vulnerable in the world (Sala et al. 2000).

The Iberian Peninsula, in particular, is a Mediterranean sub-region with many endemic species. The high biodiversity derives from the fact that this area was one of the major glacial refugia in Europe during the Pleistocene (Hewitt 1996) and a diversification centre afterwards (Gómez and Lunt 2006; Pinho et al. 2007). Biodiversity richness in this area is also influenced by the climatic heterogeneity, since the climate transition between Atlantic and Mediterranean allows the co-occurrence of species with African and Euro-Siberian affinities, which means that the Iberian Peninsula is a biogeographic crossroad (Spector 2002).

In face of climate change challenges, conservation organizations are being asked to take proactive measures to mitigate impacts on biodiversity. To select appropriate measures we need to be able to predict the impact of climate change on biodiversity and evaluate the ability of biodiversity to adapt to those impacts. The combination of this information can be used to determine biodiversity vulnerability, which in turn becomes the basis for prioritizing species and defining management strategies (Kareiva et al. 2008).

Species distribution models (SDMs) are frequently used to assess the impacts of climate change on species distributions (e.g. Araújo et al. 2006). These statistical tools relate present day distributions with current environmental conditions and then use future potential climate conditions to predict future species distributions (Pearson and Dawson 2003). Predicting the impacts of climate change on species is a challenging task because SDMs include parameters with many sources of uncertainty (Webster et al. 2002) mostly related to: a) the statistical tool used for modelling species distributions; b) the global circulation models used to predict future climate conditions (Beaumont et al. 2008; Pearson et al. 2006; Thuiller 2004); and c) uncertainty derived from scale effects (Seo et al. 2009). Recently, advances in SDMs have made it possible to significantly reduce prediction uncertainties. For example, several robust statistical modelling methods have been developed to predict species distributions (see Elith et al. 2006 for review), while advanced methodologies in ensemble forecasting allow us to overcome the problem of variability in predictions made by different modelling techniques or different global circulation models (Araújo and New 2007; Marmion et al. 2009; Pearson et al. 2006). Additionally, climate predictions have been improved at smaller spatial scales (Hijmans et al. 2005).

In this study, we will evaluate potential impacts of climate change on the distribution of amphibians and reptiles in the Iberian Peninsula. We focus on endemic and nearly endemic species, the later defined as species that have aproximatelly more than two thirds of their entire range in the Iberian Peninsula. We then use information about species adaptability and vulnerability to make conservation recommendations.

Araújo et al. (2006) identified the Iberian Peninsula as one of the areas in Europe where amphibians and reptiles are likely to undergo major contractions in their ranges. Therefore, a detailed analysis of the Iberian Peninsula at a scale appropriate for establishing management strategies is urgently needed. We complement Araújo et al.'s (2006) European-wide research by providing a more detailed analysis of the impact of climate change on amphibian and reptile's distribution within the Iberian Peninsula. In particular, we used the most recent distribution data which are geographically more detailed than the one used in Araújo et al. (2006) (10x10 km in opposition to 50x50km) and incorporate recent taxonomic discoveries, that significantly increases the number of endemics (21 species vs. 12 species). Additionally, we project species ranges to three times in the future (2020, 2050, 2080 instead of 2050 only), which may assist conservation decision making in terms of prioritizing the allocation of conservation funds through time.

We provide specific recommendations to conservation practitioners for enhancing the probability of species persistence by answering the following questions: In the Iberian Peninsula, which endemic and nearly endemic amphibian and reptile species are predicted to lose and gain suitable habitat in the future? For species predicted to lose suitable habitat, is the loss rate constant throughout time or are there more critical periods? Which areas will be more impacted by species loss? Which species should be under priority conservation action? Which conservation measures are most likely to increase the probability of species persistence?

7.3 Methods

7.3.1 Study area

The study region is the continental Iberian Peninsula, situated in the extreme southwest of Europe (bounded by 9º32′ to 3º20′E and 35º56′ to 43º55′N). With an area of 582 860 km^2, it includes the continental territories of Portugal and Spain. It is bordered to the south and east by the Mediterranean Sea and to the north and west by the Atlantic Ocean. The Pyrenees and the Strait of Gibraltar separate most of the region from the remainder of Europe and Africa, respectively (Figure 1). The dominant climate type of the region is Mediterranean, but the north and northwest of the Iberian Peninsula and the major mountain systems are characterised by an Atlantic climate.

7.3.2 Species and distribution data

Distribution data for 37 endemic and nearly endemic species (15 amphibians and 22 reptiles) were collected from the most recent herpetological atlases of Portugal (Loureiro et al. 2008) and Spain (Pleguezuelos et al. 2002), which are referenced to the UTM grid of 10x10 km. Taxonomy was defined according to the most recent revision of the taxonomic list in Carretero et al. (2009). We excluded from our analysis records from the Portuguese atlas for *Triturus marmoratus* because that data does not distinguish between *Triturus marmoratus* and *T. pygmaeus*. We followed the same method for Portuguese records of *Pelodytes punctatus* because they represent two species: *Pelodytes punctatus* and *P. ibericus*. Our data contained only two records of *Iberolacerta martinezricai* so we were unable to develop a plausible predictive model.

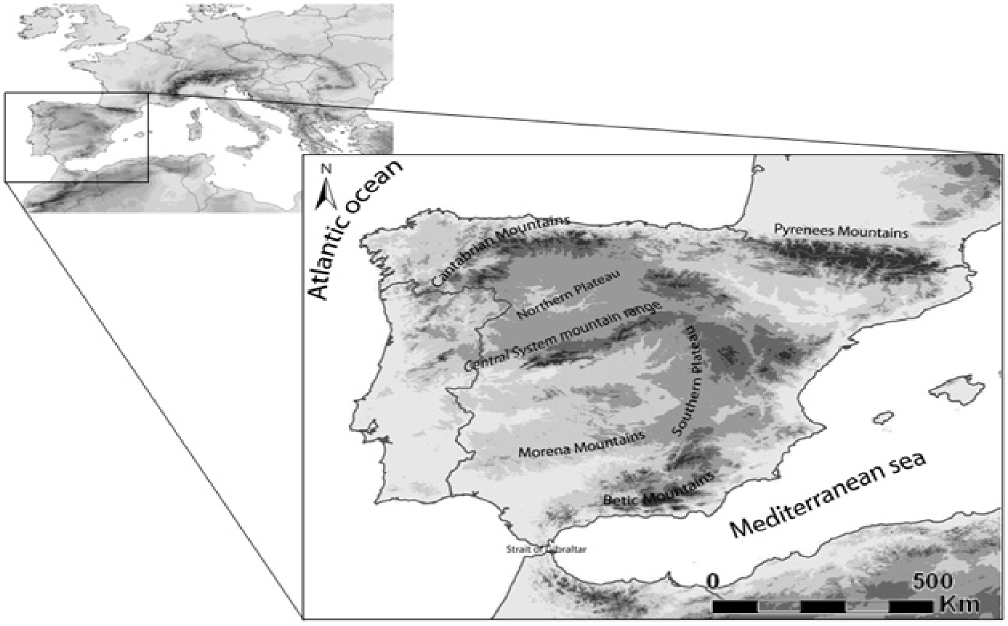

Figure 7.1 Location and map of the Iberian Peninsula depicting elevation and major geographic features. Elevation is represented in a range of grey colours where darker areas represent higher altitude.

7.3.3 Climate data

Current bioclimatic data were downloaded from WorldClim database (Hijmans et al. 2005) which is a set of global climate layers generated through interpolation of climate data from weather stations. We used nine variables that were not tightly correlated with each other (with a Pearson correlation coefficient between them lower than 0.75): temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality and altitude. All variables were downloaded in a 2.5 arc-minute resolution. We converted these data to match with the same grid format as the species distribution data by averaging the variable's values inside each grid cell.

We used future climate data for three Global Circulation Models (GCM) (CCCMA, HADCM3 and CSIRO) and two IPPC 3rd assessment storylines (A2 and B2). The IPCC storylines describe the relationships between the forces driving greenhouse gas and aerosol emissions such as demographic, social, economic, technological, and environmental developments (IPCC-TGICA, 2007). The two storylines used for this study assume regionally oriented economic growth, with population and economic growth being higher in A2 than B2. Future climate data were downloaded from WorldClim, for three different future years (2020, 2050 and 2080) creating six storyline-GCM combinations for each future year. We downloaded monthly averages of maximum and minimum temperatures and total precipitation and calculated the bioclimatic variables according to the same methodology used to calculate them for current climate conditions (Hijmans et al. 2005).

7.3.4 Species distributions: current predictions and future projections

We used a set of nine modelling techniques to predict the distribution of each of the 37 species in four different times (current, 2020, 2050 and 2080): Maximum Entropy (MXT), Generalised Linear Models (GLM), Generalised Additive Models (GAM), Classification Tree Analysis (CTE), Artificial Neural Networks (ANN), Generalised Boosting Models (GBM), Breiman and Cutler's random forest for classification and regression (RF), Mixture Discriminant Analysis (MDS) and Multiple Adaptive Regression Splines (MARS).

To produce Maximum Entropy models we used Maxent software (Phillips et al. 2004). Maxent estimates the range of a species with the constraint that the expected value of each variable (or its transform and/or interactions) should match its empirical average, i.e. the average value for a set of sample points taken from the species-target distribution (Phillips et al. 2006; Phillips and Dudík 2008). We used the default "auto features" option, logistic output, the recommended default values for the convergence threshold (10^{-5}) and the maximum number of iterations (500).

The remaining eight models were built within BIOMOD (Thuiller et al. 2009). BIOMOD is a collection of functions running within the R software v. 2.8.1 (R Development Core Team 2006) for ensemble forecasting of species distributions and a summary of model statistics is described in Thuiller et al. (2009). The majority of model-techniques requires data about presences and absences, thus we determined pseudo-absences for each species by using the "random strategy" in BIOMOD. The number of selected pseudo-absences for each species was equal to the number of its occurrences, whenever possible. In cases where the number of locations where species was not recorded was less than the number of occurrences, we selected all non-occurrences as pseudo-absences. All models were produced using default BIOMOD parameters where possible (Thuiller et al., 2009). Further parameters were as following: GLMs were generated using quadratic terms and a stepwise procedure with the AIC criteria. GAMs were generated with a spline function with 4 degrees of smoothing. ANNs were produced with two cross-validations. BIOMOD allows evaluation of model performance on different data split runs and then allows using 100% of the data to make a final calibration of the models for prediction. Thus, we randomly assigned 80% of occurrence data to train the model with the remaining 20% for testing. Each model was run ten times to avoid bias resulting from randomly splitting the data into training and testing.

To evaluate the performance of individual models from each technique, we calculated the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997; Zweig and Campbell 1993). For each of the 37 species we produced nine models for the current time and climate (with different modelling techniques) and 54 models (combination of nine modelling techniques, three GCM and two storylines) for each of the three times in the future (2020, 2050 and 2080), in a total of 171 models per species.

For each year in the future (2020, 2050 and 2080) we calculated an ensemble forecast for current time and for each IPCC scenario for the future (A2, and B2). For this purpose, we used weighted average consensus method based on AUC values, because this method is considered to significantly improve the predictive accuracy of single models (Marmion et al. 2009). Thus, AUCs values of each model technique were assigned the weights of the weighted average in order to enhance contributions of those models with higher model performance values (equation 7.1).

$$WA_i = \frac{\sum_m (AUC_m \text{ x } p_{mi})}{\sum_m AUC_m} \qquad \text{(equation 7.1)}$$

where i is the index of the grid cell, m is the model technique and p is the probability of occurrence of the species (according to model m in grid cell i).

To investigate if species ranges were predicted to contract or expand, we needed to convert the consensus forecasted probabilities of occurrence in each year to a binary value of predicted presence/absence. For each model technique, we calculated the threshold of the receiver operating characteristic curve that maximizes both correctly predicted presences and absences, relative to the evaluation data (Liu et al. 2005). Subsequently, we determined a consensus threshold (CT) by calculating the weighted average threshold, assigning the AUC value of each model as a weight (equation 7.2).

$$CT = \frac{\sum_m (AUC_m \text{ x } t_m)}{\sum_m AUC_m} \qquad \text{(equation 7.2)}$$

where m is the model technique and t_m is the optimised threshold of model m.

Potential range shifts of each species and time period were measured under two extreme dispersion scenarios: unlimited dispersal (scenario D), assuming that species can disperse to any grid cell with suitable habitat, and no dispersal (scenario ND), assuming that species are not capable to disperse even if suitable habitat is available. To predict species presence under the D scenario, we transformed the consensus probability value in each grid cell into 0 if it was lower than CT and to 1 if it was equal to or higher than CT. To predict species presences under the ND scenario, we transformed predicted presences to absences in grid cells where species is not presently predicted to occur. We evaluated the degree of uncertainty of projections for each year and scenario by calculating the standard deviation of predicted occurrence of species by grid cell.

Subsequently, we calculated predicted species richness in each grid cell for the three future periods. Future species richness was estimated by summing the number of species predicted to occur in each grid cell under each of the storylines and the dispersion scenarios. Species turnover (T) is the dissimilarity index between the present and future species composition of a given area. It accounts both for species gain and losses and its relation to the overall number of species occurring in the grid cell in present and future. Thus, a turnover value of 0 indicates that the predicted assemblage in the future would be the same as the current assemblage, whereas a turnover value of 100 indicates that the assemblage would be completely different under climate change. To determine it, we first calculated the number of species lost (L), i.e., the number of species predicted to lose suitable habitat in each grid cell, and the species gain (G), i.e., the number of species predicted to gain suitable habitat in each grid cell. Percentage of species turnover by grid cell was then calculated according to equation 7.3.

$$T = 100x\frac{L+G}{SR+G} \qquad \text{(equation 7.3)}$$

where *SR* is the current predicted species richness.

7.4 Results

Model predictions within different modelling techniques, GCMs, and storylines showed high variability in the projection of range shifts, with most species being projected to both lose and gain suitable habitat, depending on the scenario (Appendix 7.1). However, when analysing the ensemble model results (Tables 7.1 and 7.2), we found that 46% of the species are consistently predicted to have a smaller distribution in both storylines (9 amphibian species and 8 reptile species), 28% of the species are consistently predicted to have a larger distribution (3 amphibian species and 8 reptile species) and the remaining species show increases and decreases depending in the time period and storyline. For example *Algyroides marchi* is predicted to have a smaller distribution until 2050 and then increase its distribution by 2080, while, *Alytes cisternasii* and *Lissotriton boscai* are predicted to have a larger distribution until 2020 and then have a smaller distribution.

Several species are predicted to lose a significant fraction of their current range (Figure 7.2) and 10 species are predicted to lose their entire suitable distribution at some time in both storylines. Three other species are predicted to lose all suitable range in one of the storylines only (Table 7.3). Surprisingly 5 to 10 of the 13 species that are predicted to lose all their suitable distribution, lose it by 2020 (Table 7.3). Additionally, 9 of these species are also threatened by other causes, and currently considered “critically endangered”, “endangered” or “vulnerable”, in Portuguese or Spanish red data books (Tables 7.1 and 7.2).

If we assume that species have no ability to disperse, 34 species are predicted to contract their distribution and 10 species are predicted to completely lose their entire distribution in both storylines.

It is noteworthy that for species predicted to have a smaller distribution in the future, both the magnitude of contraction and the rate of contraction differ between species (Figure 7.3). While for most contracting species, the rate of range contraction is greater

Table 7.1 Amphibian species list, conservation status under IUCN criteria (NE – not evaluated, LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered), number of grid cells where each species is currently predicted to occur (current), number of grid cells where habitat is predicted to become unsuitable (negative values) or become suitable (positive values) in the future and overall tendency under storylines A2 and B2 and unlimited dispersal assumption. * indicates species strictly endemic to the Iberian Peninsula.

Species	IUCN	Current	2020	2050	2080	Tendency	2020	2050	2080	Tendency
*Alytes cisternasii**	NT	2123	2460	-1263	-2114	Expansion/ Contraction	1496	760	-1164	Expansion/ Contraction
*Alytes dickhilleni**	VU	415	-415	-414	-415	Contraction	-415	-415	-415	Contraction
*Calotriton asper***	NT	385	-200	-384	-385	Contraction	-173	-316	-385	Contraction
*Chioglossa lusitanica**	VU	790	-727	-750	-788	Contraction	-790	-734	-774	Contraction
*Discoglossus galganoi**	NT	2472	-2286	-2472	-2472	Contraction	-2337	-2428	-2416	Contraction
*Discoglossus jeanneae**	NT	1474	1991	3922	4684	Expansion	2805	2439	5052	Expansion
*Lissotriton boscai**	LC	2371	3571	-40	-1776	Expansion/ Contraction	3148	1177	553	Expansion
Pelobates cultripes	NT	3087	3988	4232	3936	Expansion	3998	4097	3933	Expansion
*Pelodytes ibericus**	LC	927	-2	487	-648	Contraction/ Expansion/Contaction	86	228	210	Expansion
Pelophylax perezi	LC	5607	-864	-47	-1849	Contraction	-617	-752	-526	Contraction
Pleurodeles waltl	NT	2826	-689	-1751	-284	Contraction	-974	-1710	1	Contraction
*Rana iberica**	VU	1324	-370	-1115	-1324	Contraction	-673	-946	-1132	Contraction
*Rana pyrenaica***	VU	89	-89	-89	-89	Contraction	-89	-89	-89	Contraction
Triturus marmoratus	LC	2080	-2075	-2080	-2080	Contraction	-2080	-2080	-2080	Contraction
*Triturus pygmaeus**	NT	1358	1277	1849	1585	Expansion	1649	1674	1849	Expansion

Table 7.2 Reptile species list, conservation status under IUCN criteria (NE – not evaluated, LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered), number of grid cells where each species is currently predicted to occur (current), number of grid cells where habitat is predicted to become unsuitable (negative values) or become suitable (positive values) in the future and overall tendency under storylines A2 and B2 and unlimited dispersal assumption. * indicates species strictly endemic to the Iberian Peninsula.** indicates species endemic to the Pyrenean Mountains.

Species	IUCN	Current	2020	2050	2080	Tendency	2020	2050	2080	Tendency
Acanthodactylus erythrurus	NT	2545	4004	4354	4627	Expansion	3753	4065	4341	Expansion
*Algyroides marchi**	VU	204	-155	292	305	Contraction/ Expansion	49	257	-65	Expansion/ Contraction
*Blanus cinereus**	LC	2778	1725	2152	2398	Contraction	1787	1620	2416	Expansion
*Chalcides bedriagai**	NT	2344	2891	3553	3510	Expansion	2432	2679	4110	Expansion
Chalcides striatus	LC	2937	1108	-263	-249	Expansion/ Contraction	714	-702	741	Expansion
Coronella girondica	LC	2899	4606	2082	4572	Expansion	2484	2432	4689	Expansion
Hemorrhois hippocrepis	LC	2583	1313	2325	2326	Expansion	1275	1962	2720	Expansion
*Iberolacerta aranica***	CR	23	-23	-23	-23	Contraction	-23	-23	-23	Contraction
*Iberolacerta aurelioi**	EN	19	-19	-19	-19	Contraction	-19	-19	-19	Contraction
*Iberolacerta bonnali***	VU	64	-64	-64	-64	Contraction	-64	-64	-64	Contraction
*Iberolacerta cyreni**	EN	867	-427	-588	-750	Contraction	-426	-538	-742	Contraction
*Iberolacerta monticola**	VU	524	-469	-524	-524	Contraction	-524	-524	-524	Contraction
*Lacerta schreiberi**	NT	1560	778	-367	-875	Expansion/ Contraction	-95	-54	-401	Contraction
*Podarcis bocagei**	LC	807	-761	-806	-807	Contraction	-807	-807	-806	Contraction
*Podarcis carbonelli**	VU	519	212	-226	-499	Expansion/ Contraction	209	-193	-7	Expansion/ Contraction
Podarcis hispanica	LC	4522	2233	2367	2926	Expansion	2235	2294	3033	Expansion
Psammodromus algirus	LC	4311	2643	1170	-1220	Expansion/ Contraction	1842	1349	1470	Expansion
Psammodromus hispanicus	LC	2882	1705	2403	2524	Expansion	1959	2416	3736	Expansion
Rhinechis scalaris	LC	2674	4742	4915	4927	Expansion	4832	4911	4922	Expansion
Timon lepida	LC	4080	-1325	-1219	-1950	Contraction	-1974	-1310	-20	Contraction
Vipera latastei	VU	2688	3865	3873	3630	Expansion	3344	3890	3139	Expansion
*Vipera seoanei**	EN	873	-867	-873	-873	Contraction	-873	-873	-873	Contraction

now (until 2020), for some species there is almost a constant rate of predicted distribution loss (e.g. *Rana iberica*), while for a minority of species the period of greatest contraction is later (e.g *Psammodromus algirus*).

