Università degli studi del Molise

Facoltà di Scienze Matematiche Fisiche e Naturali

MODELLI DI IDONEITA' AMBIENTALI PER LA LONTRA EUROASIATICA A DIVERSE SCALE

Multi – scale habitat suitability models for the Eurasian otter *Lutra lutra* (Mamalia, Carnivora, Mustelidae)

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Da

Carmen Cianfrani

Tutor: Prof.ssa Anna Loy

Co-turor: Prof Antoine Guisan

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Summary

Durante gli ultimi cinquanta anni, l'areale europeo della lontra euroasiatica (*Lutra lutra*) si è drammaticamente ridotto. Attualmente la lontra sembra stia recuperando in alcuni paesi europei, ma alcune popolazioni sono ancora frammentate e la specie è tuttora quasi assente dall' Europa centrale. In Italia la situazione è particolarmente critica, con un piccola popolazione che sopravvive nei bacini merdionali, a sua volta divisa in due nuclei isolati. Promuovere l'espansione delle popolazioni redisidue è di vitale importanza per assicurare il mantenimento della diversità genetica e la persistenza a lungo termine della specie. A questo proposito i modelli di idoneità ambientale (HSM) rappresentano potenti strumenti per valutare la qualità degli habitat e produrre carte di distribuzione potenziale e dispersione naturale della specie. Il progetto di ricerca ha avuto come obiettivo primario l'individuazione dei fattori che influenzano la distribuzione della lontra in Italia e la messa a punto di modelli in grado di predire la distribuzione potenziale della specie a diverse scale, regionale e europea.

Il modello a scala regionale riguarda il nucleo settentrionale dell'areale della lontra in Italia, principalmente costituito dalla regione Molise. Per quest'area è stato sviluppato un modello di idoneità ambientale deduttivo, basato sull'opinione degli esperti. Questo modello è stato utilizzato come base per effettuare un'analisi di connettività, longitudinale e laterale.

Nella stessa area di studio sono stati sviluppati modelli inferenziali per testare la capacità di individuare potenziali aree di espansione per la specie. Per testare la capacità di predizione dei modelli sono usati usati dati raccolti in due campagne di rilevamento, una effettuata prima della colonizzazione e l'altra dopo la ricolonizzazione. Sono stati utilizzati l'ENFA (Environmental Niche Factor Analysis) e il GLM (Generalised Linear Model). Il primo approccio utilizza solo i dati di presenza, il secondo anche quelli di assenza. I due modelli sono stati calibrati con dati raccolti prima della colonizzazione e poi con i dati raccolti sul fiume ricolonizzato. I modelli sono stati comparati e i modelli sviluppati con i dati pre-colonizzazione sono stati validati con i dati post-colonizzazione. Questo studio ha dimostrato che i dati di assenza in una situazione di instabilità tra la specie e le aree idonne occupate porta ad errori di predizione.

Nel modello a scala europea sono state considerate sia le condizioni climatiche attuali sia le predizioni relative ai cambiamenti climatici futuri. Nell'analisi sono state considerate le variabili ambientali che posso essere in relazione ai requisiti ecologici della specie, ovvero alla disponibilità di acqua, alla disponibilità di risorse trofiche, di siti di rifugio e al disturbo antropico. Gli scenari futuri sono stati ottenuti utilizzando i parametri disponibili relativi al raddoppio della CO_2 nell'atmosfera (modello CCM3). I risultati hanno mostrato come a scala europea la distribuzione della lontra sia influenzata principalmente dalla disponibilità di acqua.

La distribuzione attuale potenziale mostra larghe aree di habitat non idonei nel centro Europa, che limitano la connettività tra le tre sub-popolazioni occidentale, orientale e italiana. Gli scenari futuri indicano una potenziale perdita di habitat idonei nelle regioni occidentali, mentre in Europa centrale e orientale il modello predice un incremento. Le previsioni future indicano anche una diversa localizzazione dei corridoi di habitat che potrebbero favorire l'espansione e il collegamento delle popolazioni. Il modello è stato quindi integrato con i dati relativi alle aree protette. Il confronto ha permesso di individuare le aree più critiche che attualmente e in futuro dovranno essere preservate per garantire la sopravvivenza e il flusso genico delle popolazioni di lontra in Europa.

CHAPTER 1 - INTRODUCTION

1.1 Habitat suitability models - A tool for the conservation of the biodiversity

Habitat suitability models (HSMs) are empirical models relating field observations to environmental predictor variables based on statistically or theoretically derived response surfaces (Guisan and Thuiller, 2005, Fig. 1). By integrating known occurrences of species with environmental GIS layers that summarize meaningful niche dimensions, it is possible to determine the key combinations of environmental conditions enabling a species to grow and reproduce.

HSMs take advantage of revolutionary advances in the field of geographical information systems (GIS) and biodiversity informatics (Graham et al., 2004; Kozak,) which result in the higher availability and quality of two major sources of data:

1) Environmental predictors, including global coverage of digital terrain, climate, soil, and land-cover surfaces are now available at relatively fine spatial resolution (mostly 1km grid), thank to recent advances in interpolating climatic data from meteorological stations and remote sensing technologies. Environmental predictors can exert direct or indirect effects on species (Austin, 2002), and are optimally chosen to reflect the three main type of influences on the species: (i) *limiting factors* (or *regulators*) defined as factors controlling species eco-physiology (e.g. temperature, water, soil composition); (ii) *disturbances*, defined as all type of perturbations affecting environmental systems (natural or human-induced) and (iii) *resources*, defined as all compounds that can be assimilated by organisms (e.g. energy and water).

2) Species data sets from biological surveys and natural history collections. Species data can be simple presence, presence-absence or abundance observations based on random or stratified field sampling, or observation obtained opportunistically, such as those in natural history collection (Graham et al., 2004). The accessibility of such data is improving dramatically as a result of rapid advances in the digitization of museum and herbarium specimen collections which contain the locations of observation or collection for large numbers of species across a wide range of higher taxa (Bisby, 2000; Graham et al., 2004).
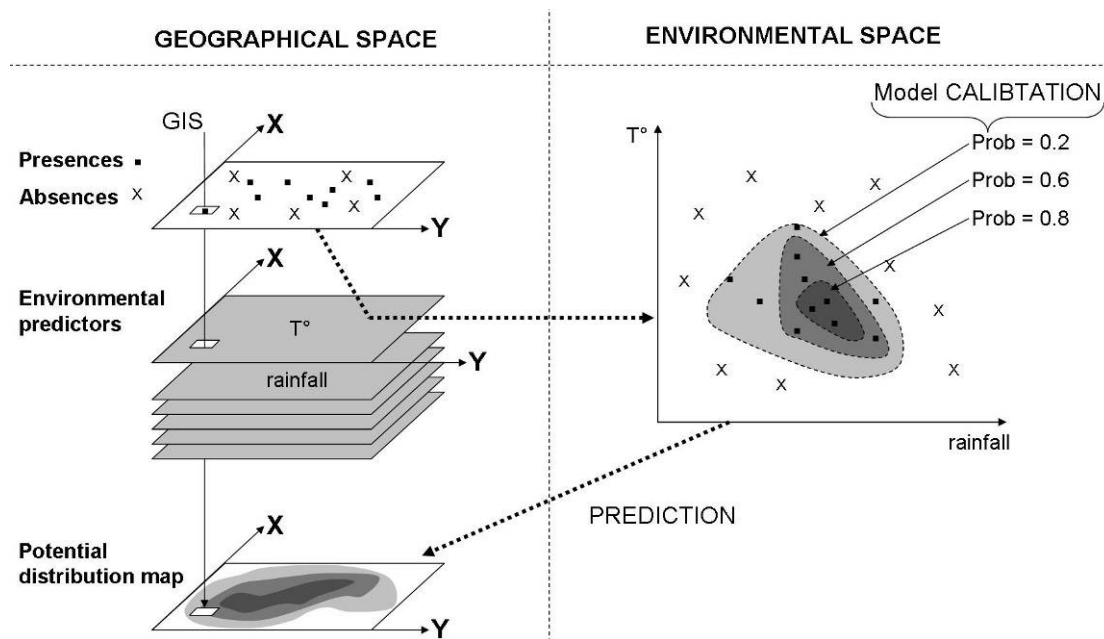
Fig. 1 – Schematic representation illustrating the main steps of habitat suitability modelling. The distribution of the species data are shown on geographical and environmental spaces. The presences (squared) and absences (crosses) data are linked to environmental predictors in a geographical information system (GIS) and environmental values are attributed to them. Statistical response surfaces are then derived in the environmental space and predicted back to the geographical space to build a potential distribution map. The predictions on the map indicate the probability of presence of the species in each regions of the study area.

Today, an impressive diversity of modelling techniques are available for modelling species distribution (see Guisan & Thuiller, 2005, tab. 2), depending on the type of response variable and predictors at hand. The choice of statistical method in a specific modelling context is now supported by many published comparison (Elith et al., 2006; Elith & Graham, 2009). These modelling techniques usually include an algorithm to select the most influential predictor in the model (Johnson & Omland, 2004). The most popular – but also controversial – technique consists in the stepwise selection procedure (see Guisan et al., 2002). Starting with a full model including all the variables, variables are sequentially introduced and removed in the model. At each step, predefined rules such as deviance reduction inform to keep or remove the specific predictor.

HSMs are useful if they are robust. Addressing ecological questions with a model that is statistically significant but only explains a low proportion of variance might lead to weak, possibly erroneous, conclusions (Mac Nally, 2002). Similar problems may well arise in the opposite case, when a model is over-fitted. Even though no absolute measure of

robustness of a model exists (Araujo et al., 2005), techniques for statistically evaluating models and their predictions are available and have considerably improved in many way (Fielding & Bell 1997, Pearce & Ferrier, 2000, see also Box 2).

Tool	Reference	Method implemented
BIOCLIM	Busby 1991	CE
ANUCLIM	See BIOCLIM	CE
BAYES	Aspinall 1992	BA
BIOMAPPER	Hirzel et al 2002	ENFA
BIOMOD	Thuiller 2003a	GLM, GAM, CART, ANN, BRT, RF, MDA, MARS
DIVA	Hijmans et al 2001	CE
DOMAIN	Carpenter et al 1993	CE
ECOSPAT	Unpublished data	GLM, GAM
GARP	Stockwell & Peters 1999	GA (incl. CE, GLM, ANN)
GDM	Ferrier 2002	GDM
GRASP	Lehmann et al. 2002b	GLM, GAM
MAXENT	Phillips et al. 2006	ME
SPECIES	Pearson et al. 2002	ANN

Tab. 1 – Published predicted NBM packages, reference paper, related modelling methods. ANN, artificial neural networks; BA, Bayesian approach; BRT, boosted regression trees; CE, climatic envelop; CART, classification and regression trees; ENFA ecological niche factor analysis; GA, genetic algorithm; GAM generalised additive model; GDM, generalized dissimilarity modelling; GLM, generalized linear models; ME, maximum entropy; MDA, multiple discriminant analysis; MARS, multiple adaptive regression splines; RF, random forest. From Guisan & Thuiller 2005.

The calibration of HSMs should be proceed by an initial conceptual phase, which consist in defining an up-to-date conceptual model of the system to be simulated based on sound ecological thinking and clearly defined objectives (Austin, 2002). Notably, a special attention must be drawn on the setting of working hypotheses (e.g. *pseudo-equilibrium; Guisan & Thiller 2005*), the assessment of available and missing occurrence data, the relevance of environmental predictors for the focal species and the given scale and choice of the appropriate spatio-temporal resolution and geographic extent for the study. These aspects have been reviewed in a recent paper by Guisan and Thuiller (2005).

Lacks of consideration in these aspects can be potentially leading to:

i) Poor predictive ability (e.g. due to taxonomic and geographic biases, missing of relevance of environmental predictors at particular scale or missing availability of absence data).

ii) Consistent over- or under-optimism in predictions with new data (e.g. due to spatial autocorrelation, wrong choice of the modelling technique, small samplings).

iii) Apparent responses to environmental conditions inconsistent with biological understanding (e.g. due to spatial autocorrelation, small sampling, spurious response curves on incompletely sampled gradient.

Niche based models relying on data from natural history collection contribute significantly to conservation efforts that are directed toward species of concern, multi-species

Conservation prioritization schemes of the spread of the endangered species and predictions of biodiversity consequences of climate change (Coetzee et al., 2009).. HSMs techniques thus offer unique opportunities to track distributional changes in relation to threatening processes and thereby anticipate future impacts.

The choice of the appropriate scale in HSMs

A central and recurrent issue in HSMs building is identifying the appropriate scale for modelling. Scale is usually best expressed independently as resolution (grain size) and extent of the study area, because modelling a large area does not necessarily imply considering a coarse resolution. No question in spatial ecology can be answered without referring explicitly to these components at which data are measured or analysed. A first possible mismatch can occur between the resolution at which species data were sampled (e.g. plot size in field surveys, grid size in atlas surveys) and the one at which environmental predictors are available. Optimally, both should be the same, but such coherence is not always possible. For instance, the minimum resolution for GIS data might be too large to realistically allow an exhaustive field sampling of biological features to be conducted in the field, and thus smaller sampling units may need to be defined within larger modelling units or at the intersection of grids. Furthermore, many environmental data are indeed provided in a grid lattice format – i.e. regular point data – rather than a true raster format, which complicates the story, somewhat. This is for instance the case of many digital elevation models (DEM) and derived data (e.g. topographic and interpolated climatic maps). Indeed, designing field sampling in order to match raster units will work well in the case of true rasters (e.g. satellite images and derived products, such as CORINE land-cover), whereas placing sampling plots at intersections of a grid may prove more appropriate in the case of lattice grids. The problem then is to combine these different types of data in a single model. Aggregating these to a coarser resolution can sometimes