Predicted patterns of species richness are substantially different between the two dispersion scenarios, but higher species richness was commonly predicted in South-western Iberian Peninsula, the Central System Mountain range and Morena Mountains (Figures 7.4 and 7.5). Major species gain, in the unlimited dispersion scenario, was predicted for the Central Plateaus, the Central-western coast of the Iberian Peninsula, and the Cantabrian Mountains (Figure 7.6). Major loss of species ranges is predicted for the Atlantic climate regions, mostly along the northwest of the Iberian Peninsula and the main mountain ranges, such as the Central System and the Morena Mountains (Figure 7.6). Spatial patterns of predicted species richness are similar in both storylines, although storyline B2 predicted slightly higher species losses for 2020 and storyline A2 predicted higher species loss for 2080 (Figures 7.4 and 7.5).

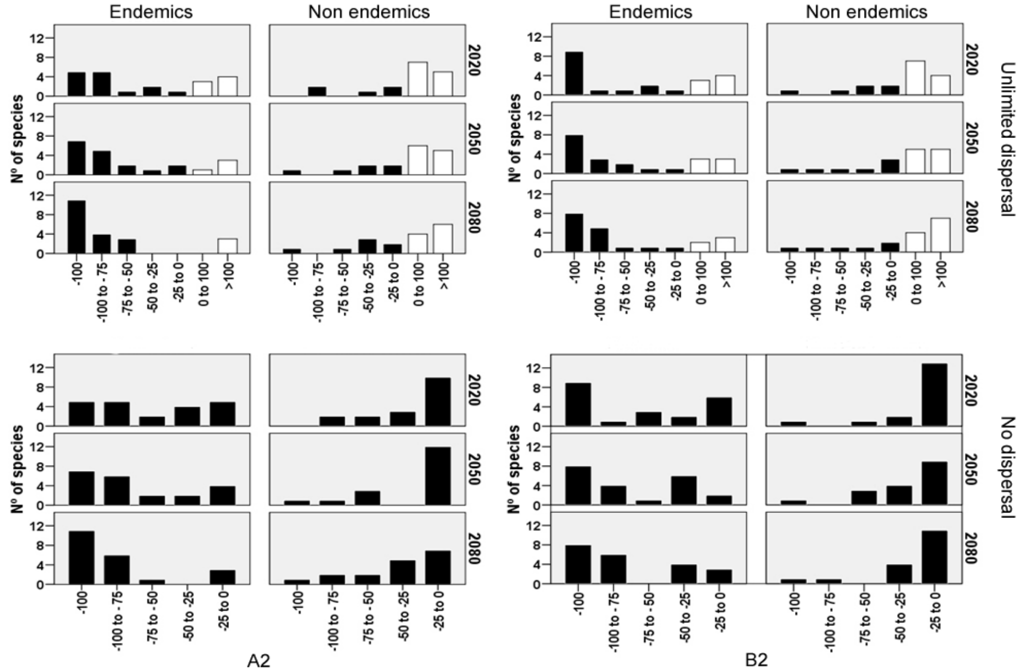

Figure 7.2 Number of species predicted to gain or lose suitable habitat under different dispersion assumptions (unlimited dispersal and no dispersal) and storylines (A2 and B2), categorized by the percentage of range contraction or expansion relatively to present (x axis). Endemics and non endemics species are represented separately, with endemics representing species strictly endemic to the Iberian Peninsula and species endemic to the Pyrenean Mountains. Black columns represent species predicted to lose suitable habitat while white columns represent species predicted to gain suitable habitat.

Table 7.3 Species predicted to completely lose distribution range in the Iberian Peninsula until each of the periods (2020, 2050 and 2080) according to storylines (A2, B2 or both) and under the unlimited dispersal scenario. * indicates species strictly endemic to the Iberian Peninsula.** indicates species endemic to the Pyrenean Mountains.

Species	2020	2050	2080
*Alytes dickhilleni**	A2/B2	B2	A2/B2
*Calotriton asper***	-	A2	A2/B2
*Chioglossa lusitanica**	B2	-	-
*Discoglossus galganoi***	-	-	A2
*Iberolacerta aranica***	A2/B2	A2/B2	A2/B2
*Iberolacerta aurelioi**	A2/B2	A2/B2	A2/B2
*Iberolacerta bonnali***	A2/B2	A2/B2	A2/B2
*Iberolacerta monticola**	B2	A2/B2	A2/B2
*Podarcis bocagei**	B2	B2	A2
*Rana iberica**	-	-	A2
*Rana pyrenaica***	A2/B2	A2/B2	A2/B2
Triturus marmoratus	B2	A2/B2	A2/B2
*Vipera seoanei**	B2	A2/B2	A2/B2

7.5 Discussion

7.5.1 Main findings and relation with previous projections

Our results suggest that climate change might have serious impacts on the distribution patterns of the endemic and nearly endemic amphibians and reptiles of the Iberian Peninsula, particularly for species with Atlantic climate affinities such as *Chioglossa lusitanica*, *Rana iberica* and *Vipera seoanei* and particularly high altitude species with Atlantic climate affinities such as *Rana pyrenaica*, *Iberolacerta monticola*, *I. aranica, I. aurelioi*, and *I. bonnali*. It is also possible that other species may be more affected by climate change than predicted by the models, such as *Iberolacerta cyreni*. This species is an endemic with a current range restricted to the Gredos Mountains in Spain. However, the ensemble model for this species predicted a current range much larger than probably the one where the species actually occurs. This indicates that predicted future range may also be overestimated. On the other side, models for *Pelodytes ibericus*, *Triturus marmoratus* and *T. pygmaeus* were built only based on Spanish records, although they also occur in Portugal. This methodological caveat may have conduced to an under estimation of current and future ranges of those species.

Our analysis indicates that the most critical period for the majority of these species will be the next decade. This result emphasises the need for immediate conservation action in the Iberian Peninsula to ameliorate the impact of climate change.

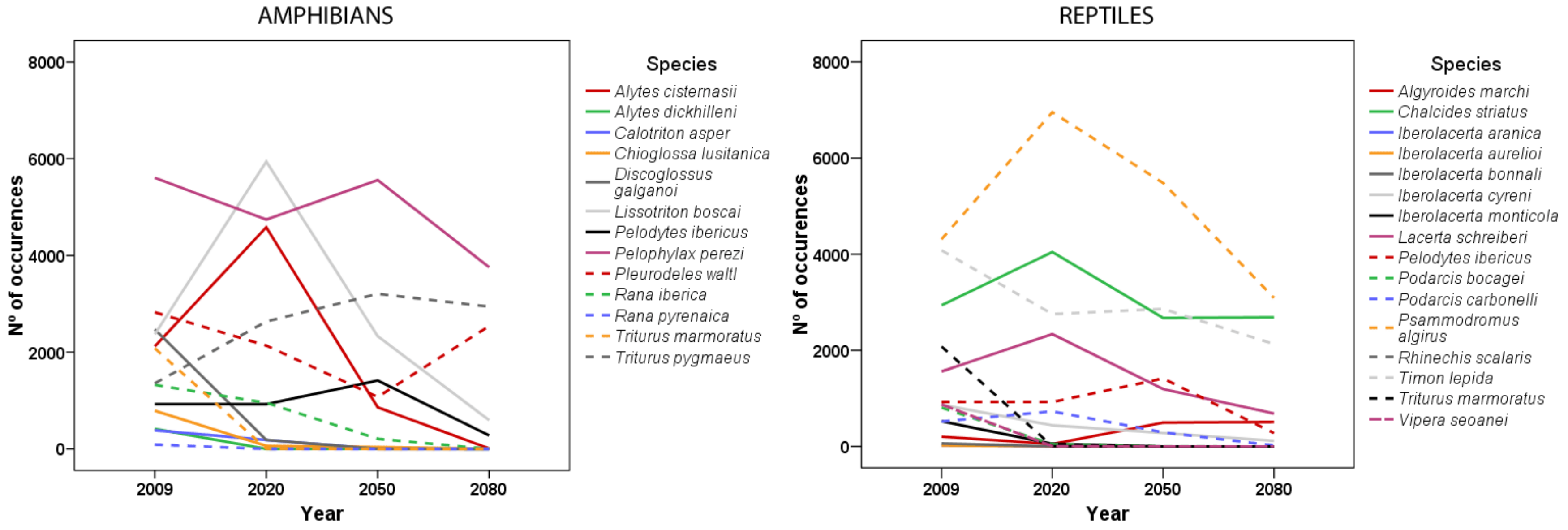

Figure 7.3 Variation in the predicted number of occurrences through time for species predicted to lose suitable habitat according to the unlimited dispersion scenario and storyline A2.

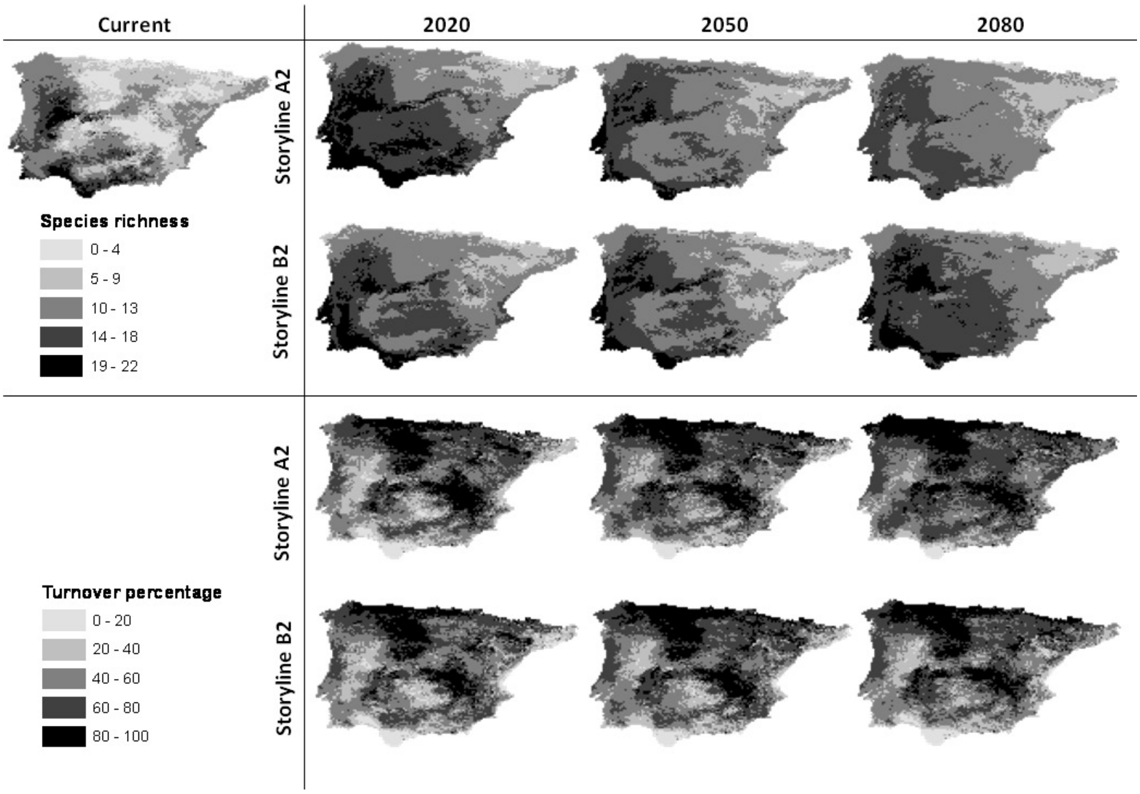

Figure 7.4 Spatial distribution of predicted current and future (2020, 2050 and 2080) species richness and turnover percentage according to storylines A2 and B2 and under the unlimited dispersion scenario.

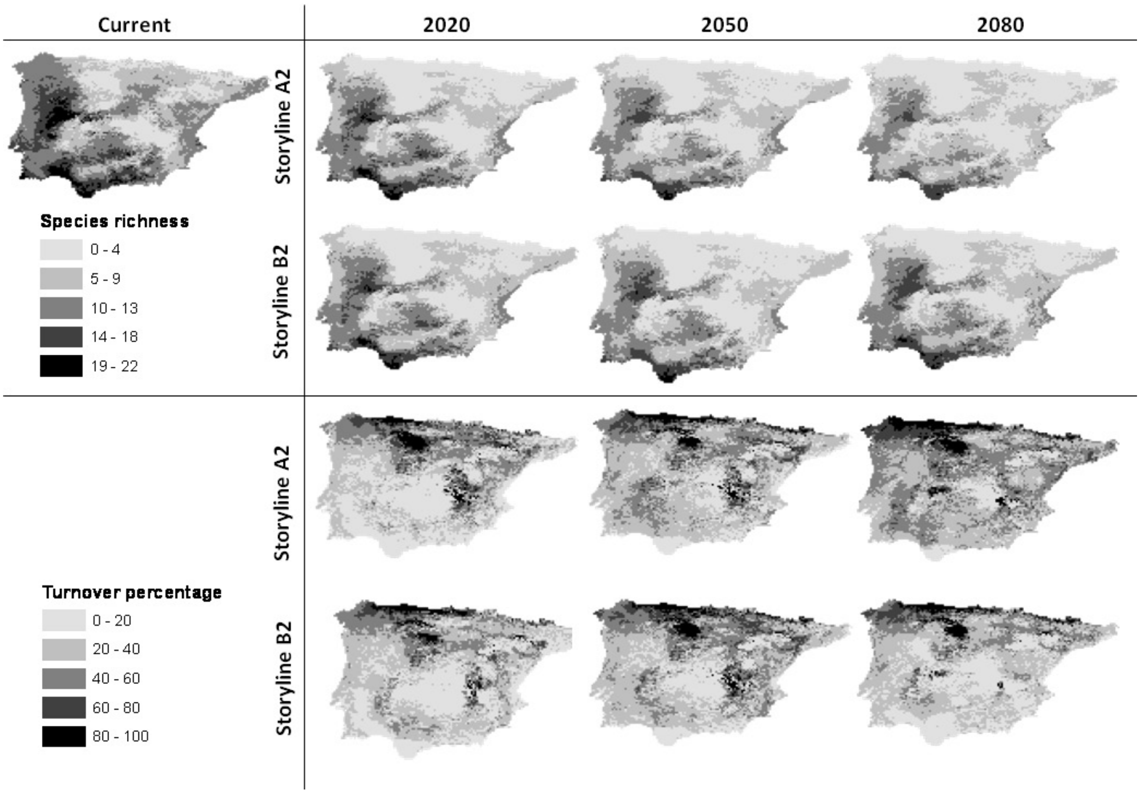

Figure 7.5 Spatial distribution of predicted current and future (2020, 2050 and 2080) species richness and turnover percentage according to storylines A2 and B2 and under the no dispersion scenario.

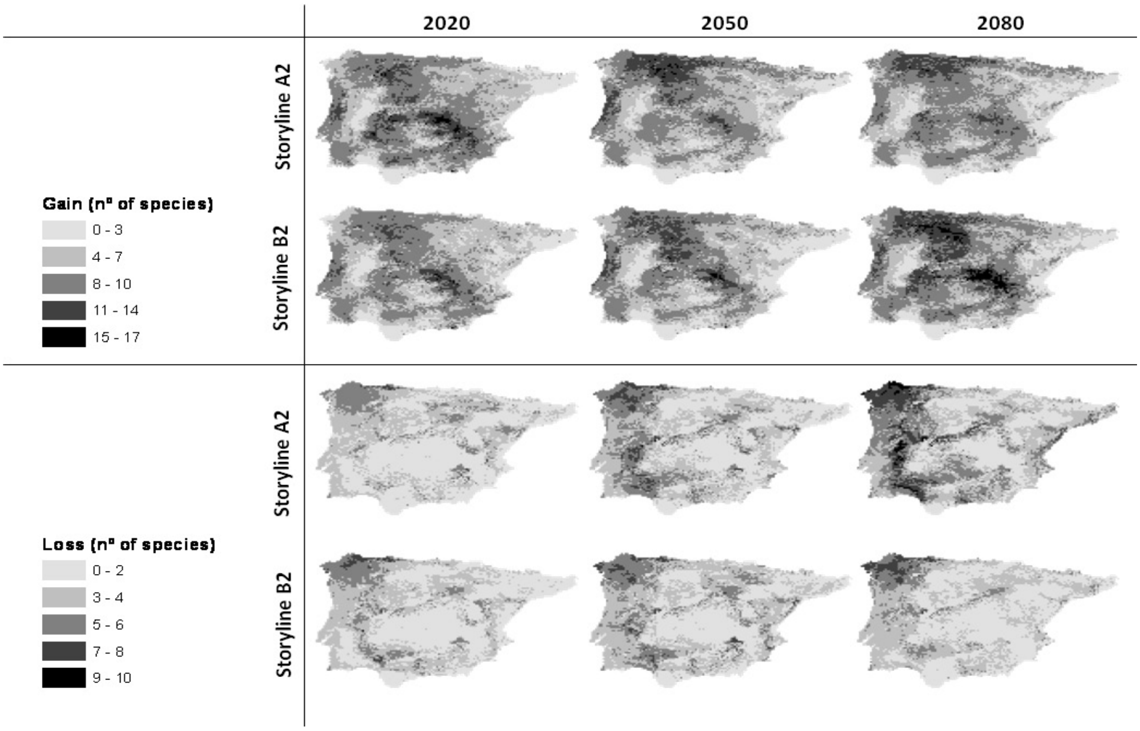

Figure 7.6 Spatial distribution of predicted gain (under the unlimited dispersion scenario) and loss (in both dispersion scenarios) of number of species in the future (2020, 2050 and 2080) according to storylines A2 and B2.

Previous macroscale studies have called attention to the vulnerability of biodiversity in the Mediterranean Basin. This region was considered one of the most vulnerable in the world (Sala et al. 2000) and one of the biodiversity hotspots likely to undergo major losses due to climate change, along with the Cape Floristic Region, the Caribbean, Indo-Burma, Southwest Australia, and the Tropical Andes (Malcolm et al. 2006). The Iberian Peninsula is considered the Mediterranean sub-region most likely to be affected by future climate change (EEA 2004). Our analysis confirm the vulnerability of species occurring in the Iberian Peninsula to climate change, but curiously, species with Atlantic climate affinities were predicted to be more affected by climate change than the Mediterranean ones. The Atlantic climate region is much more restricted in the Iberian Peninsula than the Mediterranean. Due to predicted drops in precipitation and temperature raise it is likely that the all Iberia became dominated by a Mediterranean climate. Thus, it seems logical that Atlantic species become more affected by climate change than the Mediterranean ones. Climate change impacts on Atlantic species was exacerbated by the region being a peninsula so dispersal out of the region to other Atlantic climate regions is restricted. Similar patterns should be found in other Mediterranean Peninsulas that present different climatic types (e.g. the Italian Peninsula and the Balkans).

Our results are consistent with those found by Araújo et al. (2006), in the sense that climate change is predicted to cause a major contraction in the distribution of a considerable number of amphibian and reptile species in the Iberian Peninsula. However, our results revealed that major losses for endemic and nearly endemic species will occur in substantially different areas than the ones predicted by Araújo et al. (2006) for the all amphibians and reptiles. We predict that the north-west of the region, the Central System and the Morena Mountains will lose many species in contrast to their results where there is expected to be species gain. The reasons for this difference may be our focus on endemic and nearly endemic species rather than all species, but it could also be differences in spatial scale or methods used to construct the ensemble models. Dissimilarities in areas predicted to gain species may also be related to the colonization of non endemic or nearly endemic species and non Iberian species not included in our analysis. These divergent results highlight the importance of finer-scale analyses for areas identified as vulnerable in broader continental-scale studies.

Interestingly, a previous study of climate change threats to plant diversity in Europe (Thuiller et al. 2005) also identified the Iberian Peninsula as one of the European regions likely to undergo major species loss. Garzón et al. (2008) identified the north and northwest of the Iberian Peninsula and the main mountain ranges, as the Iberian areas likely to have the highest tree species loss, which is partially coincident with our results. Thus, if changes in vegetation communities are also predicted, it means that amphibians and reptiles will face a synergistic impact of climate and habitat change, which ultimately will also be coupled with the impact of changes in biotic interactions resulting from changes in the community of species. These results also suggest that the impacts of climate change on species ranges might be similar across different biodiversity groups that occur in the same area, which calls for the need to evaluate possible climate change impacts on those groups.

7.5.2 From predicted impacts (models) to vulnerability

Our dramatic predictions should be interpreted with caution given all the uncertainties in the process: the statistical methods used for modelling species distributions, the global circulation models used to predict future climate conditions (e.g. Araújo and New 2007, Beaumont et al. 2008), the scale of the analysis (Seo et al. 2009), and specific dispersal abilities. Additionally, species distribution models disregard important biological parameters that ultimately are the determinants of species capability to adapt to climate change.

Different modelling techniques, GCM and storylines provided fairly different results for the number of predicted occurrences of a species. The ensemble methodology allows us to distinguish the strongest signal emerging from the noise associated with different model outputs but it is not immune from uncertainty. Taking uncertainty into account, for example by using as an uncertainty measure the standard deviation of the total number of occurrences predicted by the different models for each species (appendix 7.1A and 7.1B), the most likely impact of climate change will be on species whose ranges are predicted to contract more (relatively to their current extent), or to become more restricted (considering their future absolute extent) with less uncertainty. For example, analysing only the year 2020 projections for storyline A2, species that fulfil both criteria are *Discoglossus galganoi* (considering the species whose ranges are predicted to contact more) and *Iberolacerta aranica,* (considering the species whose ranges are predicted to become more restricted or disappear).