provide a simple yet efficient solution, as for instance allowing passing from locally valid point data (e.g. forest/non-forest information at a series of points) to some estimate of frequency in a cell (e.g. quantitative estimate of forest cover within a cell). Similar problems arise when SDMs are used to make projections of species future distribution. Until recently, General Circulation Models (GCM) were the only source of data to make such projections. However, GCM typically involve much coarser scales (generally several orders of magnitude coarser) than those of the species and environmental data used to calibrate the SDM. Statistically downscaled GCM data can in part address this issue however, these products are still typically too coarse for local assessment or where spatial heterogeneity is high, for example in mountainous areas. The development of Regional Climate Models and fine scale GCM will also help in addressing this issue. These future climate surfaces are also limited by the resolution of the surfaces representing current climate as these current surfaces are perturbed with anomalies calculated from the GCM data. Despite the availability of relatively fine-scaled climate data sets these products are limited by the frequency of climate station data and the interpolation techniques used to create continuous climate surfaces. Understanding the theory and processes driving the observed distribution patterns is also essential to avoid a mismatch between the scale used for modelling and the one at which key processes occur (Fig. 2). Patterns observed on one scale may not be apparent on another scale. How an overly constrained extent can lead to an incorrect interpretation if only part of an important environmental gradient is sampled, e.g. when using political instead of natural boundaries (e.g. including a whole species range). For instance, the resulting response curves of a species might appear truncated – possibly expressing a negative (e.g. on the colder part of the temperature gradient), a positive (e.g. on the warmer part of the temperature gradient) or nearly no relationship (e.g. on the intermediate part of the temperature gradient) – when the full response should be unimodal. In such case, the use of different geographical extents might thus provide contradictory answers to the same ecological question (see alsoThuiller, 2003). A similar reasoning holds for resolution. For instance, interspecific competition can only be detected at a resolution where organisms interact and compete for the same resources. The same environmental parameter sampled at different resolutions can thus have very different meanings for a species. This is in part because of the various aggregation properties and the possible problem of released matching between various attributes within a cell at coarser resolution, when no more spatial matching is ensured between the predictors and the species occurrence. For some species, like sessile organisms, it will not be sufficient that a combination of suitable conditions occur within the same cell (as e.g. obtained by

aggregating data), but these must additionally overlay at least at one specific location within the cell. In turn, for other species, like mobile animals, spatial matching of resources within the cell may not be necessary. Hence, the selection of resolution and extent is a critical step in HSMs building, and an inappropriate selection can yield misleading results. This issue is directly related to the transmutation problem, or _how to use ecogeographic predictors measured on one scale on another scale. Their integration into a multiscale hierarchical modelling framework (e.g. Pearson, Dawson & Liu, 2004) may provide the solution required to solve this spatial scaling paradigm (Wiens 2002), for instance, by associating scale domains to those environmental predictors identified as having dominant control over species distributions (see Fig. 2). Pearson et al. (2004) developed an interesting approach to evaluate the impact of climate change on plant species in UK. As the modelled species were not endemic to UK, they first developed HSMs over Europe at a rather coarse resolution (50 km grid) to ensure capturing the full climatic range of the selected species. They then projected the species distributions in UK on a 1 km grid using previously fitted models and additionally incorporating land cover data information. They showed that the incorporation of land cover at the finer resolution improved the predictive accuracy of models, compared with what had been shown at the coarser European resolution. Such hierarchical approach could benefit from a Bayesian implementation, as carried out, for example, by (Gelfand, Banerjee & Gamerman, 2005). Although these latter authors mainly used it for combining HSMs with prior information on sampling intensity, the same approach could be extended to combine environmental information from different spatial scales. The additional advantage here would be the possibility to integrate current modelling approaches (as GLM or GAM) and uncertainty analyses into a more general, hierarchical framework (Gelfand et al. 2005). The choice of scale is also closely related to the type of species considered (e.g. its detectability and prevalence in the landscape).
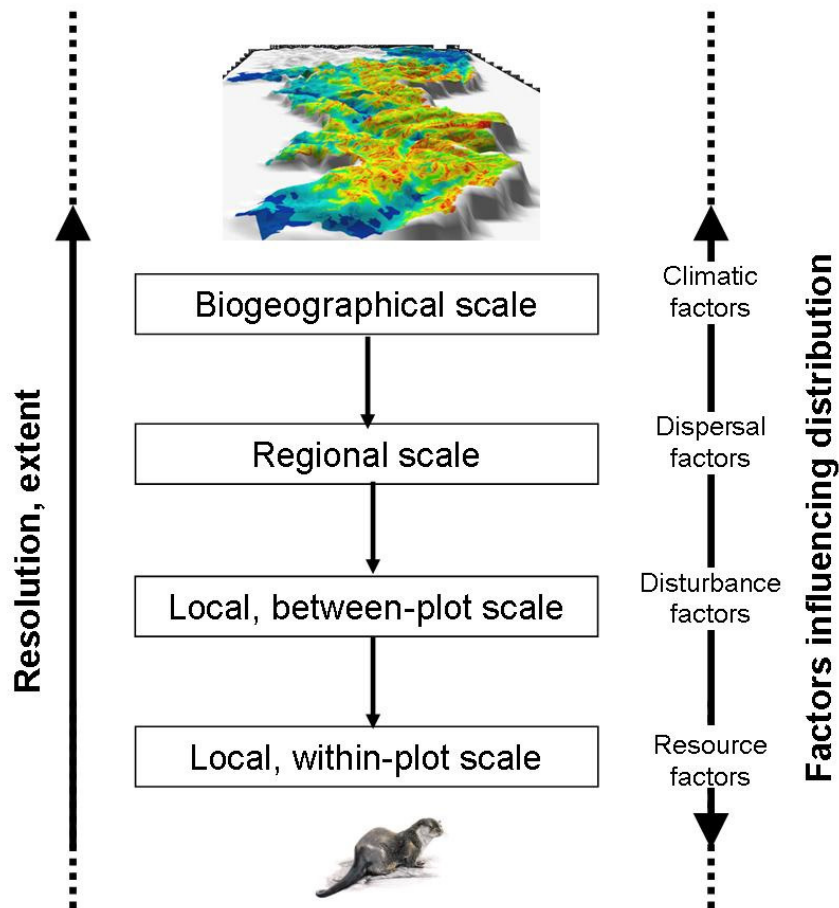
Fig. 2 – Conceptual model of relationships between resolution, factors influencing distribution and scale.

HSMs in conservation planning

NBM research within the field of conservation planning has mainly focused on the development of theories and tools to design reserve networks that protect biodiversity in an efficient and representative manner (e.g. Cabeza et al., 2004). Predicted species distribution data from NBMs are commonly used for conservation planning because the alternative (e.g. survey data) are often incomplete or biased spatially (Andelman & Willig, 2002). Moreover, HSMs and reserve selection algorithms are used together to investigate the pertinence to reserve networks under future global climate change. Several studies have assessed the ability of existing reserve-selection methods to secure species in a climate change context (Coetzee et al. 2009). They concluded that opportunities exist to minimize species extinctions with reserves, but that new approaches are needed to account for impact of climate change on species; particularly for those projected to have temporally non-overlapping distributions. Such achievement can be carried out with HSMs coupled with very simple dispersal model and reserve-selection methods to identify minimum-dispersal

corridors allowing species migration across networks under climate change and land transformation scenarios.

Box 2 – AUC validation
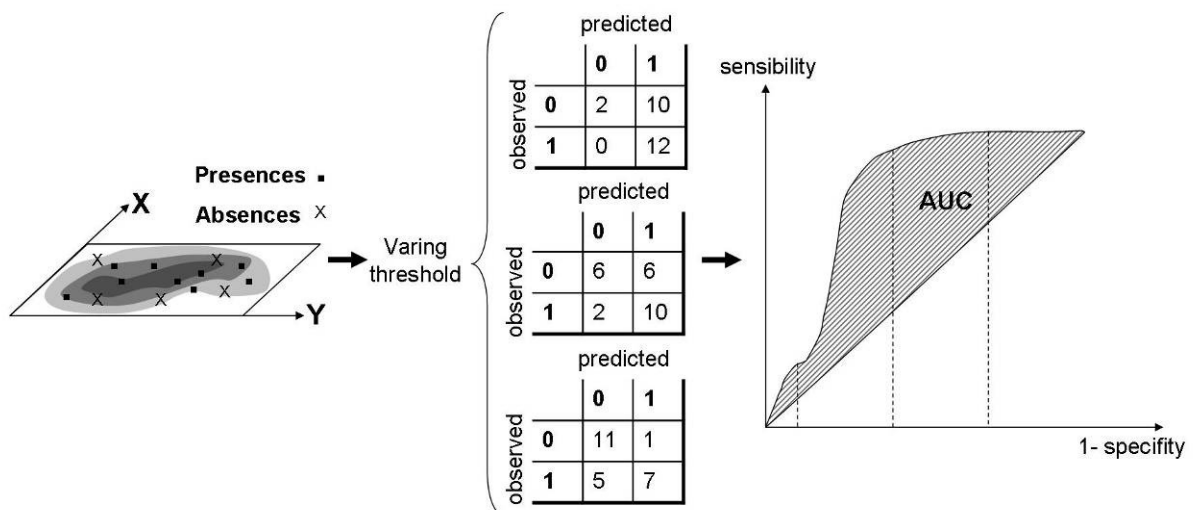
The predictive power of a model can be assessed through the area under the curve (AUC) or a receiver –operating characteristic plot (ROC; Fielding & Bell, 1997; Elith et al., 2006). A varying threshold is applied to transform the prediction into a binary response. At each threshold, the sensibility (the number of true positive) and the 1 – specificity (the number of false negative) is plotted. The area under the ROC curve indicates (AUC) the degree of matching between the known an predicted distribution of the species. Following Swets' scale (Swet, 1988), predictions are considered random when they do nor differ from 0.5, poor when they are in range 0.5-0.7, and useful in the range 0.7-0.9. Predictions greater than 0.9 are considered good to excellent (1=perfect). AUC values under 0.5 reflect counter predictions (omission and commission rates higher than correct predictions).

Habitat suitability predictions often include areas in which species is currently not known to occur. This is especially helpful in the case of rare and endangered species, and in the case of expanding species. Habitat suitability predictions in these cases are promising tools (Guisan et al., 2006) as a way to establish efficient conservation strategies of species of conservation interest. Moreover, the approach is also helpful to determine schemes to mitigate species decline or to target candidate sites for reintroduction programs.

Projecting HSMs into future climates

Even though increasing evidence shows that recent human-induced environmental change have already triggered species' range shift, changes in phenology and species extinction, accurate projections of species' responses to future climate changes are adopt proactive conservation planning measures using forecast of species responses to future environmental changes. To predict the future distribution of a species, HSMs quantify the species environment relationships in the present and project the response curves on altered climate data translating climate change (i.e. climate change scenario). The percentage of species turnover (defined as the index of dissimilarity between the current and future species composition within a given area) and the percentage of species that could persist in, disappear from, and colonize that area are often considered as a good measures of the degree of ecosystem perturbation, and have been used to assess the potential impact of climate change at regional to continental scale (Pearson, Dawson & Liu, 2004). Since the development of finer scale climate change scenarios in the past decades (e.g. Smith et al., 2000), niche-based models that project future suitable habitat from current distributions have suggested that species turnover may be very high in some regions, potentially resulting in modifications of community structure strong enough to lead to ecosystem disruption (e.g. Erasmus et al., 2002 ; Peterson et al., 2006; Thomas et al., 2004). The application of NBMs to climate change analyses was highlighted by a recent, massive study assessing global species extinction risk (Thomas et al., 2004).

1.2 The otter – The situation in Europe and in Italy

The Eurasian otter (*Lutra lutra* L., 1758) is a semiaquatic carnivore whose habitat is usually linked to the existence of freshwater, available shelter (riparian vegetation, rocky structures and others) and abundant prey (Ruiz-Olmo & Delibes, 1998). Until the end of the 19th century the otter occurred in nearly all wetland areas and water systems in Europe. During the first half of the 20th century the species became rare or disappeared completely over large areas of central Europe. The reasons of such dramatic decline are likely related at different combinations of factors appearing with regional variability in their combination and intensity (Mason & Macdonald, 1986; Macdonald & Mason, 1994). These factors include water pollution (mainly by PCBs), direct persecution, and habitat destruction. In the 1990s a reoccupation of former habitats became apparent in some European regions. Nowadays widespread populations exist mainly in western and eastern areas but a wide area covering the central part of Europe, from the southern part of Denmark to the southern Italy and from the east of France to western parts of Austria and Germany, is still more or

less free of otters (Ruiz-Olmo & Delibes, 1998; Kranz, 2000; Mason, 2004; Reuther & Krekemeyer, 2004) (Fig. 3). In Portugal the otter occupies more or less the whole country and in Spain the species is distributed almost regularly across the western half part of the country. In France the otter is present mainly in the western side. In Belgium, Netherland and Luxemburg there are not official data about natural populations. In Switzerland the otter has to be considered extinct. The current core of otter's distribution in Germany is formed by the north-eastern states and in Bavaria a small population is connected with the population in Czech Republic and in Austria. In Denmark the data of the national and regional surveys give evidence that the Danish population is still expanding. In Italy the otter is present only in the southern part of the country, and this population has to be recognised as the most endangered in Western Europe because of its complete isolation. In Austria the major occurrences were found in the northern border regions to Germany and Czech Republic and in the south-eastern border regions to Slovakia and Hungary. In the countries of the Baltic coast the otter is well distributed. In the Balkan Peninsula the otter is well widespread too (Reuther & Krekemeyer, 2004) (Fig. 3).
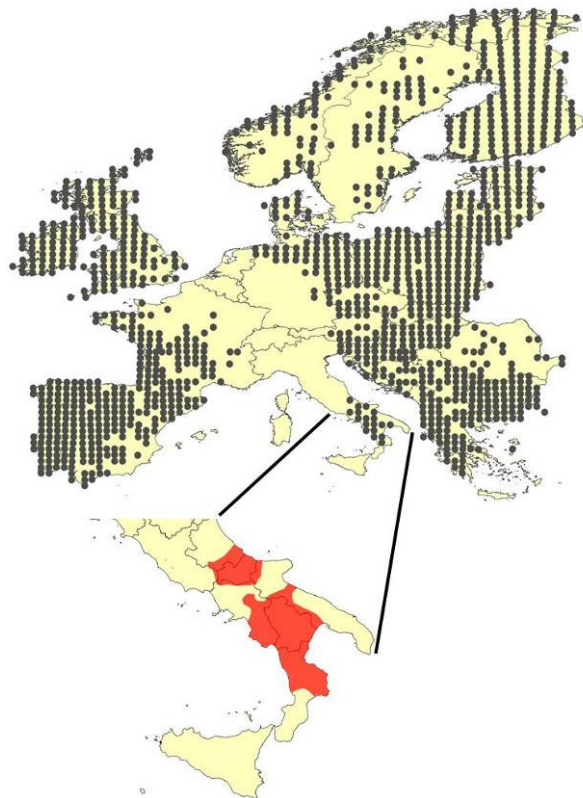

Fig. 3 – Distribution of the otter in Europe and in Italy. The grey dots indicate the presence of the species and they are referred to 50x50km grid cell (source: EIONET).