The scale of analysis may also be a relevant limitation in determining the impact of climate change, because the scale used does not account for microhabitat variability within sites. This constraint is quite relevant in the case of amphibians and reptiles because they might find suitable habitat, for instance, in small ponds, water tanks, below stones or underground (Kearney and Porter 2009). Also, the scale of the analysis probably obscures altitudinal microclimatic gradients which might allow species to move towards future suitable habitats without the need to disperse long distances.

Specific dispersal abilities may strongly determine the impacts of climate change on the future distribution of species. However, given that this parameter is difficult to determine for every species, we predicted future distributions under the assumptions of maximal and minimal possible dispersal ability for each species. We recognize that both of these assumptions are unrealistic, but they allow us to predict the largest and smallest possible future ranges. A more realistic prediction would probably be somewhere in the middle of these two extremes, but we cannot make an exact prediction with high level of certainty.

Assuming these limitations we do not argue that species predicted to completely lose their distribution under our analysis will go extinct. Rather, we consider that the degree, the certainty and the time of predicted range contractions provides a relative measure of the magnitude of the impact of climate change on each species. Ultimately, the vulnerability of a species to a given impact will depend also on the species resistance, i.e. the ability of a species to withstand an environmental perturbation, and resilience, i.e. the ability of a species to adapt and recover from a perturbation (Isaac et al. 2008; Williams et al. 2008). Thus, prioritizing species for management actions would require a further analysis of the specific factors that determine resistance and resilience. In general, the species traits that are predicted to promote species resistance to climate change are physiologic climatic tolerance (Calosi et al. 2008), geographical range size and local abundance.

Overall, reptiles are usually considered more resistant to global warming effects than amphibians because they have evolved a set of adaptations to water scarcity, such as eggs with calcareous shells (while amphibian eggs are enclosed by simple gelatinous membranes), and the excretion of metabolic wastes in the form of urea or uric acid, which is an adaptation to retain body-water (Gibbons et al. 2000). Additionally, most reptiles are not dependent on water for reproduction. Although more specific climatic tolerances might be difficult to determine, they may be inferred by morphological traits or by the complete climatic envelope of species. Also, the climatic envelope of phylogenetic related species might provide some clues, if one considers niche conservatism (Hawkins et al. 2007). For example, species belonging to clades that evolved under warm environments may be more tolerant to global warming.

Species with restricted ranges are relatively more vulnerable to climate change because contractions of their small range will not be balanced elsewhere. From this point of view, species with very restricted distributions predicted to completely lose suitable habitat in the Iberian Peninsula such as *Iberolacerta aranica*, *I. aurelioi*, and *Rana pyrenaica* may be more impacted by climate change than more widespread Iberian species such as *Lissotriton boscai* or *Chalcides bedriagai*.

Demographic parameters are also important factors in determining resistance to climate change (Keith et al. 2008). Species with restricted ranges but with high local abundance may have more chances to adapt because genetic variation and potential response to selection pressures are positively correlated with population size. Thus, biological traits that regulate abundance, such as reproductive rates, age of female sexual maturity and life span length are also relevant. *Discoglossus galganoi* and *Podarcis bocagei* are species predicted to completely lose their range in the Iberian Peninsula but have high abundance and reproductive rate, and consequently will probably be less impacted by climate change than the others will.

The adaptive capacity (or plasticity) of a species describes the intrinsic ability of a species to adapt to changing conditions. Species might be able to adjust their behaviour and phenology by switching periods of daily activity, aestivation and hibernation towards more favourable climatic conditions (Parmesan 2007). Species might also be able to evolve traits that allow them to adapt to different climatic conditions (Bradshaw and Holzapfel 2006; Harte et al. 2004). Adaptation ability may be species-specific, however, the current knowledge is insufficient to determine which species are more able to adapt and further studies and monitoring are required to fully understand it.

Species might also adapt to novel climate conditions by dispersing to other areas (Massot et al. 2008; Thuiller 2004). Dispersion ability has been identified as one of the most decisive parameters in determining species resilience to climate change as species with greater dispersion ability may be able to track climate transitions. However this parameter is also one of the most difficult to determine. A growing body of literature proposes a vast collection of complex models to predict dispersion ability (reviewed by Thuiller et al. 2008) but these require detailed data on an array of ecological processes that usually are unavailable for large numbers of species.

A preliminary analysis of the model results and previous considerations indicate that species requiring more conservation attention under a climate warming perspective may be *Rana pyrenaica*, *Rana iberica* and *Calotriton asper*, within the amphibians, and *Iberolacerta aranica*, *Iberolacerta aurelioi*, *Iberolacerta bonnali* and *Iberolacerta monticola* within the reptiles. However, this does not mean that these are the most vulnerable species to extinction, because this evaluation is only based on vulnerability to climate change, and does not account for other threats or the interaction of climate change with other threats (Brook et al. 2008). Particularly, climate change is likely to induce further habitat changes and fragmentation (due to shifts in plant species distribution and an increase in fire incidence) and the spread of agents of infectious diseases such as the chytridiomycete fungus which is already across the Iberian Peninsula (Garner et al. 2005). These factors are already considered the primary threats to amphibians and reptiles, along with pollution, invasive species, road kills and genetic depression.

7.5.3 From vulnerability to conservation actions

Recommendations to address climate change impacts on biodiversity include a wide variety of measures, with the most popular being monitoring species (with emphasis on the physiological, behavioural and demographic response), restoring habitats and system dynamics, expanding reserve networks, performing assisted dispersal (Hoegh-Guldberg et al. 2009), reducing other threats and increasing connectivity between suitable habitats (Heller and Zavaleta 2009; Lawler 2009). Probably the most important questions for management are whether species will be able to adapt to future climate conditions without the need to disperse or, if not, if they will be able to disperse. Because these questions are difficult to answer with current knowledge, novel management tools that promote flexible decision-making are emerging, such as adaptative management (Kareiva et al. 2008). Following this methodology, we recommend that monitoring should be directed at the most vulnerable species identified by our research. To infer species-specific conservation measures, the monitoring parameters should include: a) physiological changes in thermal tolerances; b) phenological adjustments, such as changes in aestivation and hibernation periods along the year; c) behavioural thermoregulation changes, such as burrowing or adjustments in daily activity periods; d) quantification of dispersal rates; e) changes in population parameters, such as abundance, fertility and mortality; f) incidence of infectious diseases and g) species interactions.

If species are not able to disperse, then management measures will be needed in order to assist local adaptation. Habitat restoration has been proposed as a proactive measure to enhance amphibian resilience to climate change. In particular, a denser network of ponds and water tanks has been recommended for amphibians (Blaustein et al. 2001) in Mediterranean areas. This measure, along with a careful control of river flow and water quality may increase the probability of amphibians to find suitable habitats during climate warming. Availability of freshwater habitats will be particularly important in the regions predicted to have high species loss, the northern Iberian Peninsula and main mountain systems, but also in extreme southern regions (Beja and Alcazar 2003).

Assisted colonisation has been suggested, as a measure to assist climate change adaptation (Mueller and Hellmann 2008). This triggered intense debate (McLachlan et al. 2007) because translocation of species originated catastrophic impacts in many existing cases. However, assisted dispersal is particularly relevant for amphibians and reptiles due to their low dispersal ability, and therefore we cannot disregard this management possibility under an extreme probability of extinction scenario. However, we agree with

(Hoegh-Guldberg et al. 2008) in that assisted dispersal should only be considered for a given species if at least one of a set of assumptions is met, namely: a) the species should be in immediate risk of extinction; b) species should have low dispersal ability; and c) the species range should be highly fragmented. Moreover, those authors suggest that translocations should only be undertaken within biogeographic regions, i.e., regions that share similar species composition, and an assessment of translocation risks should be performed previously, including ecological and socio-economical risks. Translocation risk should subsequently be balanced against those of extinction and safeguarded by detailed scientific understanding.

Protected areas have long been considered one of the most effective tools to conserve biodiversity (Rodrigues et al. 2004), but their effectiveness in securing species under rapid climate change is uncertain (Araújo et al. 2004). However they contribute to minimising threats such as, habitat destruction and fragmentation, road kills and pollution, which ultimately may assist to protect species threatened by climate warming. Therefore, it is important to evaluate if present protected areas would be effective in securing species given their predicted range shifts and whereas there is habitat connectivity between current and future species distributions. This could be achieved using reserve selection algorithms (e.g. Moilanen, 2009), which allow the identification the minimum set of areas necessary to represent all species at a given target. Ultimately, the ability of species to adapt to climate change within nature reserves will depend on the management actions undertaken in each of them. Reserve selection algorithms may also assist in identifying areas within nature reserves where the return of the management investment will be greater for a higher number of species.

If species are able to disperse to new habitats, than management actions will be needed to facilitate dispersal, including the increase of habitat connectivity, in particular of freshwater habitats.

Finally, biodiversity conservation can only be successful under climate change scenarios if socio-economical and environmental policies are integrated and if governments cooperate. Although climate change is a global issue, there is a tendency for actions to be taken by governments individually or by local administration, even with a common European environmental policy. It is recommended that the Portuguese and the Spanish governments embark on joint efforts to conserve Iberian biodiversity, particularly Iberian endemics.

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Appendix 7.1

Table S.7.1.1 - Maximum (Max), Minimum (Min) and standard deviation (STDV), of the number of occurrences predicted for each amphibian species in each year and in each storyline, within the 9 modelling methods and the 3 global circulation models.

	2020						**2050**						**2080**					
	A2			**B2**			**A2**			**B2**			**A2**			**B2**		
Species	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**
Alytes cisternasii	7293	71	2242.1	7535	34	2370.0	7207	2	2740.5	7023	8	2479.8	7602	0	2647.8	7602	0	2653.5
Alytes dickhilleni	5358	0	1406.3	5822	0	1795.8	5529	0	1792.7	5598	0	1695.5	7602	0	2315.4	7602	0	2305.5
Calotriton asper	7599	0	2858.6	7600	0	1755.6	4292	0	1090.9	7581	27	2156.2	7434	0	2258.4	7587	0	2203.3
Chioglossa lusitanica	1064	0	350.9	886	0	295.2	1584	0	391.5	7385	0	1393.2	3156	0	709.1	2428	0	524.7
Discoglossus galganoi	7420	0	2234.4	6310	0	1748.5	4614	0	1809.2	4777	0	1737.1	7602	0	2906.3	7602	0	2683.6
Discoglossus jeanneae	7602	228	2569.2	7602	374	2461.3	7602	776	2443.3	7602	749	2360.1	7602	197	3010.9	7602	710	2608.1
Lissotriton boscai	7595	1076	2196.3	7345	167	2069.3	7199	31	2082.1	7212	490	1917.1	7602	0	2607.7	7602	0	2444.6
Pelobates cultripes	7602	52	2273.2	7602	162	2235.3	7569	148	2406.4	7521	122	2220.9	7602	0	2709.4	7602	0	2592.4
Pelodytes ibericus	7387	13	2051.0	7584	268	2059.7	7516	509	2088.5	6857	22	1866.0	7519	0	2373.3	7328	0	2256.2
Pelophylax perezi	7601	372	2572.3	7602	347	2523.7	7602	315	2561.0	7602	311	2424.0	7602	0	2789.7	7602	0	2794.3
Pleurodeles waltl	7170	7	2255.1	7552	291	2124.8	7308	73	1997.5	7391	154	1912.2	7602	0	2568.5	7602	212	2544.5
Rana iberica	4186	7	1271.4	7511	0	1873.9	7413	0	1834.1	7503	0	2230.5	7515	0	2163.2	7544	0	2186.6
Rana pyrenaica	7487	0	2225.4	7389	0	1954.3	7466	0	2385.7	7590	0	2394.7	7548	0	2077.4	7490	0	2383.3
Triturus marmoratus	4589	0	1458.7	6450	0	1729.7	7313	0	1841.9	3889	0	1193.0	4473	0	1266.2	4179	0	1244.7
Triturus pygmaeus	7602	248	2386.1	7590	651	2141.6	7106	133	2218.2	7034	90	2155.6	7602	0	2720.7	7602	406	2336.6

Table S.7.1.2 - Maximum (Max), minimum (Min), and standard deviation (STDV), of the number of occurrences predicted for each reptile species in each year and in each storyline, within the 9 modelling methods and the 3 global circulation models.

	2020						2050						2080					
	A2			B2			A2			B2			A2			B2		
Species	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**	**Max**	**Min**	**STDV**
Blanus cinereus	7322	591	1676.3	7524	636	1693.2	7369	850	1707.5	6521	374	1691.0	7602	34	2593.4	7602	73	2157.2
Chalcides bedriagai	7598	53	2481.0	7148	268	2297.7	7409	299	2470.3	7376	111	2394.4	7602	20	3096.2	7602	63	2818.1
Chalcides striatus	7602	328	2238.7	7466	47	2164.6	7509	157	2316.2	7307	396	2121.2	7602	59	2565.4	7602	515	2502.4
Coronella girondica	7602	182	2662.8	7602	52	2788.2	7602	157	2599.1	7602	262	2676.9	7602	74	2992.2	7602	130	2815.2
Hemorrhois hippocrepis	6982	1380	1545.2	6359	902	1468.2	7281	1241	1835.1	7121	1208	1719.0	7602	0	2510.3	7602	0	2137.0
Iberolacerta aranica	463	0	122.1	2553	0	489.7	122	0	28.3	7493	0	1441.0	7600	0	1461.8	7592	0	1458.5
Iberolacerta aurelioi	7456	0	2368.1	7527	0	2390.1	7531	0	2401.9	7527	0	2377.6	7586	0	2414.6	7533	0	2400.6
Iberolacerta bonnali	7543	0	2406.0	7570	0	2413.6	7579	0	2420.1	7573	0	2402.6	7567	0	1459.5	7577	0	2418.1
Iberolacerta cyreni	7598	0	2327.3	7598	9	2324.0	7598	0	2320.5	7597	0	2343.6	7582	0	2331.2	7596	0	2393.4
Iberolacerta monticola	7510	0	2059.9	7446	0	1973.2	5825	0	1154.0	5002	0	982.8	6755	0	2171.6	6166	0	1612.7
Lacerta schreiberi	7378	361	2302.8	7235	0	2509.0	7325	0	2491.8	7291	58	2565.3	7602	0	2564.4	7313	0	2553.4
Podarcis bocagei	1609	0	527.1	1880	0	545.7	1786	0	561.8	1289	0	474.5	7602	0	1515.4	7602	0	1938.3
Podarcis carbonelli	7522	152	2816.1	7524	15	2654.5	7487	45	2465.4	6223	43	2142.9	7602	0	2742.7	7602	0	2703.4
Podarcis hispanica	7602	380	2543.7	7602	79	2739.4	7602	565	2756.7	7602	351	2626.6	7602	0	3080.0	7602	0	2922.5
Psammodromus algirus	7602	140	2737.2	7602	317	2747.0	7602	178	2833.4	7602	383	2740.9	7602	0	3224.3	7602	0	2889.7
Psammodromus hispanicus	7417	274	2760.3	7072	164	2697.7	7439	231	2974.2	7434	271	2867.7	7602	0	3164.2	7602	0	3026.3
Rhinechis scalaris	7602	372	2233.7	7602	82	2419.2	7602	1275	2299.2	7602	1538	2096.5	7602	0	2596.5	7602	0	2587.9
Timon lepida	7602	237	2466.0	7602	82	2709.5	7602	255	2772.4	7602	591	2616.2	7602	0	3121.7	7602	0	3022.9
Vipera latastei	7594	63	2148.9	6928	71	2270.8	7222	198	2178.5	7244	556	1811.9	7570	0	2997.2	7232	0	2838.1
Vipera seoanei	3144	0	643.7	949	0	265.2	3314	0	656.8	967	0	291.6	4931	0	967.9	4811	0	940.0

Photo: Vasco Flores Cruz

"Nothing is more difficult, and therefore more precious, than to be able to decide"

Napoleon Bonaparte

Chapter 8

Conservation Planning Under Climate Change:

Accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time

Sílvia B. Carvalho, José C. Brito, Eduardo J. Crespo, Matthew E. Watts & Hugh P. Possingham

8.1 Abstract

Climate warming challenges our approach to building systems of protected areas because it is likely to drive accelerating shifts in species distributions, and the predictions of future species distributions are uncertain. There are two important sources of uncertainty intrinsic to using species occurrence predictions for reserve system design: uncertainty in the number of occurrences captured by any reserve selection solution, and uncertainty arising from the different approaches used to fit predictive models. Here we used the present and future predicted distributions of Iberian herptiles to analyze how dynamics and uncertainty in species distributions may affect decisions about resource allocation for conservation in space and time. We identified priority areas maximizing coverage of current and future (2020 and 2080) predicted distributions of 65 species, under mild and severe uncertainty. Next, we applied a return-on-investment analysis to quantify and make explicit trade-offs between investing in areas selected when optimizing for different times and with different uncertainty levels. Areas identified as important for conservation in every time frame and uncertainty level were the ones considered to be robust climate adaptation investments, and included chiefly Iberian mountains. Areas identified only under mild uncertainty were considered good candidates for investment if extra resources are available and were mainly located in northern Iberia. However, areas selected only in the severe uncertainty case should not be completely disregarded as they may become climatic refugia for some species. Our study provides an objective methodology to deliver “no regrets” conservation investments.

8.2 Introduction

Systematic conservation planning (Margules and Pressey 2000; Margules and Sarkar 2007; Moilanen et al. 2009c) is a framework developed to identify efficient conservation areas with clearly stated quantitative objectives of species representation and persistence. Reserve selection algorithms used within this framework are computational tools that seek to efficiently allocate limited resources available for conservation (see Moilanen et al. 2009b for review).

Reserve selections algorithms tacitly assume that observations or predictions of species occurrences are complete and certain (e.g. Gaston and Rodrigues 2003; Grand et al. 2007; Wilson et al. 2005) and that species distributions are static in space and time (Drechsler et al. 2009; Possingham et al. 2009). However, none of these assumptions are realistic. Observed data on current species distributions are frequently incomplete and rely on multiple sources of uncertainty (see Carvalho et al. 2010b; Regan et al. 2009; Rondinini et al. 2006 for ideas and discussion). Ideally, areas selected for conservation should be locations combining high conservation value with low uncertainty (Moilanen et al. 2006a). Despite this, uncertainty in species distributions was seldom taken into account in reserve selection studies (but see Carroll et al. 2009; Fuller et al. 2008; Halpern et al. 2006; Hodgson et al. 2009; Langford et al. 2009; Moilanen et al. 2006b), probably because of methodological complexity. Moreover, human-induced changes are leading to a more dynamic geographic rearrangement of biodiversity and to species extinctions (McCarty 2002; Root et al. 2003; Sala et al. 2000; Thomas et al. 2004; Walther et al. 2002). Climate warming, in particular, has been recently declared as a major challenge to conservation planning, because several studies predicted that it will cause species to shift their range away from current protected areas (e.g, Araújo 2009b; Araújo et al. 2004; Hannah et al. 2007), while areas that are unprotected now may become more important for conservation actions if we are to achieve adequate and representative species conservation in the future (Barry and Elith 2006; Buisson et al. 2010).

To overcome the problem of data incompleteness and to predict future species ranges, Species Distribution Models (SDMs) are frequently used. SDMs are statistical tools that quantify the relationship between observed species occurrences and their habitat (Franklin 2009; Guisan and Zimmermann 2000). This statistical relationship is then used to predict species occurrences in sub sampled locations or under future climate scenarios. Although several advantages of using SDMs predictions in conservation planning have been acknowledged (e.g. Araújo 2009a; Elith and Leathwick 2009a), they should be used with caution as they also introduce uncertainty when used in reserve selection algorithms.

One important source of uncertainty derived by SDM predictions is the variance in the expected number of occurrences for a species resulting from the use of probabilities of occurrence (Moilanen and Cabeza 2005). SDMs predictions usually describe the probability of a species being present in a given location, with values ranging from zero to one. This probabilistic information allows planners to discern between sites of different habitat quality, which may be useful for achieving persistence goals (Araújo and Williams 2000). However, the straightforward use of probabilities of occurrence adds statistical uncertainty to the reserve selection problem. For example, if we select two planning units each of which with a 50% chance of containing the species, and those probabilities are independent, then, on average, one occurrence of the species is conserved, but there is a 25% chance we fail to conserve the species. In contrast, if we select two planning units where in one of them the probability of occurrence of the species is 100% and the other is 0%, on average, one occurrence of the species is conserved also, but in this case there is 100% certainty that one occurrence is conserved. Generally, reserve selection algorithms aim to capture the average number of species occurrences, ignoring uncertainty. Consequently, solutions found may often contain many sites that have intermediate probabilities, and high uncertainty (Moilanen and Cabeza 2005).

SDMs predictions are also subject to considerable uncertainty arising from the different possible mathematical approaches used to fit the models – the probabilities themselves are uncertain (Araújo and New 2007; Elith et al. 2006; Elith and Leathwick 2009b). This limitation is even more evident when predicting future species distributions under climate change because, in this case, uncertainty also arises from models used to predict future climatic conditions (Beaumont et al. 2008; Buisson et al. 2010; Pearson et al. 2006; Thuiller 2004), and from uncertainty in species dispersal abilities (Hodgson et al. 2009; Pearson and Dawson 2003). Distinct SDM predictions would produce considerably different solutions when used in a reserve selection algorithm and this prediction variability compromises their usefulness in guiding conservation decisions (Araújo and New 2007). Thus, quantifying and accounting for uncertainty in predictions about the distribution of species is critical for natural resource managers to effectively integrate climate change considerations into spatial conservation priority setting (Moilanen et al. 2006a; Moilanen et al. 2006b; Regan et al. 2009).

There are different tools to account for uncertainty in making decisions and several of them have been applied in the conservation field (Halpern et al. 2006; Regan et al. 2009). For instance, scenario analysis (Peterson et al. 2003) assists decision-makers in testing different management scenarios and making strategic decisions. When coupled with a return-on-investment analysis, scenario analysis highlights the benefits of alternative investment options and can be used to strategically maximize conservation gains (Murdoch et al. 2007).

Amphibians and reptiles are taxonomic groups believed to be very vulnerable to climate change (Araújo et al. 2006; Carey and Alexander 2003; Gibbons et al. 2000; Wake 2007). This is particularly true for the Iberian Peninsula where several species are predicted to have their future distribution entirely or severely reduced (Araújo et al. 2006; Carvalho et al. 2010a).

However, predictions of the distributions of species were significantly variable among different modeling techniques when different future climatic predictions were assumed and even more variable when different dispersal scenarios were considered (Araújo et al. 2006; Carvalho et al. 2010a). These critical but uncertain projections pose considerable challenges to conservation. In face of uncertainty, some recommend that the best strategy is the one that assumes the worst case scenario (Cooney 2004; Steele 2006). However, this approach may prevent us from investing in species predicted to completely lose their range (Bottrill et al. 2008) and defining exactly what is "worst case" is problematic. Such a strategy would need to be very confident that the predictions about future distributions are really true. Conversely, deciding to invest conservation efforts in a valuable but uncertain location may result in a waste of resources. Thus, the best decision should be a trade-off between the predicted range of conservation values of each location over a particular time period, and the certainty of the models and data.

Because decision-makers need to choose how best to invest limited climate adaptation resources, the aim of this study is to illustrate a methodology to account for uncertainty in species distributions and make trade-offs in investment options explicit. What will be the gain and loss if one decides to allocate resources to high value but risky areas rather than areas where we are very certain of the information? The most confident investment will be in areas that are 1) consistently identified as belonging to a near-optimal investment option across different scenarios (Moilanen et al. 2006a); and 2) identified as maximizing the return of investment in most scenarios.

To achieve our goals, we developed a modified version of the software Marxan (Ball et al. 2009), which is a decision support tool for spatial conservation prioritization. This modified version deals with uncertainty in the expected number of occurrences, assuring that species' occurrence targets are met with a selected level of confidence - e.g. a species meets its conservation target with a 90% chance. Subsequently, we use scenario analysis to identify important areas for conservation under different uncertainty assumptions and for multiple times. Finally, we use return-on-investment thinking to evaluate the relative benefits of competing investment options.

8.3 Methods

8.3.1 Study area

The study region is the continental Iberian Peninsula (Appendix 8.1), situated in the extreme southwest of Europe (bounded by 9º32' to 3º20'E and 35º56' to 43º55'N). With an area of 582 860 km^2, it includes the continental territories of Portugal and Spain.
The study area was divided into 7 603 ten square kilometer grid cells, hereafter referred as planning units (PUs).

8.3.2 Protected areas data

The location of protected areas is essential for evaluating the existing reserve system, and identifying gaps in protection. Data on existing protected areas was compiled from three digital sources: a) the world data base on protected areas (IUCN and UNEP-WCMC 2010); b) Instituto da Conservação da Natureza e da Biodiversidade (ICNB), for Portuguese protected areas (http://portal.icnb.pt) and c) Spanish Ministerio de Medio Ambiente y Medio Rural y Marinho (http://www.mma.es), for Spanish protected areas. Protected areas missing from all cited sources were digitized from topographical maps. Spain has many kinds of conservation tenure. In this study, only National Parks, Nature Parks, Regional Parks, Nature Reserves, Integral Nature Reserves, Microreserves, Partial Nature Reserves, Wildlife reserves and Natura 2000 sites were considered.

8.3.3 Scenarios and species distribution data sets

We built eight data sets containing species probabilities of occurrence under six scenarios, combining three times - present, 2020 and 2080 - with two uncertainty levels – Mild and Severe (Figure 8.1). Methods used to assemble the eight data sets are described next.

To predict the probability of occurrence of each species in each planning unit in the present time and for the years 2020 and 2080, we used SDMs for 37 endemic and nearly endemic Iberian amphibian and reptile species described in Carvalho et al. (2010). We applied the same methodology to make similar predictions for the remaining 28 amphibian and reptile species occurring in that area (see Appendix 8.2 for the complete list of species). Species distributions for the present time were predicted using nine modeling techniques (Figure 8.1). Species distributions for the years 2020 and 2080 were predicted by projecting present relationships between species distributions and current climatic conditions determined by each of the nine model techniques for six future climatic scenarios, combining two IPCC storylines (A2 and B2) and three Global Circulation Models (CCCM3, CSIRO and HADCM3), leading to a total of 54 (= 9×2×3) predictions of each species' distribution.

Probabilities of occurrence for a species in each PU and time can be quite similar or fairly different when predicted with different modeling techniques, Global Circulation Models and storylines. The highest and the lowest probability of occurrence for a species in each planning unit for a given time, frame an uncertainty interval. The higher the difference between the two extremes, the higher the uncertainty in the prediction of probability of occurrence. Ensemble forecasting attempts to reduce uncertainty in these multiple predictions by calculating a consensual solution (Araújo and New 2007), and methods based on average function algorithms are believed to increase significantly the accuracy of species distribution predictions (Marmion et al. 2009). Thus, we build the "Mild uncertainty" scenarios by calculating the weighted average consensus based on AUC values (Marmion et al. 2009). However, these average predictions do not consider how far the average is from the extremes. Hence, to account for extent of variation between

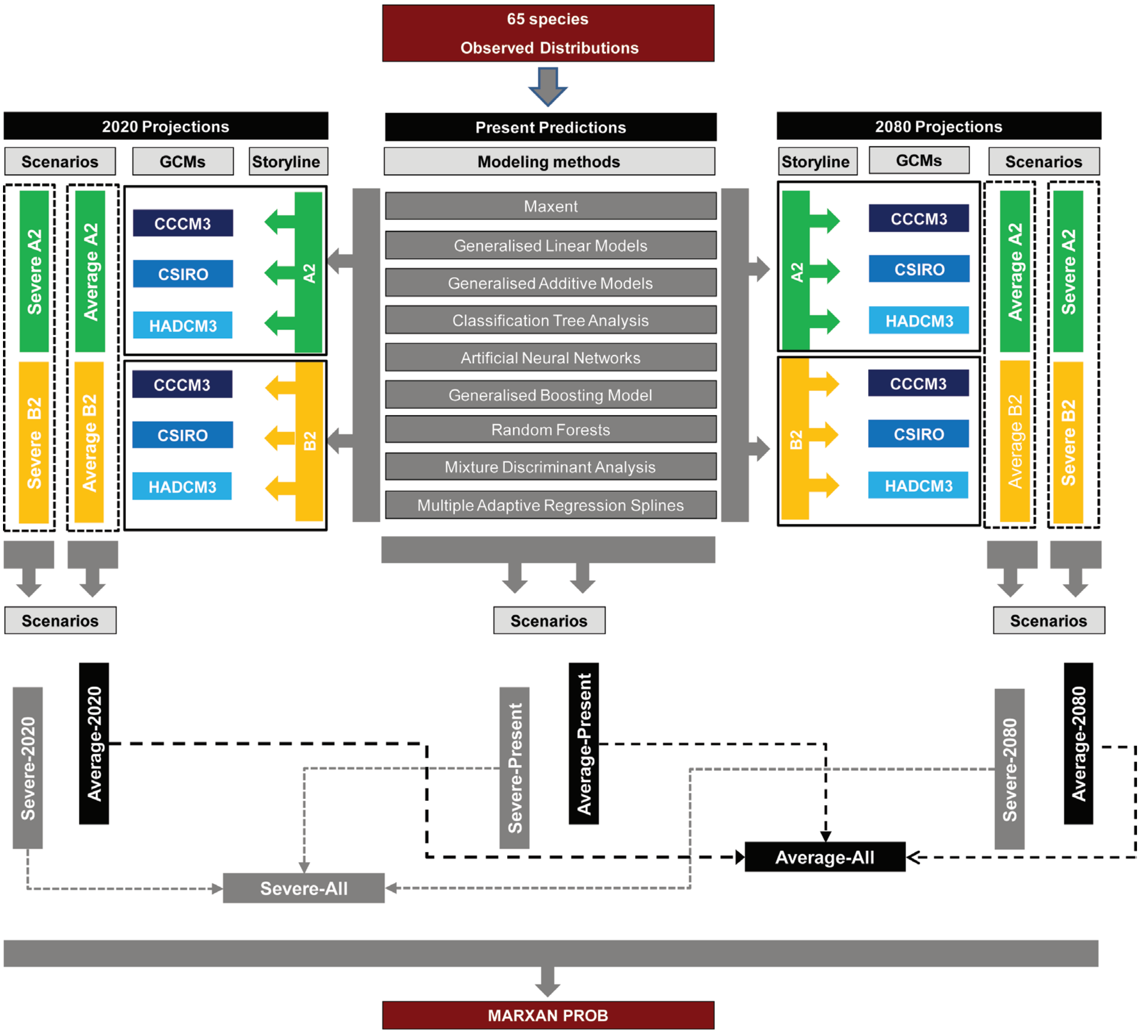


Figure 8.1 - Schematic representation of the methodology used to build the species distribution data sets used to selected priority areas for conservation under six combined time-uncertainty scenarios. Complete present distributions of 65 species were predicted from observed occurrences and current climatic conditions, using nine modeling methods. Future distributions were predicted by projecting the predictive models to the years 2020 and 2080 under six different climatic scenarios combining two IPCC storylines and three Global Circulation Models. Predicted distributions were ensembled for each time and under two uncertainty scenarios –Mild and Severe uncertainty.

models in each time, we built a second scenario, which we called "Severe uncertainty", where the probability of occurrence of a species in a planning unit was reduced by the uncertainty in that probability (following the distribution discounting methodology proposed by Moilanen et al. 2006b). As a measure of uncertainty, we used one standard deviation of the probabilities of occurrence predicted by model in each planning unit.

Ensembles of future species distributions were first made separately for storylines A2 and B2. These predictions were joined in order to obtain only one data set for each time. Hence, data sets for 2020 and for 2080 contained two predictions for each species (one for storyline A2 and another for B2), thereby creating a total of 130 conservation features that need protection. The rationale underlying this procedure was to ensure that the solutions attained by the reserve selection algorithm achieved species targets in each time-scenario regardless of the storyline. We also built other data sets containing all five predictions for each species, in each uncertainty scenario: one prediction for the present, two predictions for 2020 and two predictions for 2080. Accordingly, the rationale to produce these data sets was to ensure that solutions attained by the reserve selection algorithm achieved conservation targets for all species at all three times, regardless of the storyline.

This way, we obtained eight data sets containing the predicted probability of occurrence of each species in each planning unit: six with predictions for a given time and separately for different levels of uncertainty (Mild-Present, Mild-2020, Mild-2080, Severe-Present; Severe-2020 and Severe-2080) and two with predictions for the three times simultaneously and separately for different uncertainty levels (Mild-All and Severe-All) (Figure 8.1).

8.3.4 Identifying near-optimal investment options within and across scenarios

We used a "minimum set" approach (Moilanen et al. 2009a) to identify the near-optimal set of areas for conservation investment for each of the eight species distribution data sets. Predictions of probabilities of species occurrences were used as input data into a modified version of the software Marxan (Ball et al. 2009), developed to deal with uncertainty in the variance in the expected number of occurrences. The main difference of the modified version is that it has a new term on the objective function which penalizes solutions that do not achieve the occurrence target with a desired level of certainty. The new term in the objective function also includes a weighting factor which allows balancing penalties for not achieving level of certainty against the other terms of the objective function. This weighting factor is hereafter referred as "probability weighting" (see Appendix 8.3 for details on modified version of Marxan).

In the present study, we set species occurrence targets as 10% of the number of planning units where each species is currently predicted to occur and the level of certainty of reaching that target at 50% for all species. To run Marxan, we used the following parameters: algorithm - simulated annealing; number of runs - 100; penalty cost for not achieving the occurrence target - 1; iterations per simulation – 10 000 000; temperature decreases per simulation – 10 000; initial temperature and cooling factor - adaptive. Probability weight was set to 100 and the boundary length modifier to 0.1 after a preliminary sensitivity analysis.

Species conservation and management will be more efficient in the future if we are able to allocate resources to intensively managed existing protected areas instead of managing areas outside them or designating new ones. Thus, in order to favour the selection of currently protected planning units, we set the cost of protected planning units as half that of the non protected ones. We considered a planning unit protected if it had more than 10% of its area inside a currently designated protected area or a Natura 2000 site.

For each of the eight species distribution data sets, we identified the best set of planning units selected out of the 100 Marxan runs. Sunsequently, we overlapped the planning units found in those best solutions in order to identify those planning units selected in multiple solutions. We used this procedure to find planning units selected concurrently in present, 2020 and 2080 scenarios (which we refer to as the T1 set) and concurrently in 2020 and 2080 scenarios (which we refer to as the T2 set). We used this procedure separately for each of the uncertainty scenarios, resulting in four solutions: overlap T1M and overlap T2M for the Mild uncertainty scenarios, and overlap T1S and overlap T2S for the Severe uncertainty scenarios. We also identified planning units selected in both uncertainty scenarios in each of the three times separately (we refer to these as the overlap UPresent, U2020 and U2080) and for the three times simultaneously (overlap UAll). Finally we identified those planning units selected concurrently in both uncertainty scenarios and in all three times (overlap T1U), and planning units selected in both uncertainty scenarios and in both 2020 and 2080 scenarios (overlap T2U).

8.3.5 Evaluating the relative benefits of competing investment options

In order to evaluate the relative benefits of investing conservation resources in a particular solution, we analyzed the overall performance of each solution in achieving all species targets, and the performance in achieving each species target individually.

We started by evaluating the cost-effectiveness of different solutions by measuring two metrics:

a) Summed probability of achieving occurrence target (*Sp*) – measures the probability of each species meeting the occurrence target, summed across all species. For data sets where we had more than one prediction per species per planning unit (scenarios 2020, 2080 and All), we calculated the average probability of each species meeting the target. The value of *Sp* approaches the number of species (65) when all species achieve their level of certainty, and approaches zero when no species achieve their level of certainty;

$$Sp = \sum_{j=1}^{65} S_j = \sum_{j=1}^{65} (1 - P_j) \qquad \text{(expression 8.1)}$$

, where *j* is the index for species and *Pj* is the probability of species *j* not achieving the occurrence target.

b) Efficiency (E) – measures the efficiency of any solution by dividing *Sp* by its cost:.

$$E = \frac{Sp}{\sum_{i}^{7603} X_i C_i} \qquad \text{(expression 8.2)}$$

,where *j* is the index for the planning units, $X_i = 1$ if a planning unit is in the Marxan best solution (zero otherwise) and C_i is the cost of planning unit *i*.

These metrics allow us to identify the best possible investment in each scenario, if we knew correctly which uncertainty scenario, Mild or Severe, will occur in the future. Thus, because we are considering two uncertainty scenarios, to make a smart decision, we need to minimize the waste of resources if an alternative scenario to the one planned for takes place. Thus, the questions we need to answer are: Which species and how much of their ranges will we be covering if we optimize the selected planning units for a specific uncertainty scenario and the alternative takes place? In essence, how wrong could we be?

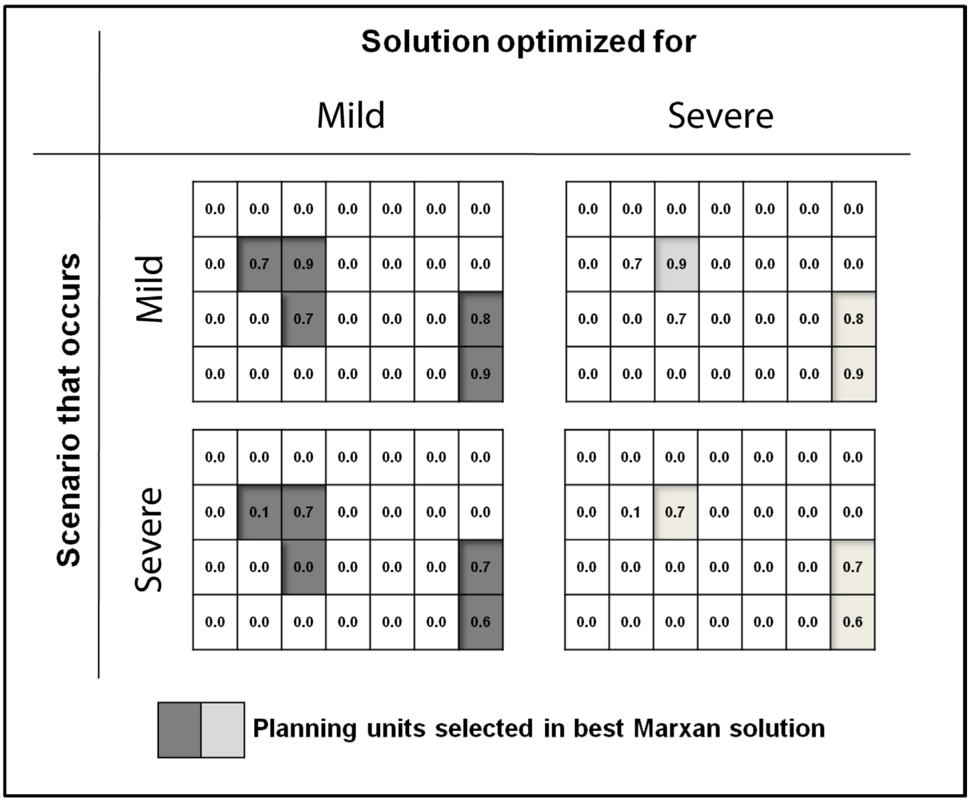
To answer these questions, we evaluated the performance of the planning units selected when optimizing the solution for a given uncertainty level (Mild or Severe uncertainty) assuming that the alternative occurs (Figure 8.2). We expect to achieve better performances when the scenario optimized for, and the scenario that actually occurs, are the same.

We can think of a "no regrets" or robust strategy as one where we invest in planning units that are selected in all six scenarios (every combination of time and level of uncertainty). It is interesting to see which species are adequately conserved in a "no-regrets" solution. To answer this question we analyzed the performance of the Overlap T1U solution in achieving targets for species individually. This approach allows decision-makers to identify which species would be covered by conservation investment if they decided to invest in sites over which that there is no doubt they are valuable. Also, the knowledge of which species are covered by this solution and the ones which will only be covered by investments that are less certain, will allow decision makers to favor, or otherwise, particular species in conservation management once the "no regrets" actions are taken. Thus, for the Overlap T1U solution, we analyzed the probability of each species meeting the level o certainty (*Sj*). We repeated the same approach for the extra planning units only selected when optimizing for the Mild uncertainty scenario, and for the extra planning units only selected when optimizing for the Severe uncertainty scenario. Similarly to the evaluation we made for the overall solution, we calculated the probability of each species achieving the occurrence target, first assuming that the uncertainty scenario that we optimized the solution is the one that will occur, and subsequently assuming that the opposite scenario is the one that will occur (Figure 8.2).

8.4 Results

8.4.1 Identifying near-optimal investment options within and across scenarios

We identified priority areas for conservation of amphibians and reptiles in the Iberian Peninsula for each of the eight data sets (Figure 8.3). The number and location of planning units selected varied between scenarios. The number of planning units required to achieve targets increased through time, i.e, more planning units were selected in the 2080 scenarios than in the present and 2020 scenarios. Also, the number of currently non protected planning units selected increased considerably through time (Figure 8.4). The number of planning units necessary to simultaneously achieve targets in all of three times was about twice the number needed to achieve targets in the present, both in the Mild and Severe uncertainty scenarios.