At European level the otter is included in the List of Rare and Threatened Mammals of the Council of Europe, in Appendix II of the Berne Convention, in Appendices II and IV of the Habitat Directive of the European Union, in Appendix I of the CITES. Until the 2007 the species was classified as *vulnerable* in the IUCN Red List of Threatened Species (Hilton-Taylor, 2000). In the 2007 the species was downgraded to *near threatened* (IUCN, 2007), but its status could be raised if causal factors are not remediated (IUCN, 2007).

In Italy the species was distributed over the whole Italian country before 1950 (Cagnolaro et al., 1975), but by the end of he XX century it was confined to a small part of southern Italy (Spagnesi, Toso & De Marinis, 2002). Causes for this decline include hunting, food shortages (mainly of fish), and the destruction of riparian vegetation (Mason, 1989; Conroy & Chanin, 2000). Presently, the otter's Italian population consists of two, apparently isolated, populations (Fig. YY) (Fusillo, Marcelli & Boitani, 2007). The otter was then included as a *critically endangered* in the Italian vertebrates red lists (Calvario & Sarrocco, 1997).

The need for conservation strategies for the otter

The fragmentation and the separation of the European distributions could not assure the genetic diversity necessary to ensure the long term persistence of the species (Reuther & Krekemeyer, 2004). The conservation of the otter would benefit from large scale conservation policies aiming to promote the population expansion and reconnection. Thus the identification of the large scale factors that affect wild population, the recognition of gaps of unsuitable habitats and suitable habitat for species recovering are crucial to efficiently define conservation actions (Robitaille & Laurence, 2002).

In this sense habitat suitability models are a fundamental tool for the conservation of the otter as they provide a geographic perspective for conservation strategies. For the conservation of the species it is important to understand what are the factors that affect otter distribution at large scale and to develop an habitat suitability map for the otter in Europe to predict the otter recovering in a medium to a long term.

The implications for the otter's conservation are several; for example:

• To address conservation actions on environmental features that affect population survival;

• To identify suitable areas susceptible to be re-colonised where it would be important to limit perturbations and habitat destruction;

- To identify critical areas for dispersal, so as to improve connectivity between suitable patches;
- To discover unknown nucleus in areas of high habitat suitability (model-based sampling).

Instead, the Italian population has been slow to recover, and signs of the species' expansion are only beginning to appear (Prigioni, Balestrieri & Remonti, 2007). The budding expansion process, the relatively small size of the otter Italian population and the presence of two disjoint populations all lend importance to the establishment of effective conservation strategies. Among conservation priorities are (i) the protection of the areas of potential otter recolonization, and (ii) a better understanding of the otter's habitat requirements at fine scale.

1. 3 Objectives and content of the main chapters

The general aim of this PhD thesis is to assess the usefulness, effectiveness and shortcomings of habitat suitability models applied at different spatial scales to identify suitable areas susceptible to be re-colonised by the otter to establish effective conservation strategies for the species.

Given the broad scope of the issue, this will be achieved by conducting specific studies aiming to investigate important unsolved limitations and suggest new approaches.

Chapter 2 presents an approach combining a fine scale Habitat Suitability (HS) model and connectivity analysis to identify areas where the otter could potentially expand in the short-medium term within and around the south-central Italian subpopulation. The HS model was also used to identify rivers with particularly suitable habitats that could provide source populations.

Chapter 3 presents a study to test the capacity of HSMs in identifying the locations and characteristics of the areas potentially suitable for the recovery of the European otter in Italy. More generally, we expected the results to help in defining guidelines for a right use of the HSMs, especially in non-equilibrium situations, such as spreading species. We considered two species distribution datasets: the first was collected before, and the second after, a recolonization event. We assumed that the first situation was not at equilibrium, and that the second had reached a sub-equilibrium state. For HSMs, we used two common methods, one dealing with presence-only data, and the second using presence and absence data of the species. We computed and cross-validated models based on the pre-

colonization dataset and then externally validated them with the post-colonization dataset. The modeling methods were deliberately chosen among the commonly used methodologies, as we wanted our results to be useful to other researchers and conservation practitioners.

Chapter 4 presents a study with the aim in determining which factors influence the otter distribution and use them to predict the potential distribution of the species in Europe, under current and future climate. The environmental variables used are related to water availability, food supply, resting site and human disturbance using six different modelling approaches. Future projections are derived by running the CCM3 climate model under a $2xCO_2$ increase scenario. At the European scale, the otter is mostly influenced by water availability. The current potential distribution reveals large gaps of unsuitable habitats limiting connectivity between otter populations in Europe. Climate change would have different effects on otter habitat suitability in Europe. In the Western part, the model predicts losses of suitable habitats, whereas gains are predicted in central Europe and Eastern Europe shows equal rates of losses and increases of suitable habitat. Our results are important in helping setting up conservation actions and promote otter recovery in Europe.

Chapter 5 describes the project which is in progress aiming to assessing the potential of Swiss landscapes to sustain the reintroduction of otter populations, through the development and application of a habitat suitability model, calibrated at the European scale, then projected and refined with local environmental predictors at a finer scale over Switzerland, and verified in the field.

CHAPTER 2 – HABITAT SUITABILITY AND CONNECTIVITY FOR THE OTTER

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Otter *Lutra lutra* population expansion: assessing habitat suitability and connectivity in southern Italy

Anna Loy[1]*, Maria Laura Carranza[1], Carmen Cianfrani[1], Evelina D'Alessandro[1], Laura Bonesi[2], Piera Di Marzio[1], Michele Minotti[1] and Gabriella Reggiani[3]

[1] *Università del Molise, Contrada Fonte Lappone, I-86090 Pesche, Italy; e-mail: a.loy@unimol.it*

[2] *Università di Trieste, Via Weiss 2, I-34127 Trieste, Italy*

[3] *Istituto di Ecologia Applicata, Via Cremona 71, I-00161 Roma, Italy*

Abstract

The Eurasian otter is one of the most endangered mammals in Italy and its distribution is now restricted in two isolated portions in southern Italy. However, in recent times, this species has shown a tendency to expand its range, especially northwards. It is therefore important to identify suitable areas on the border of its expansion range where the species can establish and disperse, so that these areas can be targeted for conservation actions. To this aim, the distribution, quality and connectivity of habitats of seven river catchments located in the northern portion of the current otter range in Italy were assessed. Catchments included both rivers where the otter currently occurs and where it is likely to expand in the short-medium term. An expert-based Habitat Suitability (HS) model was developed and validated using otter presence-absence data based on standard field surveys. Fine scale riverbank land cover, extra-riparian coarse scale land cover, altitude, bank slope, and human disturbance were considered as the main factors in the HS model. These variables were available or newly created in the form of digital maps (layers) and the HS model was built by sequentially filtering these layers. Connectivity was assessed within and between river basins through landscape algorithms by taking into account variables that could influence otter dispersal. The results indicated that the seven rivers considered are heterogeneous both in terms of habitat suitability and in terms of connectivity. Among these, one river in particular (the river Volturno), where otters are currently present, showed one of the largest extensions of suitable habitats and the best connectivity both within the river and between the river and the neighbouring catchments, suggesting that this river could play a strategic role in the survival and expansion of otters in the surrounding areas.