Solution optimized for Mild – Scenario that occurs Mild:

0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.7	0.9	0.0	0.0	0.0	0.0
0.0	0.0	0.7	0.0	0.0	0.0	0.8
0.0	0.0	0.0	0.0	0.0	0.0	0.9

Solution optimized for Severe – Scenario that occurs Mild:

0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.7	0.9	0.0	0.0	0.0	0.0
0.0	0.0	0.7	0.0	0.0	0.0	0.8
0.0	0.0	0.0	0.0	0.0	0.0	0.9

Solution optimized for Mild – Scenario that occurs Severe:

0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.1	0.7	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.7
0.0	0.0	0.0	0.0	0.0	0.0	0.6

Solution optimized for Severe – Scenario that occurs Severe:

0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.0	0.1	0.7	0.0	0.0	0.0	0.0
0.0	0.0	0.0	0.0	0.0	0.0	0.7
0.0	0.0	0.0	0.0	0.0	0.0	0.6

Figure 8.2 - Schematic example of the methodology used in the evaluation procedure. The performance of the solutions attained when optimizing for the Mild uncertainty scenario were evaluated assuming that the Mild uncertainty scenario will occur or that the Severe uncertainty scenario will occur. The same method was applied to the solution found when optimizing for the Severe uncertainty scenario. The numbers in the figure are hypothetical predicted probabilities of occurrence of a species and grey shadows represent hypothetical selected Pus.

A large number of planning units (1155) were selected in every scenario (overlap T1U) – the “no-regrets” planning units. These planning units were mostly located in mountains such as the Cantabrian, Central System, Morena, Nevada, Burgos, Peneda-Gerês, Alvão, and Montesinho (Appendix 8.1). There were other less mountainous areas with concentrations of “no regrets” planning units, such as Southwestern Portugal, Southern Spain (around the Strait of Gibraltar) and Northeastern Portugal (along the border with Spain). A substantial proportion of the planning units selected in overlap T1U were already protected (1079 PUs) including the large nature parks of study area, Sierra de Aracena y Picos de Aroche, Doñana, Los Alcornocales, Sierras de Andújar, Sierras de Cazorla, Segura y Las Villas and Baixa Limia-Serra do Xurés (in Spain) and Peneda-Gerês, Vale do Guadiana and Sudoeste Alentejano e Costa Vicentina (in Portugal) (Appendix 8.1).

Planning units selected in the Mild uncertainty scenarios but not in the Severe uncertainty ones, were chiefly located along Northern Iberian Peninsula (red areas in Figure 8.3), while planning units selected in the Severe uncertainty scenarios but not in the Mild ones were mainly located on the Northwestern and southern Iberian Peninsula (around the Strait of Gibraltar) and some scattered planning units along the Southeastern and Northern coasts (yellow areas in Figure 8.3).

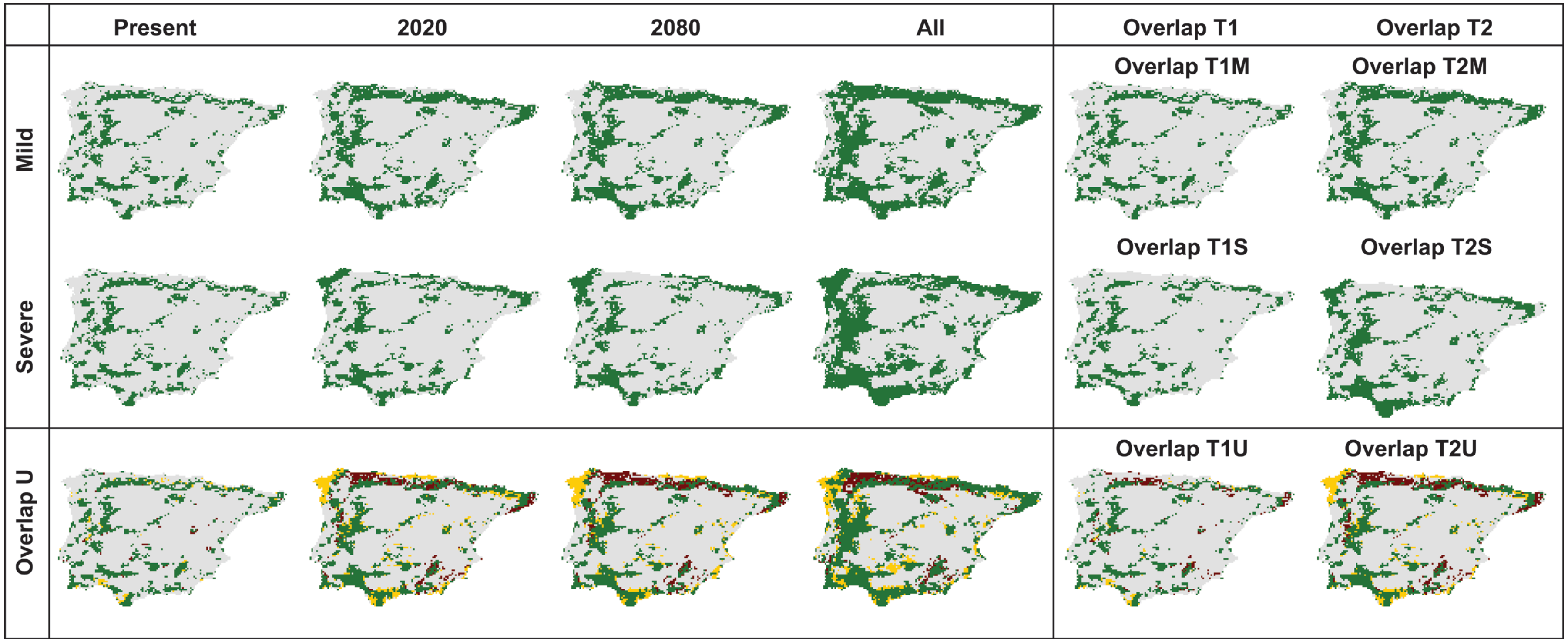


Figure 8.3 - Planning units selected when optimizing for each time-uncertainty scenario, and planning units selected concurrently in different scenarios: Overlap T1 represents planning units common to present, 2020 and 2080 scenarios in each uncertainty scenario; Overlap T2 represents planning units common to 2020 and 2080 scenarios in each uncertainty scenario. Overlap U represents planning units common to Mild and Severe uncertainty scenarios (dark green), planning units selected only in the Mild uncertainty scenario (red), and planning units selected only in the Severe uncertainty scenario (yellow). Overlap T1U represent planning units selected in both uncertainty scenarios and common to present, 2020 and 2080 solutions and Overlap T2U represent planning units selected in both uncertainty scenarios and common to 2020 and 2080 solutions.

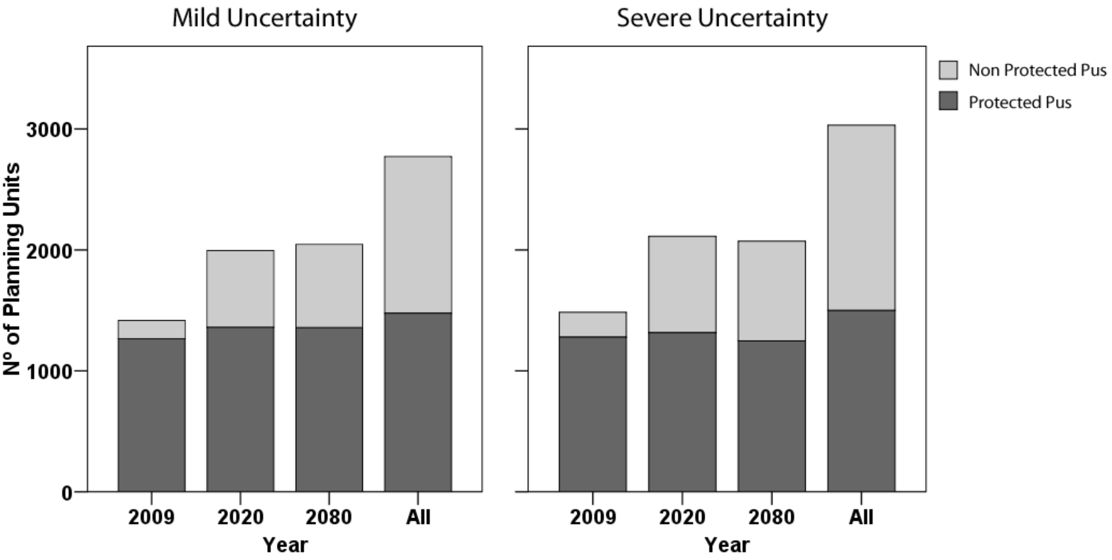


Figure 8.4 - Number of protected and non protected planning units selected in each time (present, 2020 and 2080) and in all times simultaneously (All).

8.4.2 Evaluating the relative benefits of competing investment options

The performance of the selected planning units varied through time and uncertainty scenarios (Figure 8.5).

The planning units selected attained good performance in terms of probabilities of achieving occurrence targets for the present climate, as *Sp* values (our measure of protected area performance) were close to 65 (the maximum possible value). However, such good performances were not achievable with the solutions found for the 2020 and the 2080 scenarios. The performance was even worse if we assumed that the severe uncertainty scenario is the one that will occur.

As expected, *Sp* values were always equal or higher when the uncertainty scenario that we optimize for and the one actually occurring were the same than when they were different. For example, assuming that the Mild scenario occurs, *Sp* values when we optimized the Marxan solution for the Mild uncertainty were similar to the ones obtained when optimizing for the Severe uncertainty scenario. Differences between performances achieved by the solutions were more pronounced when we assumed that the Severe uncertainty scenario will occur: we always achieved higher *Sp* values when we optimized for the Severe uncertainty scenario than when we optimized for the Mild one. However, efficiency results indicate that solutions obtained when we plan for the Mild scenario are always more cost-efficient, as *E* achieved higher values, regardless of the uncertainty scenario occurring.

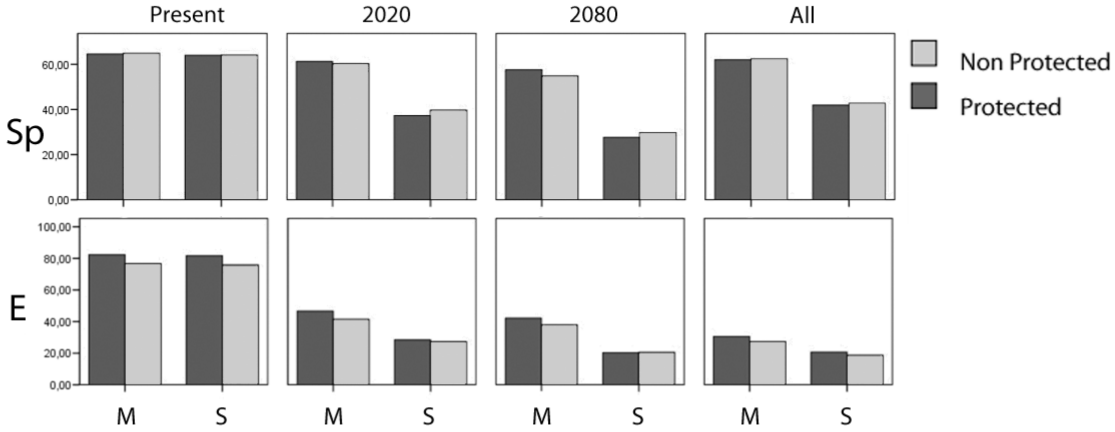


Figure 8.5 - Values obtained by summed probability of achieving occurrence target (*Sp*) and Efficiency (*E*) in each time scenario (Present, 2020, 2080 and All) assuming that a given uncertainty scenario will occur (M-Mild and S-Severe).

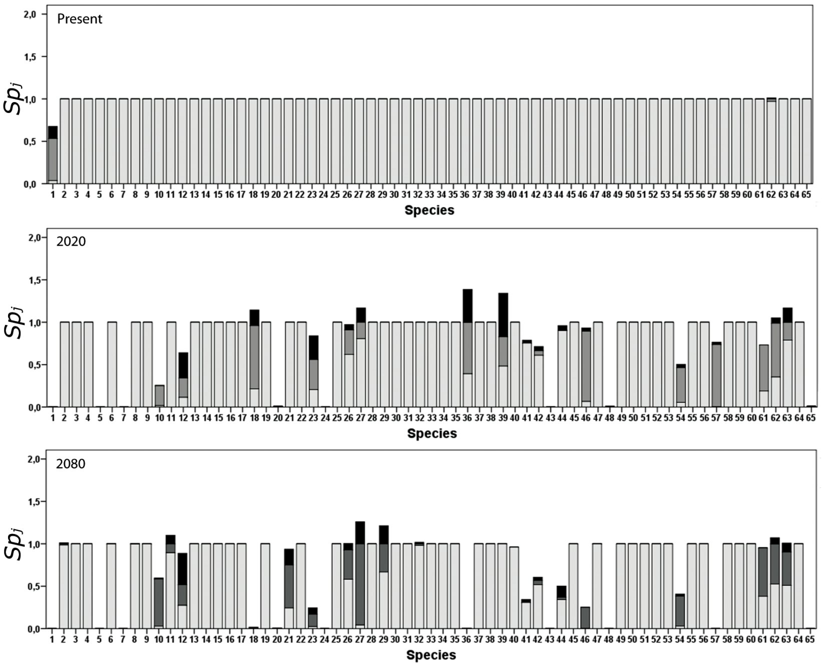
8.4.3 Evaluating which species would be covered and which would be missed

If we only conserve the no-regrets planning units (overlap T1U) then most species achieve their occurrence targets with high probability assuming their distribution does not change in the future (Figure 8.6). The only exceptions were *C. lusitanica* and *T. hermanni* (for both uncertainty scenarios) and *T. graeca* (if the Severe uncertainty scenario occurs). However, if we consider future predicted distributions, with the "no regrets" planning units, most species will not meet their occurrence targets with a high probability. For example, if we consider species distribution predictions for 2020, 19 species will have a less than a 50% chance of reaching their occurrence targets with the no-regrets solution, in both Mild and Severe uncertainty scenarios. Moreover, 27 other species will also have less than a 50% probability of achieving the occurrence target if the Severe uncertainty scenario occurs. The performance of the "no regrets" solution is even more reduced when we consider species distributions predictions for 2080, since 21 species will have very reduced probability of achieving the occurrence target (prob<0.5) regardless of the uncertainty scenario that occurs. If the Severe uncertainty scenario is the one that occurs, only five species will have a better than 50% chance of achieving their occurrence target in 2080.

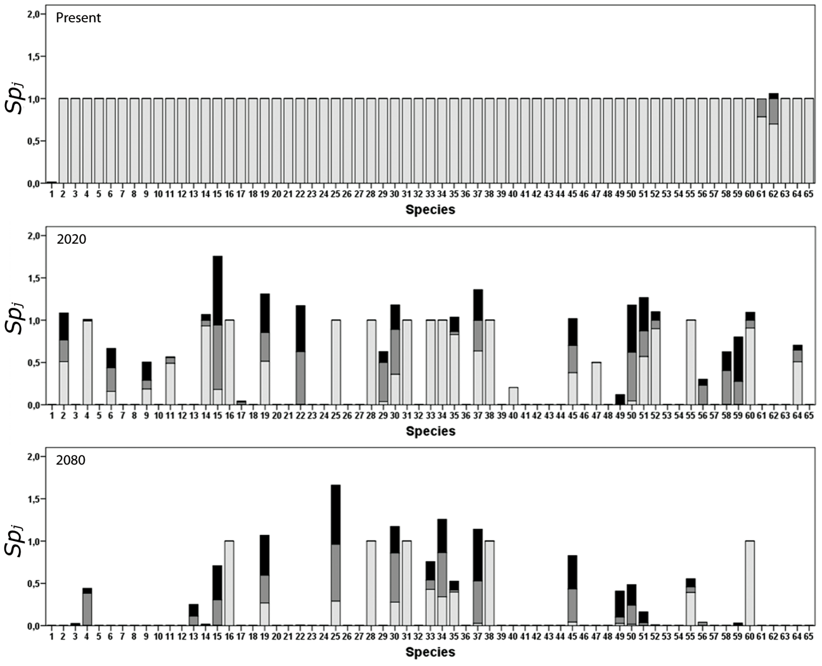
It is noteworthy that even the concurrent solution to all time-scenarios in each uncertainty scenario (overlaps T1M and T1S) are not enough for all species to achieve the occurrence target with high probability, particularly considering species distributions predictions for 2020 and 2080. Examples of species with reduced probabilities of achieving occurrence targets (prob < 0.5) are: *C. lusitanica*, *M. alpestris*, *L. helveticus*, *R. dalmatin*a, *R. temporaria*, *L. bilineata*, *Z. vivipara*, *P. bocagei* and *V. seoanei*.

Another interesting result is that the expected representation of each species varies

a) Mild uncertainty



b) Severe uncertainty



■ Probability of each species achieving the occurence target when selecting PUs identified exclusivelly in the Severe uncertainty scenario

▨ Probability of each species achieving the occurence target when selecting PUs identified exclusivelly in the Mild uncertainty scenario

□ Probability of each species achieving the occurence target, when selecting PUs identified both in the Mild and Severe uncertainty scenarios

Species
1 *Chioglossa lusitanica*
2 *Calotriton asper*
3 *Pleurodeles waltl*
4 *Salamandra salamandra*
5 *Mesotriton alpestris*
6 *Lissotriton boscai*
7 *Lissotriton helveticus*
8 *Triturus marmoratus*
9 *Alytes cisternasii*
10 *Alytes dickhilleni*
11 *Alytes obstetricans*
12 *Discoglossus galganoi*
13 *Discoglossus jeanneae*
14 *Pelobates cultripes*
15 *Pelodytes punctatus*
16 *Bufo bufo*
17 *Bufo calamita*
18 *Hyla arborea*
19 *Hyla meridionalis*
20 *Rana dalmatina*
21 *Rana iberica*
22 *Pelophylax perezi*
23 *Rana pyrenaica*
24 *Rana temporaria*
25 *Acanthodactylus erythrurus*
26 *Algyroides marchi*
27 *Anguis fragilis*
28 *Blanus cinereus*
29 *Coronella austriaca*
30 *Coronella girondica*
31 *Coluber hippocrepis*
32 *Coluber viridiflavus*
33 *Chalcides bedriagai*
34 *Chalcides striatus*
35 *Chamaeleo chamaeleon*
36 *Zamenis longissima*
37 *Rhinechis scalaris*
38 *Emys orbicularis*
39 *Hemidactylus turcicus*
40 *Lacerta agilis*
41 *Iberolacerta aranica*
42 *Iberolacerta aurelioi*
43 *Lacerta bilineata*
44 *Iberolacerta bonnali*
45 *Timon lepida*
46 *Iberolacerta monticola*
47 *Lacerta schreiberi*
48 *Zootoca vivipara*
49 *Macroprotodon brevis*
50 *Malpolon monspessulanus*
51 *Mauremys leprosa*
52 *Natrix maura*
53 *Natrix natrix*
54 *Podarcis bocagei*
55 *Podarcis carbonelli*
56 *Podarcis hispanica*
57 *Podarcis muralis*
58 *Psammodromus algirus*
59 *Psammodromus hispanicus*
60 *Tarentola mauritanica*
61 *Testudo graeca*
62 *Testudo hermanni*
63 *Vipera aspis*
64 *Vipera latasti*
65 *Vipera seoanei*

Figure 8.6 - Probability of each species meeting the occurrence target (*Sj*) in each time scenario and assuming that a given uncertainty scenario will occur: a) Mild and b) Severe. For each species it is represented the probability of achieving the occurrence target by the planning units selected when optimizing both for the Mild and Severe uncertainty scenarios and by the planning units selected exclusively when optimizing for one of those scenarios.

according to the scenario that we optimized the solution for and according to the scenario that actually occurs. For example, if the Mild uncertainty scenario is the one that actually occurs, species such as *A. dickhilleni, H. arborea*, *R. iberica*, *R. pyrenaica*, *A. marchi*, *A. fragilis*, *Z. longissima*, *I. monticola*, *P. bocagei*, *P. muralis*, *T. graeca*, *T. hermanni* and *V. aspis* achieve significantly higher probabilities of meeting the occurrence targets with the concurrent solution optimized for the Mild scenarios (overlap T1M) than with the concurrent solution optimized for the Severe uncertainty scenario (overlap T1S). However, other species reach higher probabilities of meeting the targets with units selected concurrently in present, 2020 and 2080 scenarios under the Severe uncertainty scenario overlap T1S (*D. galganoi*, *H. turcicus*, *I. aranica* and *I. bonnali*). Curiously, if the Severe uncertainty scenario is the one that actually occurs, the concurrent solution when optimizing for the Mild uncertainty scenario (T1A) achieves better performance for several species. For example, considering the 2020 predictions, *L. boscai*, *A. obstetricans*, *B. calamita*, *P. perezi*, *C. austriaca*, *C. girondica*, *M. monspessulanus*, *P. hispanica*, *P. algirus* and *V. latasti* achieve significant higher probabilities of meeting the occurrence targets with overlap T1M then with overlap T1S. A similar result was observed for *S. salamandra*, *C. girondica*, *C. striatus* and *P. hispanica*, considering species distributions predicted for 2080.