Introduction

The Eurasian otter (*Lutra lutra* L.) is a semi-aquatic carnivore that underwent a strong decline in Europe between the 1960s and the 1980s (Mason & Macdonald 1986, Mason 1989, Macdonald & Mason 1994). Several factors have been suggested to explain this decline, including the reduction of food supply, pollutants, human persecution, and the destruction of riparian vegetation (Mason & Macdonald 1986, Macdonald & Mason 1994, Conroy & Chanin 2000, Kruuk 2006). The decrease in the concentration of harmful pollutants in the environment due to more stringent regulations (Pacyna 1999) and the enactment of legal protection have allowed otter populations to gradually recover since the 1980s in several European countries (Conroy & Chanin 2000, Roos et al. 2001, Mason & Macdonald 2004). Compared to other populations in Europe, the Italian population has recovered rather slowly, and signs of the species expanding its range have only recently started to become apparent (Prigioni et al. 2007). Despite the fact that the IUCN Red list and the European Mammal Assessment consider the Eurasian otter as *near threatened* (Temple & Terry 2007, 2009; Ruiz-Olmo et al. 2008), this animal is still considered a critically endangered species in Italy (Bulgarini et al. 1998). At present, the Italian range of the otter is confined to the southern part of the Italian peninsula (Fig. 1), while originally the species was distributed all over the country (Cagnolaro et al. 1975). The residual population is relatively small (Prigioni et al. 2006a, b) and it is geographically isolated and genetically differentiated from other European populations (Randi et al. 2003). Furthermore, this population is currently separated into two isolated subpopulations (Fig. 1): the largest one located in southern Italy and the smallest one, only recently discovered, located in south-central Italy (Loy et al. 2004, Fusillo et al. 2004, 2007, Prigioni et al. 2007).
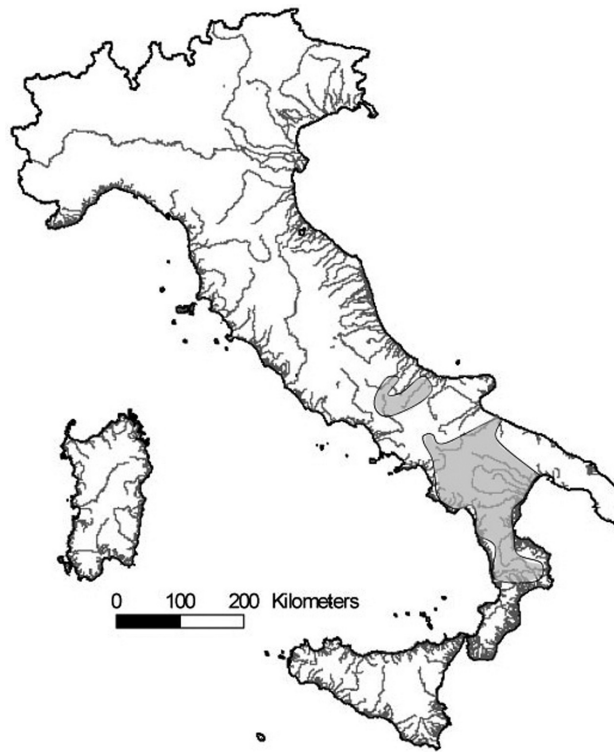
Fig. **1 -** Distribution range of the otter *Lutra lutra* in Italy.

The subpopulation of south-central Italy is currently expanding northward (De Castro & Loy 2007) while there is no indication that otters are currently colonising the gap that separates the two subpopulations. Given the small size and the current expansion trend of the south-central subpopulation, it is important to identify rivers that can potentially host otters in the area and also to identify the rivers and land areas through which the species could disperse to better target conservation actions aimed at promoting the recovery of the species.

In this study, an approach combining a fine scale Habitat Suitability (HS) model and connectivity analysis was adopted to identify areas where the otter could potentially expand in the short-medium term within and around the south-central subpopulation. The HS model was also used to identify rivers with particularly suitable habitats that could provide source populations. HS models for otters have been produced on different geographic scales (Ottino et al. 1995, Prigioni 1995, Prenda & Granado-Lorencio 1996, Antonucci 2000, Reggiani et al. 2001, Barbosa et al. 2001, Boitani et al. 2002) with a resolution which is usually greater than 1 km. However, fine scale approaches are still lacking. The fine scale approach is particularly critical for otters, as some important habitat requirements such as riparian vegetation cover may not be related to the available coarse scale environmental GIS variables usually used to build HS models.

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Study Area

The study area comprised seven river catchments of south-central Italy (Sangro, Biferno, Trigno, Fortore, Saccione, Sinarca, and the upper part of the River Volturno) located mostly in the Molise region (Fig. 2). These catchments comprise both rivers where otters are currently present and neighbouring rivers where otters are likely to expand in the near future.

The total length of the water courses considered in the study was 1 943 km. A standard survey run in the years 2000-2004 (Fusillo et al. 2004, Loy et al. 2004) revealed that otter occurrence was restricted to the Biferno and upper Volturno catchments. Sporadic records of otters were also reported for the river Fortore, while otters were seemingly absent from the rivers Sangro, Trigno, Saccione, and Sinarca (Fig. 2). A more recent survey in 2006 revealed signs of otter occupation on the river Sangro, which is located in the north-western part of the study area (De Castro & Loy 2007).
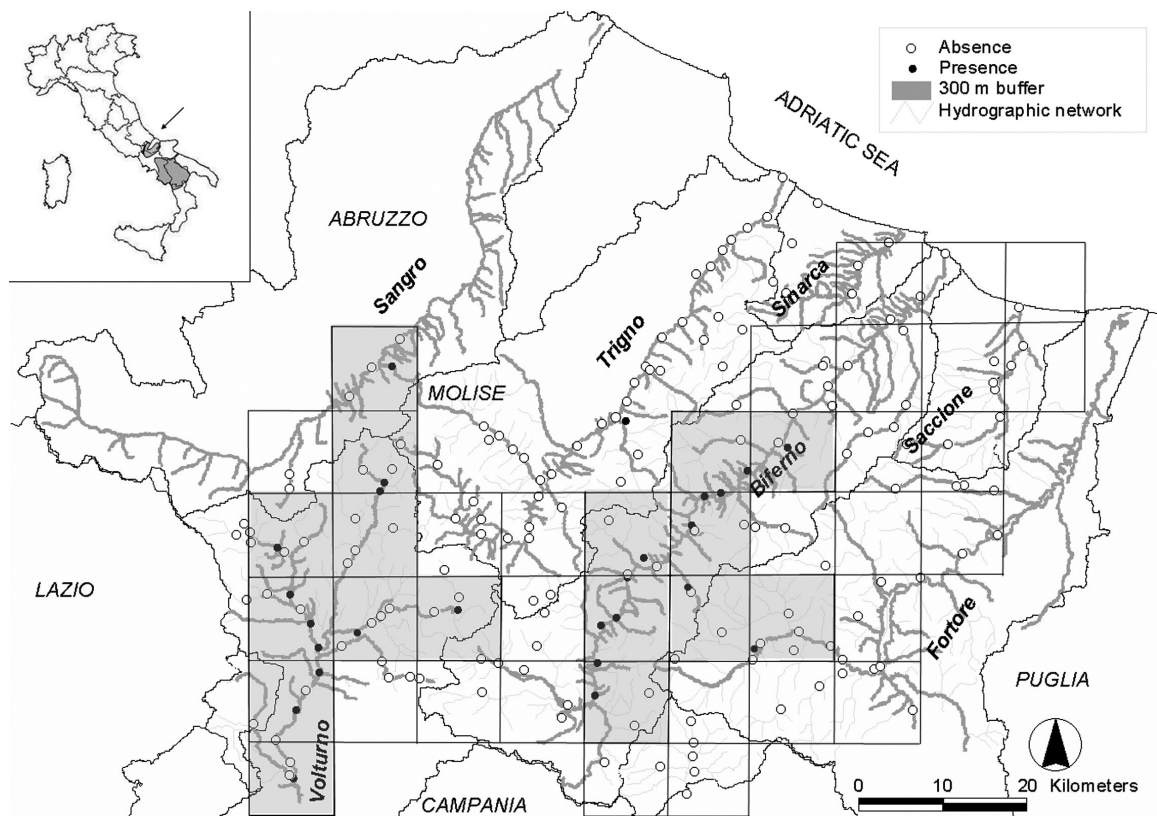