8.5 Discussion

In this study we used the Iberian herptiles present and future predicted distributions to analyze how uncertainty in species distributions may affect decisions about resource allocation for conservation in space and time. Our approach allowed us to quantify and make explicit trade-offs between investing in different locations, optimized according to three time frames and two levels of uncertainty.

Our findings indicate that the current protected areas are nearly sufficient to cover 10% of the current distribution of all studied species, however, a different result is expected under future climates. Indeed, contractions and rearrangements of species distributions due to climate warming will make the current protected areas ineffective in achieving representation goals. Our results indicate that to continue representing 10% of the distribution of the amphibians and reptiles in the future decades, we will need to make the protected area estate 1.4 to 2.0 times bigger. However, even if current protected areas are expanded that much, it will not be possible to meet occurrence targets for some species because their distribution in the Iberian Peninsula is predicted to contract to less than 10% of their current range.

Predictions that an increase in protected areas will be necessary to maintain species representation targets in the future have been reported in other studies, focusing on different species and places (e.g, Araújo 2009b; Coetzee et al. 2009; Hannah et al. 2007; Hole et al. 2009). Investment in protection of such large areas is probably an impractical objective within the current economical and social context. Thus, identifying and prioritizing investment options within these areas is mandatory (Murdoch et al. 2007).

Priority of investment should be given to those areas are more robust to uncertainty and deliver the largest return on investment. From this point of view, planning units selected consistently in both uncertainty scenarios and at any future time offer less investment risk (areas represented by overlap T1U in Figure 8.3). Most of these areas are already protected areas but investment can be directed to conservation actions within those areas, such as monitoring or habitat restoration. However, these areas are not sufficient to represent all species, and investment conservation in places where there is no certainty about our return is important.

Our results indicate that investing in the areas selected only under the Mild uncertainty scenario will be a more cost-efficient investment if the Severe uncertainty scenario occurs than vice versa. This result shows that disregarding uncertainty and applying the precautionary principle would not be best strategy in this case. This result was probably attained because several species are predicted to have their distribution severely or completely reduced under the Severe uncertainty scenario, and consequently they are not accounted for in the Marxan optimized solution. We consider that areas selected under the Mild uncertainty scenario would be good candidates for investment, subject to the implementation of a dynamic management plan that considers shifting actions from actively managing species and habitats to surveying species abundances or halting conservation investment according to the probabilities of the species targeted being extant (Chadès et al. 2008). Despite being less cost-efficient, we do not suggest that areas selected only in the Severe uncertainty scenario be completely disregarded from conservation efforts because those areas may become climatic refugia for some species, including species from other taxonomic groups (Pyke and Fischer 2005).

Our study shows how to account for uncertainty in predicted future species distributions. The return-on-investment analysis based on different uncertainty scenarios provides decision-makers with the knowledge and tools to support robust investment options.

For the sake of simplicity, we constrained the number of uncertainty scenarios arising from the different possible mathematical approaches used to fit the models to two (Mild and Severe), but there are many possibilities between and beyond the bounds of these two. Similarly, we used only one level of desired probability of achieving species occurrences targets (we set the level o certainty in Marxan to 0.5). Additionally, we did not account for uncertainty in all variables that can affect future species distributions. Where possible, we attempted to minimize the influence of other sources of uncertainty in our results. For example, we aimed to minimize the uncertainty arising from the storylines assumed in future climate change predictions. To do so, we identifed priority areas for the future by replicating the possible distribution of each species in each of the two storylines considered in this study. This approach may have induced an overestimation of the selected areas needed to meet representation targets in the future. Ideally, uncertainty derived from all storylines described in the Special Report on Emissions Scenarios (Nakicenovic and Swar 2000) should be considered individually in the reserve selection exercise. Another important source of variability and uncertainty that we attempted to minimize was the dispersal ability of each species. We used only the worse-case scenario regarding dispersal, i.e., we assumed that species could not disperse and therefore future ranges must be contained within current ranges. This is a cautious approach that acknowledges many herptiles have low dispersal capacity. However, dispersal uncertainty is a very important issue in the identification of priority areas for conservation under climate change, particularly with respect to the connectivity of priority conservation areas (Halpern et al. 2006; Hodgson et al. 2009; Williams et al. 2005). If we had assumed unlimited dispersal ability most species ranges would be predicted to be larger that our predictions (data not shown), consequently the probability that more species would co-occur in planning units would increase and the areas selected by Marxan for the 2020 and 2080 scenarios would be smaller.

Uncertainty in future species distributions can also derive from uncertainty in other variables not accounted for in this study. For instance, the rate of habitat fragmentation and degradation (Burgman et al. 2005; Polasky et al. 2008), uncertainty in habitat variables, errors in distributional data and uncertainty in metapopulation parameters, such as abundance, reproduction and mortality rates.

There are other methodological aspects that if approached differently could have returned dissimilar results. For instance, we used the number of protected and non-protected areas selected as a surrogate for cost. We used this simple approach to reduce the complexity of our study, but a more realistic estimate of the cost of conservation could consider acquisition, transaction, damage and opportunity costs (Adams et al. 2010; Naidoo et al. 2006), the cost of conservation actions (Carwardine et al. 2008; Naidoo et al. 2006), or the cost of other ecosystem services (Naidoo and Ricketts 2006). Additionally, we measured the benefits as the number of species meeting occurrence targets with at least 50% probability, and we set the same relative target for all species (10% of present range). By doing this, we considered all species has having equal value. However, it is reasonable to think that some species could be valued higher than others, for instance, the endemics, the ones with most concerning conservation status, or the ones that are more phylogenetically distinct (Faith 1992; Vane-Wright et al. 1991) could have been valued higher. Thus, we encourage conservation authorities of this area to set their own conservation objectives and evaluation metrics instead of simply assuming that the areas identified in this work are the only possible and optimal solution.

There is still a long way until we are able to deal with the extreme complexity of the biological systems, the parameters regulating their persistence and their intrinsic uncertainty, the dynamics of species distributions in space and time, the difficulty in incorporating realistic costs and making decisions involving multi objectives. However, this case study illustrates one method of making spatially explicit robust investment options for conservation despite multiple uncertainties.

8.6 Conclusion

Dealing with uncertainties in climate change and species distribution model is a major challenge for the spatial prioritization of conservation investment. This study identifies a set of sites in the Iberian Peninsula where conservation investment is prudent regardless of how the globe warms and how the climate changes distributions of amphibian and reptile species – these are "no regrets" sites for conservation. Additionally, we identified those species that will require extra investment if the no-regrets solution is implemented. We showed that investing beforehand in a precautionary strategy may not be the best option. Instead, scenario analysis coupled with return-on-investment thinking may lead to more efficient conservation investments.

8.7 Acknowledgements

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Appendix 8.1

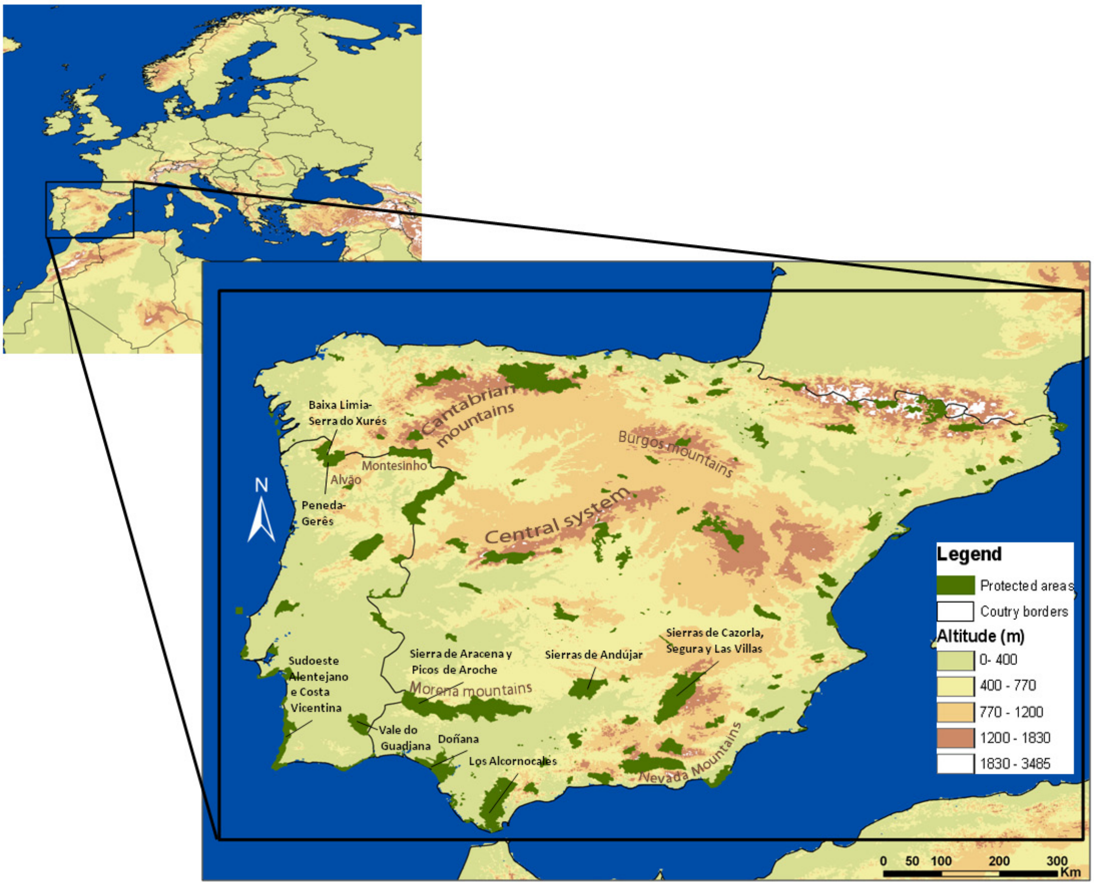

Figure S.8.1.1 - Map of the study area, altitude and protected areas, highlighting features referred in the text. Map shown in WGS84 projection.

Appendix 8.2

Table S.8.2.1 - List of amphibians and reptiles species. End – endemic species to this region are marked with an "X". CS – Conservation status according to Cox et al. (2006).

Class	Order	Family	Species	END	CS
Amphibia	Anura	Alytidae	*Alytes cisternasii* Boscá, 1879	X	NT
			Alytes dickhilleni Arntzen & García-París, 1995	X	VU
			Alytes obstetricans (Laurenti, 1768)		LC
			Discoglossus galganoi Capula, Nascetti, Lanza, Bullini & Crespo, 1985	X	LC
			Discoglossus jeanneae Busack, 1986	X	NT
		Bufonidae	*Bufo bufo* (Linnaeus, 1758)		LC
			Bufo calamita Laurenti, 1768		LC
		Hylidae	*Hyla arborea* (Linnaeus, 1758)		LC
			Hyla meridionalis (Boettger, 1874)		LC
		Pelobatidae	*Pelobates cultripes* (Cuvier, 1829)		NT
			Pelodytes punctatus (Daudin, 1802)		LC
		Ranidae	*Pelophylax perezi* (Seoane, 1885)		LC
			Rana dalmatina Fitzinger in Bonaparte, 1838		LC
			Rana iberica Boulenger, 1879	X	NT
			Rana pyrenaica Serra-Cobo, 1993	X	EN
			Rana temporaria Linnaeus, 1758		LC
	Urodela	Salamandridae	*Calotriton asper* (Dugès), 1852	X	NT
			Chioglossa lusitanica Bocage, 1864	X	VU
			Lissotriton boscai (Lataste, 1879)	X	LC
			Lissotriton helveticus (Razoumowsky, 1789)		LC
			Mesotriton alpestris (Laurenti, 1768)		LC
			Pleurodeles waltl Michahelles, 1830		NT
			Salamandra salamandra (Linnaeus, 1758)		LC
			Triturus marmoratus (Latreille, 1800)		LC
Reptilia	Chelonia	Bataguridae	*Mauremys leprosa* (Schweigger, 1812)		LC
		Emydidae	*Emys orbicularis* (Linnaeus, 1758)		NT
		Testudinidae	*Testudo graeca* Linnaeus, 1758		LC
			Testudo hermanni Gmelin, 1789		NT
	Ophidia	Colubridae	*Coronella austriaca* Laurenti, 1768		LC
			Coronella girondica (Daudin, 1803)		LC
			Hemorrhois hippocrepis (Linnaeus, 1758)		LC
			Hierophis viridiflavus (Lacépède, 1789)		LC
			Macroprotodon brevis (Günther, 1862)		NT
			Malpolon monspessulanus (Hermann, 1804)		LC
			Natrix maura (Linnaeus, 1758)		LC
			Natrix natrix (Linnaeus, 1758)		LC
			Rhinechis scalaris (Schinz, 1822)		LC

Table S.8.2.1 - (continued)

Class	Order	Family	Species	END	CS
			Zamenis longissima (Laurenti, 1768)		LC
		Viperidae	*Vipera aspis* (Linnaeus, 1758)		LC
			Vipera latastei Boscá, 1878		NT
			Vipera seoanei Lataste, 1879	X	LC
	Sauria	Anguidae	*Anguis fragilis* Linnaeus, 1758		LC
		Blanidae	*Blanus cinereus* (Vandelli, 1797)	X	LC
		Chamaeleonidae	*Chamaeleo chamaeleon* (Linnaeus, 1758)		LC
		Gekkonidae	*Hemidactylus turcicus* (Linnaeus, 1758)		LC
		Lacertidae	*Acanthodactylus erythrurus* (Schinz, 1833)		LC
			Algyroides marchi Valverde, 1958	X	EN
			Iberolacerta aranica (Arribas, 1993)	X	CR
			Iberolacerta aurelioi (Arribas, 1994)	X	EN
			Iberolacerta bonnali Lantz,1937	X	NT
			Iberolacerta martinezricai (Arribas, 1996)		CR
			Lacerta andreanszkyi Werner, 1929	x	NT
			Lacerta agilis Linnaeus, 1758		LC
			Lacerta bilineata (Daudin, 1802)		LC
			Lacerta monticola Boulenger, 1905	X	VU
			Lacerta schreiberi Bedriaga, 1878	X	NT
			Podarcis bocagei (Seoane, 1884)	X	LC
			Podarcis carbonelli Pérez Mellado, 1981	X	EN
			Podarcis hispanica (Steindachner, 1870)		LC
			Podarcis muralis (Laurenti, 1768)		LC
			Psammodromus algirus (Linnaeus, 1758)		LC
			Psammodromus hispanicus Fitzinger, 1826		LC
			Timon lepida (Daudin, 1802)		NT
			Zootoca vivipara (Jacquin, 1787)		LC
		Scincidae	*Chalcides lanzai* Pasteur, 1967	X	NT
			Chalcides bedriagai (Boscá, 1880)	X	NT
			Chalcides striatus (Cuvier, 1829)		LC

Appendix 8.3

Marxan delivers decision support for reserve system design by minimizing a combination of the cost of a set of selected planning units and the boundary length of the entire system whilst representing a set of features with a given number of occurrences (occurrence target) (Ball et al. 2009).

Mathematically, we can define the representation of feature *j* in a set of planning units as

$$R_j(x) = \sum_{i}^{Ns} x_i r_{ij} \qquad x_i \in \{0,1\} \ \forall \ i \tag{1}$$

where r_{ij} is the occurrence level (for instance, abundance or number of populations) of feature *j* in planning unit *i*, and x_i is a control variable with value 1 for planning units selected in the set, and value 0 for planning units that are not selected.

The mathematical problem that Marxan resolves can be defined as:

$$Minimize \quad \sum_{i}^{Ns} x_i C_i + b \sum_{i}^{Ns} \sum_{h}^{Nf} x_i (1 - x_h) cv_{ih} \tag{2}$$

subject to the constraint that all features meet representation targets

$$R_j(x) \geq T_j \quad \forall \ j = 1 \ldots N_f \tag{3}$$

where C_i is the cost of planning unit *i*, Ns is the total number of planning units, Nf is the number of conservation features, T_j is the occurrence target of feature *j* and b is the boundary multiplier which determines the cost of the overall selected planning units relative to the penalty to its spatial configuration. The matrix CV is the connectivity matrix with elements CV_{ih}, which reflects the cost of the connection (such as a boundary) shared by planning units *i* and *h*.

Marxan uses a simulated annealing algorithm to evaluate an objective function that combines expressions 2 and 3. The objective function in Marxan assures that all features meet their occurrence target by penalizing planning units' configurations where condition (3) is not satisfied. Hence, SPF_j represents the penalty paid for any feature *j* that does not meet its occurrence target (T_j). The penalty for not achieving conservation targets are generally to be large enough that no targets are unmet. Once the target is met the penalty is zero. There is also a penalty for planning units configurations with larger borders, which is weighted with the boundary length modifier (BLM) and an optional term that penalizes solutions exceeding a given cost t, with a penalty (CTP).

$$E\left(R_j(x)\right) = \sum_{i}^{Ns} x_i r_{ij} p_{ij} \qquad ,$$

where p_{ij} represents the probability of occurrence of feature *j* in planning unit *i*.

Consequently, the variance in the representation of each feature is:

$$Var\left(E\left(R_j(x)\right)\right) = \sum_{i}^{Ns} r_{ij}^2 p_{ij} x_i (1 - p_{ij}) \quad ,$$

According to the central limit theorem, the mean of a sufficiently large number of independent random variables, each with finite mean and variance, will be approximately normally distributed. Thus, the probability of each feature failing to meet the desired occurrence target (P_j) is given by the proportion of the normal curve that is below the desired target T_j. When the variance in the representation of each feature is higher than zero, Z-scores for each feature are calculated according to:

$$Z_j = \frac{T_j - E\left(R_j(x)\right)}{\sqrt{Var\left(E\left(R_j(x)\right)\right)}}$$

Finally, P_j is calculated according the rule

$$\text{if } Z_j \geq 0, \; P_j = 1 - \mathrm{f}(Z_j)$$
$$\text{if } Z_j < 0, \; P_j = \mathrm{f}(-1 x Z_j)$$

where f is a function that converts the normal deviate into a proportion of a normal curve.

In the modified Marxan version used in the present study there is now a penalty for not meeting a conservation target with the required level of certainty rather than a penalty for meeting the target or not.

Photo: Vasco Flores Cruz

> **"In the end we will conserve only what we**
> **love. We will love only what we understand.**
> **We will understand only what we are taught"**
>
> **Baba Dioum**

Chapter 9

General Discussion

The broad objective of this thesis was to address some unresolved issues in conservation planning, by using the Western Mediterranean region as study area and the amphibian and reptiles species occurring there as biological models. In the first part of this discussion, two main aspects are addressed: 1) key findings are summarized and integrated; 2) their implications for conservation planning science and for the conservation of amphibians and reptiles in the Western Mediterranean region are discussed. The second part of this chapter focuses on future research prospects.

9.1 Summary and key findings

9.1.1 Contribution to knowledge on the distribution of amphibians and reptiles in the Western Mediterranean

This thesis contributes significantly to the knowledge and understanding of the distribution of the amphibians and reptiles in the Western Mediterranean region.

Data on the distribution of amphibians and reptiles in the study area was already available in a spatial referenced form, since distribution atlases were available for Portugal (Loureiro et al. 2008), Spain (Pleguezuelos et al. 2002), and Morocco (Bons and Geniez 1996). However, those data sources comprised records collected from several observers, along several decades, and thus a systematic sampling was not applied. Hence, there was no information on the sampling effort and it was not know which grid cells were not sampled at all.

Species distribution models (SDMs) are potential useful tools to locate relatively under-sampled sites and direct field survey efforts (maximizing their efficiency and efficacy), and ultimately assisting in locating unknown populations of rare species (Guisan et al. 2006; Guisan and Thuiller 2005; Williams et al. 2009). In **chapters 5**, **6**, **7** and **8**, SDMs were used to predict the potential distribution of each species in the study area, although the methods applied, the area and the species under focus differed. For example, in **chapter 5**, the maximum entropy method (Phillips and Dudík 2008; Phillips et al. 2004) was used to predict potential distributions of each amphibian and reptile species in the Iberian Peninsula, but, because the aim was to test the sensitivity of reserve selection algorithms to different proportions of species occurrence data, only fractions of the overall records were used as input data. In **chapter 6**, the same maximum entropy method was used to predict the overall occurrence of amphibians and reptile species in Iberian Peninsula and Morocco, this time using all occurrence records, except to those species occurring both in the Iberia and Morocco. For those species, the number of occurrences in Iberia was reduced in order to match the density of records within the minimum convex polygon formed by all Moroccan records. In **chapter 7**, we used an ensemble of nine SDMs methods to predict the distribution of each amphibian and reptile species in the Iberian Peninsula, both for present and different future climatic conditions.