Fig. 2 - Map of the study area with the seven river catchments. Only the southern tributaries of the river Trigno and Sangro were considered, as the standard survey was limited to the river basins of the Molise region (see text). The map also shows the UTM grid cells of 10x10 km used to validate the HS model. Shadowed cells indicate otter presence. The white circles report negative otter sites, while the black ones report positive otter sites (Loy et al. 2004).

Material and Methods

Habitat Suitability model development

The HS model was expert-based, rather than inferential. There were two reasons behind this choice: 1) an inferential approach applied on the peripheral areas of an expanding species' range may fail to discriminate between suitable and unsuitable areas because suitable areas may not yet be occupied (Jason et al. 2002, Clevenger et al. 2002, Ottaviani et al. 2004); 2) European otters have been thoroughly studied and many of the factors that influence their biology and ecology are well known (Mason & Macdonald 1986, Mason 1989, Beja 1992, Madsen & Prang 2001, Bonesi & Macdonald 2004, Kruuk 2006).

As availability of water represents a main ecological factor affecting otter occurrence (Beja 1992, Prenda et al. 2001, Bonesi & Macdonald 2004, Kruuk 2006) the model was developed on those river stretches that were likely to have water all year round. Main river courses and first and second order tributaries were selected from the national hydrographical network (1:250000 map obtained from the national environmental agency, ISPRA) and included in the model. Spatial information on the distribution of the otter's resources and disturbance factors was derived from existing digital maps and. However, for the "bankside fine scale land cover" variable, a specific spatial data set was developed. Each variable was inserted into a G.I.S. system as a different layer and all categories within each variable were reclassified according to their suitability for otters (Appendix 1). More specifically, the following variables were considered:

Bankside fine scale land cover (1:5000). Many studies have found relationships between the number of otter signs and bank side cover (Jenkins & Burrows 1980, Macdonald & Mason 1982, 1985, 1988, Bas et al. 1984, Adrian 1985, Prauser 1985, Delibes et al. 1991). As this parameter is not detectable from the usual coarser CORINE land cover maps, data were obtained by digitising land cover categories derived from aerial photos taken in 2005 and considered at a resolution of 20 m. This variable was considered on a 300 m large buffer around the river. The categories used were those of the CORINE land cover classification scheme at the third level of detail (European Commission 1993). The procedure of assessing land cover from aerial photos at a scale of 1:5000 allowed us to gain a good representation of the riparian vegetation on and around the river banks. The role of riparian vegetation was then considered according to its use in providing breeding dens, enhancing the filtering of pollutants and promoting fish productivity (Jenkins & Burrows 1980, Green et al. 1984, Macdonald & Mason

1994, Rader 1997, Morrow & Fischenich 2000). The CORINE land cover categories were then re-classified accordingly (Appendix 1 – layer 1 in Fig. 3).

Bank slope. A slope layer was derived from the Digital Elevation Model at a resolution of 20 x 20 m. Cells within the buffer area with a slope of 70° or more were considered as evidence of rock cliffs, potentially providing good sites for resting and breeding dens (Chanin 2003), and were classified as highly suitable (Appendix 1 – layer 1 in Fig. 3).

Altitude. This variable is important because otters are rarely found above 2000 m a.s.l., probably due to the scarcity of food available at high altitudes (Ruiz-Olmo 1998, Kruuk 2006). We used the 20 m resolution Digital Elevation Model to classify the area into four altitudinal ranges of decreasing suitability (Appendix 1), producing a new layer (layer 2 in Fig. 3).

Human density. This variable can potentially affect the presence of otters negatively (Barbosa et al. 2001, Chanin 2003) and was derived by considering the density of people in each municipality within a buffer of 1 km surrounding the river (Appendix 1 – layer 4 in Fig. 3).

Coarse scale extra-riparian CORINE land cover (1:100 000 map, year 2000). Extra-riparian disturbance was considered within a buffer of 1 km surrounding the river. The presence of land types such as urban settlements and intensive agricultural areas were considered to have a potentially negative affect the presence of otters (Barbosa et al. 2001, Boitani et al. 2002). Land cover maps were rasterized to 1 x 1 km grid cells and reclassified according to presence/absence of a negative effect (Appendix 1 – layer 4 in Fig. 3).

All GIS layers described above and saved in a raster format at a resolution of 20 x 20 m were then integrated following the scheme presented in Fig. 3 to produce the final layer of habitat suitability for the otter. First of all, the bank slope layer was overlapped to the bank side fine scale land cover layer. Cells with bank slopes which were steeper than 70° were given a high suitability value (three). When a cell had a bank-slope value of three, this figure was retained irrespective of the value of the bank side fine scale land cover, to take into account the fact that when rock cliffs are present the surrounding land cover matrix may have little influence on otter presence. The resulting layer was characterized by 20 x 20 cells with HS integer values ranging between zero and three (layer 1). This layer was then combined with the altitude layer (layer 2) to produce four synthetic suitability classes ranked between zero (less suitable) and three (most suitable) through a logical overlay operation. This operation assigned a suitability class value to each 20 m cell by

choosing the lowest value between those of the two input layers (1 and 2). The new layer (layer 3) so created was also made of integer numbers ranging between zero and three (Fig. 3). Human disturbance was then taken into consideration by subtracting values of 0.25 or 0.50 from this new layer if, respectively, one or both disturbance factors (human density and unfavourable land cover) were present (layer 4). If no disturbance was present, the layer retained its original value. The maximum number of final suitability classes resulting from this procedure was ten, ranging in values from zero (least suitable) to three (most suitable) (Fig. 3) and these values were assigned to each 20 x 20 m cell within a buffer of 300 m surrounding the river.