Figure 9.1 represents the observed and predicted species richness as calculated with the methodology used in **chapter 6** (the only chapter where both Iberia and Morocco were considered). Differences between observed and predicted species were predominantly higher in Morocco than in Iberia, indicating that sampling effort in Morocco was probably lower. There are however, few areas in Iberia where observed species richness was higher than predicted. One of the possible explanations may be the threshold used to transform probabilities of occurrence into presence/absence data. The threshold applied to each species was the one where 90% of the occurrence records with the highest model probabilities were considered as presences. This means that 10% of the observed records are considered absences, accounting for possible “false presences” in the observed data. Differences between observed and predicted richness indicate that future sampling efforts should be directed preferentially to Morocco, and particularly to the coastal areas and higher altitudes. The lower sampling effort in Morocco in comparison with the Iberian Peninsula highlights the importance of **chapter 4**. Indeed, the 427 new records added correspond to an increment in 7% relative to the total number of occurrences of the terrestrial species published in the atlas of amphibians and reptiles of Moroco (Bons and Geniez 1996). These new records extended the known distribution of several species such as, *Discoglossus scovazzi*, *Ptyodactylus oudri*i and *Spalerosophis dolichospilus,* while feeling gaps within the known range of other 63 species.

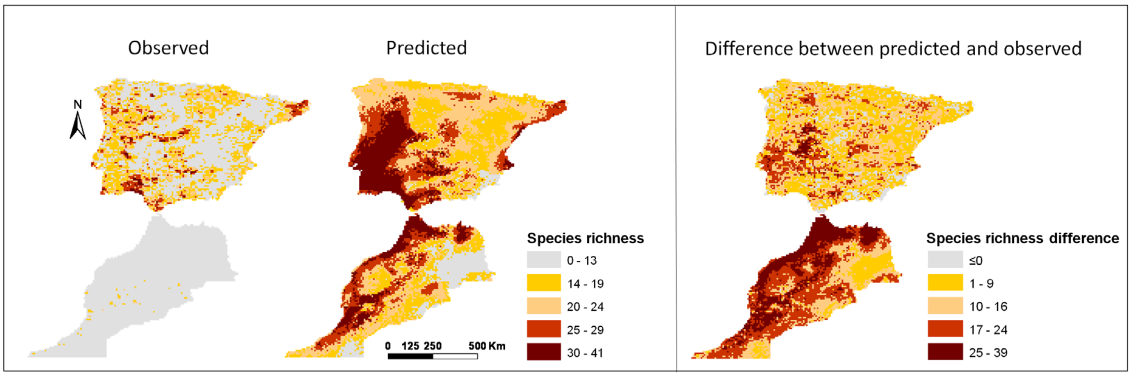

Figure 9.1 - Distribution of observed and predicted amphibian and reptile species richness in the Western Mediterranean.

A second advantage of the use of SDMs is that they allow identifying the environmental factors which contribute the most to explain species distributions (Guisan and Thuiller 2005). The variables "annual precipitation" and "precipitation of driest month" were the ones which had higher contribution for most individual species models, both for amphibians and reptiles (Figure 9.2). These two variables alone contributed more than 90% to the models of *Leptotyphlops macrorhynchus*, *Mesalina pasteuri* and *Tripiocolotes tripolitanus* (annual precipitation) and *Iberolacerta aranica* and *Iberolacerta aurelioi* (precipitation of driest month). Understanding the affinities of species distributions with environmental variables is critical to understand how they may respond to environmental disturbances.

9.1.2 Contribution to Conservation Planning Science

Along this thesis, several of the stages of the systematic conservation planning process were analyzed as well as their influence in identifying priority areas for conservation.

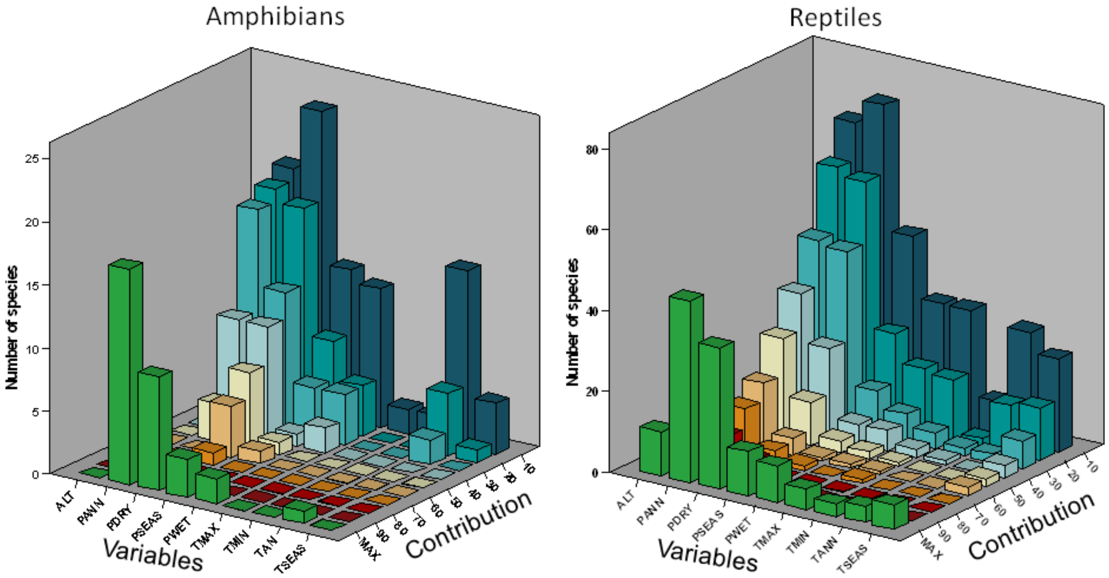

Figure 9.2 - Number of species to each variable had the maximum contribution (Max) or achieved a given percentage of contribution (10 to 90%) to the distribution model.

The main focus was given to the “objectives” subgroup (Figure 1.3). Novel approaches were proposed to deal with data limitations and uncertainty, dynamics of the spatial distribution of conservation features and the incorporation of evolutionary processes. This work contributed to enhance comprehensiveness and confidence on the process and to boost the chance of getting increased benefits for conservation actions.

One of the most important findings of this thesis was that data on spatial distribution of conservation features is decisive to the prioritization process, as it will have a strong influence in setting conservation targets and objectives, and ultimately, in the prioritization outcomes. Understanding the biological and economic consequences of data limitations can both improve the choice of conservation priorities based on such data and guide efforts to collect additional data.

In **chapter 5**, it was shown that the type of species distribution data (observed, predicted, transformed predicted or mixed) have a strong influence on the cost-effectiveness of the solutions found. Additional results not shown in this thesis also demonstrated that congruence between areas selected as priority for conservation when using different data sets was low. These results concur with the ones found in a recent study (Underwood et al. 2010). Also in **chapter 5**, it was found that, when the prioritization process starts, the degree of knowledge on species distributions has deep consequences on priority areas identified. This finding is in agreement with previous results (Grand et al. 2007), but in this thesis the analysis was extended in order to understand interactions between data completeness, data type, conservation targets and the mathematical problem statement. Although no single type of species distribution data outperformed the others (in terms of cost-efficiency) in every situation, it was possible to make recommendations for particular combinations of these four factors. For example, it was noticed that the use of observed data is not recommended in data-poor circumstances and particularly when using the minimum set approach, because, in such cases, flexibility in solutions is reduced, leading to expensive solutions. Hence, planners are recommended to first identify the circumstances that the conservation planning is being carried in terms of knowledge of the distribution of conservation features. A second assumption that emerged was that predicted probabilistic data is generally less cost-efficient than mixed and transformed predicted data in most data-knowledge circumstances. Limitations of using probabilistic data are exacerbated by adding uncertainty to the reserve selection problem, as explained in **chapter 8**. On the other hand, using probabilistic data may be advantageous when planning for persistence because it allows discerning between occupied areas of different suitability (Araújo and Williams 2000) and it allows circumventing a subjective choice for the threshold used to convert probabilities into binary data (Liu et al. 2005). These reasons motivated the development of a new version of the decision-support software Marxan, which deals with the variance in expected number of occurrences captured by a set of selected areas (**chapter 8**). Although it was not tested here whether solutions found using probabilistic predicted data in the modified version of Marxan performs better in terms of cost-efficiency than it does on the classic version, ongoing research suggests that it may be the case.

The importance of species distribution data to the prioritization process was further explored in **chapter 9,** where it was shown that predicted dynamics in species distributions derived from ecological disturbances, such as climate change, may strongly influence decisions about which areas should be preserved and when. A novel approach was developed to integrate both dynamics and uncertainty in species distributions, and two types of uncertainty were targeted: the variance in the expected number of occurrences for a species resulting from the use of probabilities of occurrence, and uncertainty arising from the different possible mathematical approaches used to fit species distribution models. As mentioned previously, a new version of the decision support tool Marxan was developed for this purpose. It was evidenced that accounting for uncertainty subjacent to current and future predictions of species distributions may be helpful to increase confidence in conservation investments. These developments are a step forward in turning the systematic conservation approach more comprehensive and realistic.

Another aspect related to the "objectives" subgroup addressed in this thesis was the incorporation of evolutionary processes into conservation planning. Evolutionary processes are extremely important both for generating biodiversity and for enhancing persistence chances of the existing one. Targeting evolutionary processes in conservation planning has been fully acknowledged in scientific literature but rarely implemented. In **chapter 6,** a novel approach was developed to find surrogates for both the neutral and the adaptive components of genetic diversity. It was found that priority areas for conservation identified when targeting evolutionary process were significantly different from the ones identified while targeting species representation only. While new methods are emerging to incorporate molecular data on conservation prioritization, most regions still lack genetic variation information. Thus, given the urgency of making conservation decisions, approaches such as the one developed in this thesis are useful because they enhance the probability of capturing evolutionary processes without requiring molecular data.

The emerging result transversal to **chapters 5**, **6**, and **8** was that priority areas identified when addressing different conservation planning issues separately were fairly different. For example, priority areas identified in the Western Mediterranean were distinct when including surrogates for evolutionary processes from solutions found when not including them (**chapter 6**). Priority areas identified also varied when incorporating predicted shifts in species distributions and accounting for data uncertainty (**chapter 8**). Moreover, priority areas identified in the Iberian Peninsula when planning for the all Western Mediterranean (**chapter 6**) were quite different from the ones identified when planning exclusive for the Iberian Peninsula (**chapter 8**). These results demonstrate that prioritization problems do not have an exclusive answer, which reiterates the role of systematic conservation planning as a decision support tool instead of a decision-making tool (Margules and Sarkar 2007). Hence, results obtained when using reserve selection algorithms should not be accepted uncritically. They should be interpreted in the context in which they were obtained and addressing methodological limitations. The challenge is to evaluate in each situation which elements are worth including and which only add complexity without any substantial improvement in outcomes. Furthermore, prioritization results should be integrated as a part of the full decision process which should also incorporate stakeholders and expert opinions, and be encapsulated by the social economic context (Figure 1.3). Conservation planning should be a dynamic process, where implemented conservation actions are monitored and evaluated, and providing feedback for future decisions.

9.1.3 Implications for the conservation of amphibians and reptiles in the Western Mediterranean

Although the main objectives of this thesis were more related with analysis and development of methodologies in conservation planning, there were few insights emerging with direct conservation application.

Foremost, it was evidenced in that climate change in the next decades may have severe effects on amphibian and reptiles distribution in the Iberian Peninsula, particularly on the endemic species with Atlantic climatic affinity such as *Chioglossa lusitanica*, *Rana iberica* and *Vipera seoanei*, and particularly in altitude species such as *Rana pyrenaica*, *Iberolacerta monticola*, *I. aranica*, *I. aurelioi*, and *I. bonnal*i. Results indicated that the next decade, in particular, will be a critical period for most of these species, which calls for immediate conservation action. In **chapter 8**, priority areas for conservation were identified taking into account potential range contraction of the species. Previous studies have attempted to identify priority areas for conservation of amphibians and reptiles in the Iberian Peninsula, but without accounting for potential range shifts, and usually using a coarser scale of analysis (e.g. Araújo et al. 2007; Lobo and Araújo 2003). Thus, the present work represents a relevant progress in the conservation context of the Iberian Peninsula.

Noteworthy, most of the priority areas identified when accounting exclusively for predicted distributions for present time are already protected (Figure 9.3a). The few exceptions are areas adjacent to Douro Internacional, Malcata and Doñana sites, and the extreme northeast of the Iberian Peninsula. If considering the “discounted uncertainty” scenario, additional areas were also identified between Donãna and Vale do Guadiana sites, west to Los Alcornocales and some other scattered areas mostly along the northern coast of the Iberian Peninsula and central-east Portugal. However, several additional areas to the current protected ones were identified as priority for conservation when accounting for future species distributions (Figure 9.3b). Gaps between priority areas identified and currently protected areas were mostly located in Southwestern Spain (area comprised between the southern border of Portugal and Spain and the Strait of Gibraltar) and in Central-Eastern Portugal, between Douro Internacional, Serra da Estrela, Tejo Internacional, Malcata and São Mamede protected areas. Additionally, several areas identified in only one of the uncertainty scenarios are neither currently protected, such as the coastal areas of Asturias province and the Northwest of the Peninsula, in Galicia province.

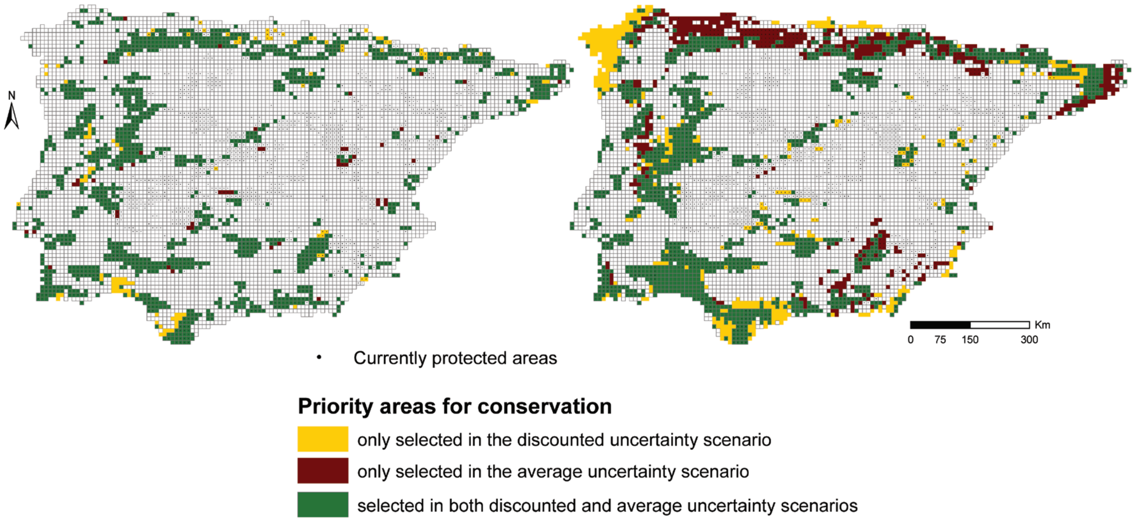

Figure 9.3 - Priority areas for conservation common to solutions obtained when optimizing for amphibians and reptiles distributions predicted for a) present time and in each uncertainty scenario; and b) 2020 and 2080 and in each uncertainty scenario. Black dots identify planning units that currently have more than 10% of its area inside a currently designated protected area or a Natura 2000 site. See chapter 8 for methodological details.

As found in **chapter 8**, given the uncertainty in future species distributions, it will probably be more cost-efficient to extend protection to areas identified under the "average uncertainty" scenario than the ones identified under the "discounted uncertainty scenario" (see **chapter 8** for methodological details). However, areas identified under the "discounted uncertainty" scenario may become important climatic refugia for many species with Atlantic climate affinities, particularly *Chioglossa lusitanica* and *Rana iberica*. Ideally, all areas identified as priority for conservation in Figure 9.3b should be protected in order to secure, with certainty, the majority of amphibian and reptile species in the next century. However, it should be outlined that in this study only amphibians and reptiles were accounted in the selection of priority areas and other spatial configurations may prove more efficient to protect several biodiversity groups simultaneously. Nonetheless, it is likely that climatic change affect different biodiversity groups in similar ways, particularly by shifting ranges northwards and towards higher altitudes (e.g. Feehan et al. 2009). For example, Garzón et al. (2008) predicted that the temperate broad-leaved tree species will be relegated to the northern mountains of the Iberian Peninsula, and that their current range will be substituted by sub-mediterranean tree species. These results concur that the North of the Iberian Peninsula and the Mountain tops will probably become climatic refugia for several species, mostly the ones with Atlantic climate affinities.

It is important to note that priority areas identified in **chapter 8** did not objectively account for economical costs, as only the parameter "area" was used as surrogate for cost. This consideration is extremely important given that a considerable proportion of priority areas identified were located in areas of economical importance and urban pressure, such as coastal regions. Therefore, attempting to conserve these areas may result in serious conflicts of interests on land-use. However, it is also relevant to point out that those areas are likely to undergo severe habitat fragmentation in upcoming years due to urban development, if not preserved. Thus, it is advisable to combine the results of future potential distributions with socio-economic, land-use and environmental models, to derive data that can be integrated into decision-making (e.g. Verboom et al. 2007), and to evaluate the effects of different land-use policies on biodiversity (e.g. Louette et al. 2010).

Another important consideration regarding the priority areas identified in **chapter 8**, is that it was assumed a "no dispersion" scenario, meaning that priority areas were identified based on areas where species are most likely to persist without dispersal, and potential areas to where they might disperse and find suitable habitat in the future were disregarded. This implicates that if species are able to disperse and expand their current range, it may be possible to find more efficient spatial configurations of priority areas, since there will probably be more combination possibilities. It also means that connectivity between priority areas, and particularly between current and future potential priority areas, would have to be accounted.

It is also relevant to mention that priority areas identified in **chapter 8** did not account for species predicted to completely lose suitable climatic habitat in the future. However, given the uncertainty in model predictions and in species adaptation abilities, predicting complete loss of suitable climatic niche does not necessarily mean that species will actually go extinct. In fact, if those species are able to persist, they may become the priority ones for conservation action. Once there is not absolute certainty of how species will respond to climate change, the implementation of a monitoring program is recommended to track species range shifts and/or behavioural, and physiological adaptation. Species predicted to completely lose suitable climatic niche in the Iberia Peninsula, and particular the endemic ones, should be the principal candidates to be included into monitoring programs. Such species comprise *Alytes dickhilleni*, *Calotriton asper*, *Chioglossa lusitanica*, *Discoglossus galganoi*, *Iberolacerta aranica*, *Iberolacerta aurelioi*, *Iberolacerta bonnali*, *Iberolacerta monticola*, *Podarcis bocagei*, *Rana iberica*, *Rana pyrenaica*, *Triturus marmoratus* and *Vipera seoanei*.

The monitoring locations should also be stratified according to current climatic variability and they should cover, in particular, areas with steep climatic gradients, such as mountain ranges. Mountain ranges played a very important role as biodiversity refugia centres in historical climatic events and it is likely that they also play an important role in species persistence in future decades. An extra reason for monitoring in mountains is because the scale of the analysis used in this work is not detailed enough to capture microclimates along slopes and valleys. Further attention should also be devoted to areas with expected high rates of turnover, because changes in assemble composition may conduct to ecosystem disruption. Such considerations should be accounted in broader monitoring programs, such as the ongoing SIMBION project aimed to monitor biodiversity in Northern Portugal. Monitoring parameters should include: a) physiological changes in thermal tolerances; b) phenological adjustments, such as changes in aestivation and hibernation periods along the year; c) behavioural thermoregulation adjustment, such as burrowing or adjustments in daily activity periods; d) quantification of dispersal rates; e) changes in population parameters, such as abundance, fertility and mortality f) incidence of infectious diseases, and g) species interactions.

Different configurations of priority areas were identified in **chapter 6**, where the study area was extended to include Morocco, and targets were set for surrogates of evolutionary processes in addition to species presence. Given the different methodology used, the priority areas identified were fairly different from the ones identified in **chapter 9**. It would be interesting to investigate which areas would be selected as conservation priority if both species range shifts, uncertainty and evolutionary processes were included simultaneously. It would also be interesting to evaluate how areas selected using surrogates for evolutionary processes would actually preserve more of the genetic diversity and particularly to test if genetic diversity has phenotypic expression in traits relevant to adaptation to climate change. For example, for species predicted to be severely affected by climate change, and which have diversified lineages, such as *Chioglossa lusitanica*, it would be interesting to investigate if different lineages have different physiological tolerances of phenologies.

9.2 Future prospects

Despite the exponential growing of systematic conservation planning in the last three decades (Moilanen et al. 2009; Pressey and Bottrill 2008), there are still important unresolved issues at every stage of the process, including the topics focused along this thesis.

9.2.1 Biodiversity data

Data paucity is still one of the most challenging issues in conservation planning, but conservation decisions have to be made in spite of bias and gaps in species information. Along this thesis, the focus was given to individual species distributions and SDMs were systematically used to circumvent the problem of biologic data paucity. However, species distributions models are not uncertainty-free. Model limitations should be accounted for when interpreting conservation prioritization results derived from predicted data and uncertainty should be fully acknowledged. The field of species distribution modeling has been evolving rapidly, and new emerging approaches are promising for conservation planning, particularly the ones developing from the Bayesian and machine learning fields (Elith and Leathwick 2009). Also promising is the link of correlative with mechanistic models (e.g. Kearney and Porter 2009), or with population models (Keith et al. 2008), and the inclusion of biotic interactions into the distribution models (Araújo and Luoto 2007).

There are other possible approaches to the individual species modeling to circumvent the data paucity limitation. Using surrogates for biological data is a common practice and there are several possibilities (Ferrier and Watson 1997; Rodrigues and Brooks 2007; Sarkar et al. 2005; Williams et al. 2006). For example, often a subset of species or other taxa are used as surrogates for all of them. Another option is to use environmental-based surrogates, because environmental variables are easier to obtain, particularly from satellite image data. A third option is using a synecological approach (Hortal and Lobo 2006), which consists in using composite biodiversity variables such as species richness, rarity, endemism, community composition or community composition turnover (either observed or estimated). Community–level approaches are claimed to be cheaper, quicker and easier to obtain than species-based ones (Ferrier et al. 2009; Margules and Sarkar 2007), conferring significant benefits for applications involving very large numbers of species and coarse areas, and particularly in data-poor regions. However, little effort has been directed to comparing the relative performance of species-based with community-based approaches. Nonetheless, in a recent prioritization approach developed to work with community-based data, maximization of complementary richness, attained reasonable levels of species representation (Arponen et al. 2009). Such results reveal a highly promising strategy for cost-effective conservation prioritization but this assumption needs to be tested more broadly.

There are still also opportunities for improving observed species distribution data sets, even because accurate model predictions depend critically on the quality of observed biological data (Graham et al. 2008; Lobo 2008). Recently, the conservation society has been putting a large amount of effort in compiling species distribution data and providing online gateways for dissemination (Bisby 2000; Graham et al. 2004; Guralnick et al. 2007). Of noteworthy mention is the Global Biodiversity Information Facility (http://www.gbif.org/), which currently contains nearly 7 500 collections representing more than 150 million occurrence records. However, these databases have some limitations that need to be overcame in order to become more useful for conservation planning. Some of the limitations have been discussed previously (e.g. Graham et al. 2004; Guralnick and Hill 2009; Guralnick et al. 2007; Hortal et al. 2007) and can be summarized as follows:

a) some records lack geographic accuracy and many are presented in the form of a textual locality description, which hinders its direct application in geographical information systems (Yesson et al. 2007);

b) data is geographically and taxonomically biased (Yesson et al. 2007);

c) most areas lack a realistic assessment of the survey effort (Soberón et al. 2007)

d) there is vast uncertainty in many records regarding the date of collection (Guralnick et al. 2007);

e) there are taxonomic misidentifications and there is no estimative of its proportion (Guralnick et al. 2007; Lozier et al. 2009);

f) a substantial percentage of records were collected prior to major alterations of native landscapes.

Nonetheless, biodiversity informatics is starting to gain impetus as a scientific discipline (Sarkar 2007). The parallel development of data portals and analysis tools, together with increased internet speed, are promising for creating new avenues of development in the biodiversity informatics field. Practical ways to overcome limitations and to create a unified global map of biodiversity have been suggested:

a) develop automated processes to convert textual or other locality format data to geographic coordinates (Guo et al. 2008; Hill et al. 2009);

b) link online taxonomic catalogues such as the Catalogue of Life (http://www.catalogueoflife.org/search.php) with species occurrence data bases, to provide valid taxonomic names to species records (Guralnick and Hill 2009; Sarkar 2007);

c) employ efforts to identify species accurately through DNA barcoding (Hajibabaei et al. 2007);

d) increase the detail of species occurrences to finer resolutions (Soberón et al. 2007);

e) evaluate the degree of completeness of occurrence data (Hortal et al. 2007; Soberón et al. 2007);

f) promote the use of social networks for exchange and upload of biodiversity records such as Scratchpads (http://scratchpads.eu/) or Biodiversity 4 all (http://www.biodiversity4all.org/) (Guralnick and Hill 2009);

g) develop and disseminate online the results of species distribution models (Guralnick and Hill 2009);

h) predict potential distributions of currently non-described species (Bini et al. 2006; Possingham et al. 2007).

9.2.2 Evolutionary Processes

In **chapter 3,** a new approach was developed to integrate evolutionary processes into conservation planning when molecular data is not available or is not geographically comprehensive, which is the common case. However, in recent years the body of information of phylogenetic relationships between taxa has been growing exponentially, as well as new approaches to bridge the fields of molecular ecology and biogeography (Hendry et al. 2010; Kozak et al. 2008). There are, however, some challenges that the scientific community face in order to make that information useful for conservation prioritization.

One of the major challenges is to integrate molecular data produced by different authors, using different molecular markers and statistical methods, to the handling of very large datasets, and the integration of different levels of genomic information (Guralnick and Hill 2009; San Mauro and Agorreta 2010). However, in the next years, a massive amount of molecular information will probably become available for a vast array of taxa. Some projects are underway with this purpose, such as the TreeBase (http://www.treebase.org), which is an online repository of phylogenetic information, with the objective to assemble a single inclusive tree of all life on Earth. There are also some online tools such as the PhyLoTA browser (http://phylota.net) (Sanderson et al. 2008) intended to systematize data available on molecular data bases such as GenBanK (http://www.ncbi.nlm.nih.gov/genbank).

Another challenge is to use such molecular data into conservation prioritization. Developing new metrics and approaches to use phylogenetic information to prioritize taxa for conservation has received a large attention lately. Several phylogenetic diversity (PD) metrics have been proposed (reviewed by Redding et al. 2008), and the PD approach has also been extended to include species threats and extinction risks, (Faith 2008 ; Isaac et al. 2007; Redding and Mooers 2006; Steel et al. 2007), endemicity (Faith et al. 2004; Posadas et al. 2001; Rosauer et al. 2009) population abundances (Cadotte and Davies 2010; Cadotte et al. 2010), spatial gradients of PD (Graham and Fine 2008) and even to incorporate the expected contribution of a taxa to future phylogenetic diversity (Steel et al. 2007). These approaches have been accompanied by the development of computational tools such as Phylocom (Webb et al. 2008), Picante (Kembel et al. 2010), and Biodiverse (Laffan et al. in press).

Another research topic deserving future attention is developing theoretical frameworks to explicitly incorporate targets for the representation and persistence of genetic diversity of multiple species. Currently, reserve selection algorithms rely on setting targets for discrete conservation features – species or vegetation types. Using phylogenies as conservation features poses new challenges in developing methodologies to cope with continuous conservation features (Diniz-Filho and Telles 2006). The challenge is exacerbated when dealing with cryptic species, generally characterized by the presence of uniparental lineages and reticulate evolution (Ennos et al. 2005), because in such cases lineages are often not spatially structured. Thus, developing suitable computational tools to deal with continuous conservation features in conservation prioritization is still an open challenge.

Frontiers of research have also been focusing on better understanding evolutionary processes that generate and maintain genetic diversity, allowing adaptation to global environmental changes. Special attention is particularly growing on the influence of environmental variation in driving genetic divergence at the intra specific level as well as in evolution of morphological, physiological and behavioural traits (Kozak et al. 2008; Smith and Grether 2008; Thomassen et al. 2010). Combining species distribution models with coalescence models is one of the possible ways to achieve understanding of the factors that contribute to the formation of population genetic structure (Carstens and Richards 2007; Waltari et al. 2007). Such understanding is critical for conservation prioritization because it will allow the identification of hotspots of evolutionary potential (e.g. Davis et al. 2007; Vandergast et al. 2008), as well as areas maximizing overall genetic diversity within populations (e.g. Rissler et al. 2006). It may also contribute to explain how species niches evolve which, in turn, will allow enhancing predictions of species range shifts under climate change (see topic below). Another relevant research topic for conservation planning is the understanding of how phylogenetic relationships among species drive community assemblage (e.g. Cavender-Bares et al. 2009; Webb et al. 2002).

9.2.3 Dynamics in conservation planning

Chapters 7 and **8** focused on one type of dynamic process in conservation planning: change in species distributions derived from climate change. Predicting future species ranges and understanding the mechanism that may facilitate adaptation to different climatic conditions is one of the primal challenges in conservation nowadays (e.g. Brooke 2009; Huntley 2007; Lawler 2009; Mawdsley et al. 2009). However, the complexity of the biological systems, which include parameters such as environmental niches, biotic interactions, extinction risks, dispersal abilities and evolutionary potentials, calls for methodological improvements if it is to guide conservation decisions (Sinclair et al. 2010).

Species distributions models have been the chief methodology employed to predict species ranges shifts derived from climate change (e.g. Araújo et al. 2006; Pearson and Dawson 2003; Thuiller et al. 2005). However, the accuracy of such approach has been questioned because they do not incorporate dispersal, demographic processes nor biotic interactions explicitly (Zurell et al. 2009). Additionally criticism relies on the fact that precise validation of biological models is difficult or even impossible (Araújo et al. 2005; Oreskes et al. 1994), particularly when predictions are made for relatively distant future times. Such questions are reasonable, but despite no clear answer can be given, better understanding on how species respond to climate change can be improved in several ways (e.g Botkin et al. 2007; Nogués-Bravo 2009).

Advances in forecasting species distributions under climate change have been proposed recently, such as incorporating species interactions (Araújo and Luoto 2007), landscape characteristics (Vos et al. 2008) and species traits (Pöyry et al. 2008). It is likely that in upcoming years, and with sophistication of computational power, statistical tools and data availability, several of these parameters may be included simultaneously in model calibration. Additionally, several statistical approaches are being developed to reduce and assess the uncertainty of the methods and data used (e.g. Diniz-Filho et al. 2009).

Understanding how species adapted and evolved in response to past climatic extremes provides essential clues to predict how they will respond to future climatic changes (Cordellier and Pfenninger 2009). The outstanding advancement of molecular biology and bioinformatics (San Mauro and Agorreta 2010) has supplied researchers with powerful tools for testing hypothesis about how past climate changes have affected species distributions (Scoble and Lowe 2010). For example, locating past climatic refugia based on phylogeographic analysis may prove concordance with projections made with species distribution models for the past (e.g. Carstens and Richards 2007; Waltari et al. 2007).

Molecular biology may also provide useful insights to test a fundamental assumption of species distribution models: that species' niche remains stable over time and thus it is sensible to transfer projections of species distribution models in time (Nogués-Bravo 2009; Varela et al. 2009). Niche conservatism theory has gained supporters (e.g. Wiens and Donoghue 2004; Wiens and Graham 2005) as it has been revealed for several taxa. However, further analysis is required to unveil the extent to which it represents a general and consistent pattern (Pearman et al. 2008), as several studies have evidenced the opposite trend, i.e. niche diversification (e.g. Broennimann et al. 2007; Knouft et al. 2006). Recent studies showed evidence that niche diversification can arise as a result of genetic divergence of traits related to climatic fitness (Skelly et al. 2007). This controversy jeopardizes confidence in species distribution models predictions for past and future times. Thus, future research should aim to improve understanding of how environmental conditions influence niche dynamics and evolution of climatic traits, such as physiological thermal tolerance. Particular emphasis should be directed to evaluate how this influence varies with the spatial and temporal scales, the focal clade, and the size of the phylogenetic trees (Pearman et al. 2008). Additionally, it was recently proposed the use of a multi-temporal approach to validate temporal transferability (Nogués-Bravo et al. 2008).

Molecular tools may also prove helpful in understanding meta-population dynamics, by identifying aspects of the landscape that hinder dispersal and disrupt gene flow (Scoble and Lowe 2010; Storfer et al. 2007). This information can be used to better understand current barriers and assess species dispersal limitations. Molecular approaches have been misused in the context of incorporating meta-population parameters in species distribution models. Nonetheless, other approaches such as using spatially explicit stochastic population models have recently emerged (Brook et al. 2009; Keith et al. 2008).

Understanding meta-population dynamics, and particularly dispersal mechanisms, is paramount to predict species responses to a set of synergistically threats such as climate changes, habitat fragmentation, invasive species and the spread of infectious diseases (e.g. Brook et al. 2008; Chazal and Rounsevell 2009; Sala et al. 2000). Recently, a greater amount of attention has been placed into the synergistic interactions among different threats (e.g. Jetz et al. 2007; Opdam and Wascher 2004; Spangenberg 2007), but such processes remain poorly understood, hampering appropriate conservation decisions. Thus, future research should focus on how climate change will interact with other main drivers of species extinctions and in how biodiversity will respond to such cascading effects.

In terms of selecting priority areas for conservation, climate change poses important challenges, once shifts in species ranges may render current protected areas inefficient in representing biodiversity (Araújo et al. 2004; Hannah 2010; Hannah et al. 2007).

Additionally, in order to assure species persistence, a paradigm shift is required in the way that protected areas are planned and managed (Araújo 2009; Baron et al. 2009). Recently, Araújo (2009) suggested that conservation planners should start reconsidering the classic "SLOSS" debate (Diamond 1975) arguing that in face of climate change, smaller conservation areas tracking pertinent climatic gradients might be preferable to large conservation areas occupying uniform climatic gradients. He suggested that at least three types of areas need to be targeted for conservation to tackle biodiversity persistence:

a) range retention areas - where species are most likely to survive despite climate changes;

b) displaced refugia – where species will be able to find suitable habitats after they have been displaced by climate change; and

c) corridors connecting range retention areas and displaced refugia – areas of high quality habitat that facilitate species dispersal between present and future climatic suitable areas.

There are several research opportunities regarding how these three types of areas should be identified and optimally arranged in space. While species distribution models may be helpful to identify range retention areas and displaced refugia, extended approaches in prioritization algorithms are required to apply the principles of complementarity, efficiency, flexibility and adequacy and to optimize connectivity. Some work has started to be done in that direction, for example, by using reserve algorithms that account for dynamics in conservation features throughout time (Drechsler et al. 2009; Game et al. 2008b; Moilanen and Cabeza 2007) or optimize connectivity corridors (e.g. Cerdeira et al. 2010; Phillips et al. 2008), but much remains to be done.

9.2.4 Uncertainty

Uncertainty is a ubiquitous issue in conservation planning. In **chapter 9,** a new approach was developed to boost conservation decisions in face of two types of uncertainty. Novel and robust statistical methods have been developed and integrated in computation tools in the conservation planning area, but opportunities for innovations remain to deal more explicitly with uncertainty (e.g. Regan et al. 2009).

Statistical treatment of uncertainty allows for the enhancement of confidence in conservation decisions, but it does not eliminate uncertainty. Thus, complementarity approaches are being advised, such as turning conservation planning more adaptive (Wilson et al. 2009). The purpose of adaptive conservation planning is to explicitly address uncertainty through learning, and subsequently adapt conservation strategies, decision frameworks and actions to reflect improved knowledge (Grantham et al. 2009).

Monitoring plays a central role in adaptive conservation because it generates new knowledge about how the system responds to conservation actions. This new knowledge provides, in turn, the feedback loop to complete the adaptive conservation cycle (see Figure 1.3) (Lyons et al. 2008). Generally, monitoring is applied to evaluate the success of implemented conservation actions, which has been seen as a passive learning process. Long-term monitoring of the conservation outcomes is desirable, but it is often hindered by the lack of financial and human resources, and because most of the times conservation action outcomes are only visible outside project's time-frames (Kapos et al. 2008).

Recently, some proposals were made to boost the speed of learning. For example, it has been argued that learning can be improved by balancing the requirements of management with the need to learn about the effects of conservation actions by experimenting different actions (McCarthy and Possingham 2007). This approach has been called "active adaptive management" and has been considered as a desirable practice, although several challenges have to be overcame in order to be applied, (Grantham et al. 2009).

Another set of proposals to boost learning focus on evaluating the past actions and comparing outcomes of conservation actions of different projects around the world. However, an important required step forward in this direction is to better report on situations where conservation actions implemented were unsuccessful in achieving conservation objectives (Ferraro and Pattanayak 2006). Negative outcomes of conservation actions are often under-reported as reported failures may lead to reductions in future funding and to professional discredit or reputation damage (Redford and Taber 2000). Until recently, the analysis of conservation actions effectiveness was also obscured by the lack of unified framework for evaluating conservation outcomes and managing information on existing conservation experience. However, this caveat has been recently circumvented by the development of specific tools by the Cambridge Conservation Forum (CCF) (Kapos et al. 2008). CCF tools provide a standardized framework that serves as a useful basis for assembling, managing, and using information about project outcomes and existing conservation experience. Potentially, with wider application, such tools may boost learning and help to circumvent uncertainties about how biodiversity will respond to conservation actions. Additionally, it may help identifying factors that affect the success of conservation activities (Kapos et al. 2009).

9.2.5 Frontiers of conservation planning

A question emerging from results obtained along this thesis is how interactions between the several stages and concepts of systematic conservation planning may affect conservation decisions. Chapters of this thesis focused on analyzing different possible approaches for a single stage or closely related stages at a time, disregarding which approaches would be followed in other stages. Due to the high complexity of the overall systematic conservation process, focusing on single or few stages has been the benchmark of scientific literature. For example, several papers have focused on:

a) prioritizing taxa and setting conservation targets (Arponen et al. 2005; Carwardine et al. 2008; Justus et al. 2008; Vane-Wright et al. 1991);

b) analyzing the performance of different surrogates (Rodrigues and Brooks 2007; Sarkar et al. 2005; Williams et al. 2006);

c) testing the performance of different types of species distribution data sets (Grand et al. 2007; Underwood et al. 2010; Wilson et al. 2005b);

d) incorporating ecological and evolutionary processes (Desmet et al. 2002; Klein et al. 2009; Rouget et al. 2003);

e) incorporating biodiversity threats and vulnerability (Game et al. 2008a; Wilson et al. 2005a);

f) planning for persistence (Cabeza and Moilanen 2001; Game et al. 2008b; Nicholson et al. 2006);

g) dealing with dynamics in species distributions and threats (Carroll et al. 2009; Visconti et al. 2010);

h) treating uncertainty in species distributions (Fuller et al. 2008; Langford et al. 2009; Moilanen et al. 2006a; Moilanen et al. 2006b; Nicholson and Possingham 2007);

i) incorporating costs (Adams et al. 2010; Bode et al. 2008; Carwardine et al. 2008; Naidoo et al. 2006);

j) integrating spatial configuration and connectivity (Briers 2002; Cabeza 2003; Van Teeffelen et al. 2006);

k) planning for implementation (Knight et al. 2006);

l) evaluating outcomes of conservation actions (McDonald-Madden et al. 2009).

These aspects do not stand alone in the conservation planning process but interact with each other. Thus, the way that each stage is addressed in the process may synergistically influence the outcomes (Figure 1.3). Future work should focus on how to address the complexity inherent to combining several of these issues.

One outstanding challenge in conservation planning is zoning areas within and beyond protected areas to reflect particularly land uses or specific conservation actions. This is because several protected areas are not exclusively devoted for conservation, but allow several human activities. Determining how different land-uses can take place in order to optimize conservation, economical and social outcomes is an issue of the utmost importance. Pioneer works have been done in integrating spatially-explicit biologic and economic models to identify trade-offs between conservation and economic benefits (e.g. Polasky et al. 2008; Wilson et al. 2010). Progress have also been made in developing computational tools to evaluate the consequences and trade-offs of alternative zoning configurations (Watts et al. 2009).

Onother interesting aspect is to integrate different types of conservation actions in order to optimize overall benefits. Conservation planning has been focusing on identifying priority areas for conservation. However, after priority areas have been identified, conservation practitioners may invest in a diverse array of actions, such as fire management, control of invasive species, predator control, revegetation or monitoring. Thus, recent approaches to conservation prioritization aim to prioritize between different conservation actions in space and time (Wilson et al. 2009). The prioritization of conservation actions proceeds in a similar framework to the identification of priority areas, balancing conservation objectives, costs and the likelihood of success of each action. New research is revealing innovative approaches to systematically planning multiple actions for multiple species (e.g. James et al. 2001; Wilson et al. 2007). Recently, the new concept of generalized complementarity was proposed, defined as the benefits of all conservation actions across the landscape evaluated jointly and how they account for the long term consequences of interactions between actions (Moilanen 2008). Theoretically, the generalized complementarity concept can be extended to a broader prioritization scheme, for example to prioritize actions benefiting the overall ecosystem services (Chan et al. 2006). Conversely, to move in that direction, global ecosystem service assessments must generate better maps of where ecosystem services are produced, flows between services need to be better understood, concordance between areas that produce ecosystem services and those that support biodiversity require further evaluation, and the likelihood of converting land uses and ecosystem services needs to be quantified (Naidoo et al. 2008). Additionally, it has been pointed out that there is still lack of understanding of how different types of interventions improve ecosystem services and human-well-being. Different authors suggested ways forward to integrate different disciplines, embrace the divide between ecosystems and social systems and to examine the impact of different decisions on the future supply of the whole range of ecosystem services (Carpenter et al. 2009; Hancock 2010; Mooney 2010 ; Steffen 2009).

Future progress in conservation planning is likely to integrate optimization in representation of biodiversity and evolutionary processes while accounting for dynamics in species distributions and landscapes, and optimizing the benefits for both biodiversity, economic activities and ecosystem services.

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