Habitat Suitability Model validation

Validation of the HS map resulting from the application of the model described above was performed using available data on the presence and absence of otters in the area derived from a standard otter survey (Loy et al. 2004). Otter presence/absence was reported in UTM grid cells of 10 x 10 km, considering only the river basins of current otter occupancy, for a total 42 UTM grid cells (Fig. 2). The river Trigno was excluded from the validation analyses as it was the furthest away from areas with otter presence. Hence, it is likely that the absence of otters along this river is due to the fact the species has yet to arrive there rather than to the characteristics of the river. The UTM grid cells were classified as positive (17 out of 42) if they contained at least one positive site where otter signs (spraints or footprints) had been recorded. Both presence and absence data were considered for the validation of the model. It must be stressed that absence data obtained for this species using the standard surveys are considered to be more reliable than for other species for which absence is more likely to mean non detection (Reuther et al. 2000). The percentage of the 300m buffer around the river covered by each of the ten suitability classes was computed within each UTM grid cell of 10 x 10 km. The percentage area covered by each HS class was then compared between 10 x 10 km UTM grid cells which were positive or negative for otters through a non parametric Mann–Whitney U-test.

Accuracy of the model was then tested through a sensitivity analysis for HS classes showing significant differences either for presence or absence of otter signs. Sensitivity analysis was performed by applying the ROC (Receiver Operating Characteristics) technique (Fielding & Bell 1977, Swets 1998, Manel et al. 1999, Greiner et al. 2000, Osborne et al. 2001). The suitability classes that successfully passed the test were used to define a threshold between two large categories of suitable and non suitable habitats.
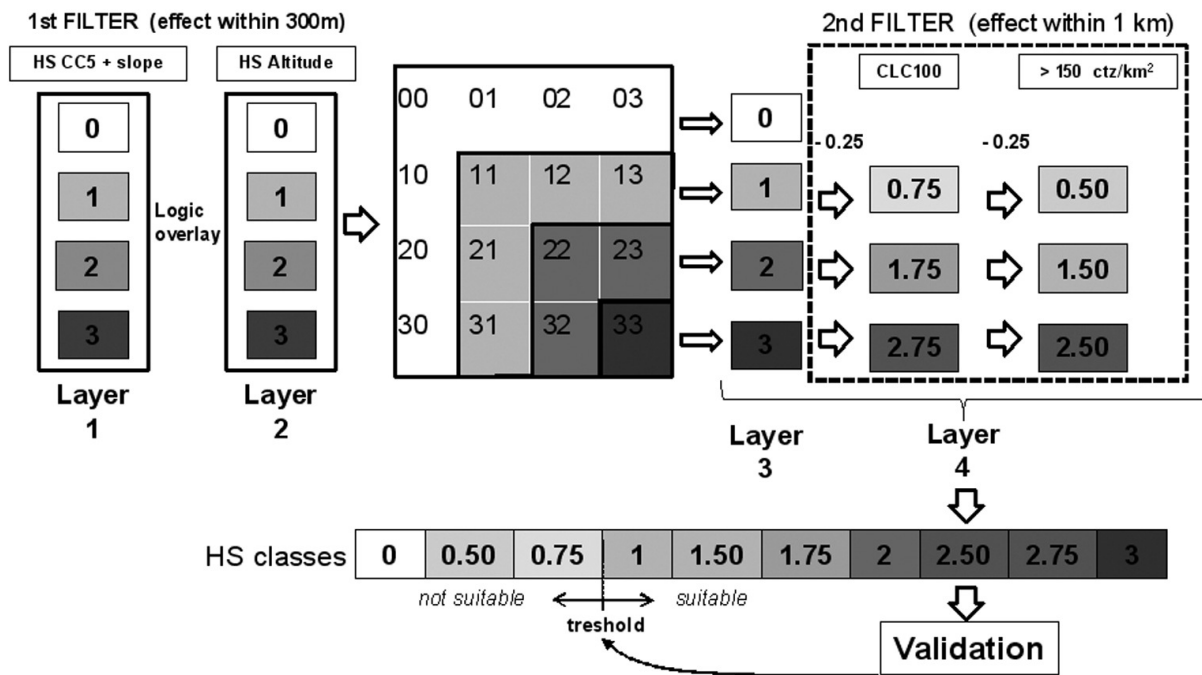
Fig. 3 - Flow chart of the procedure used to create the 10 HS suitability classes. The first number in each cell of the square matrix in the middle represents layer 1, while the second number represents layer 2. The dotted square on the right represents the process of subtracting human disturbance (human density and land cover derived from the CORINE 1:100 000) from layer 3.

Connectivity analysis

Otter habitats tend to develop along linear features of the landscape, namely the hydrographical systems (Philcox et al. 1999, Kruuk 2006). Analyses examining the connectivity of the landscape along linear features such as rivers are relatively new (Bennett 1999, Wiens 2002, Schick & Lindley 2007) and pose some specific problems in that both longitudinal and lateral connectivity must be evaluated (van Langevelde et al. 1998). Longitudinal connectivity refers to otters moving within one river system, while lateral connectivity refers to dispersal movements toward neighbouring rivers, which contribute to range expansion and the maintenance of gene flow among populations living in different river basins. As river catchments can be considered as closed systems, the longitudinal connectivity can be simply evaluated through the distribution of suitable habitat patches, while the lateral connectivity must also consider the resistance (permeability) of the land matrix to dispersal by otters between catchments (Schumaker 1996, Tischendorf 2001).

Longitudinal connectivity along rivers was analysed by summarising two classical spatial pattern statistics of suitable habitat distribution (Mac Garigal & Marks 1995, McGarigal et al. 2002). More specifically, the extension and fragmentation of suitable

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patches, as identified by the HS model, within the 300 m buffer along rivers were evaluated through their number patches (NUMPs) and mean patch size (MPSs). These data were evaluated considering the mean distance covered by an otter during its daily movements in Italian river catchments, which was respectively 10 km for males and 6 km for females (Di Marzio 2004).

Lateral connectivity was assessed by evaluating the resistance of the land matrix between neighbouring catchments to otter movements, i.e. dispersal. The following layers of the land matrix were considered to be relevant in evaluating resistance to otter dispersal: slope, land cover, altitude, human density and road networks (Philcox et al. 1999, Janssens et al. 2006). The analysis was performed within the region Molise area, for which all GIS layers were available. Source of data for slope, altitude and land cover were the same as those specified for the HS model; road networks were derived from a 1:250 000 digital map of the National Environmental Agency (ISPRA). Specifically, slopes were considered to be impermeable when greater than 45° (Cortés et al. 1998, Saavedra & Sargatal 1998, Saavedra 2002, Janssens et al. 2006); altitude, CORINE land cover map at scale 1:100 000, and roads were reclassified for permeability as listed in Appendix 1. All the reclassified layers were then rasterized at a resolution of 20 x 20 m. The logical overlay of the considered layers allowed the identification of areas which were permeable to otter dispersal between catchments. A group of contiguous 20-meter permeable cells formed a permeable patch. The efficacy of each permeable patch was analysed considering its extension and the number of river tributaries connected within it. To this aim, we considered the whole hydrographical network at a resolution of 1:250 000 (source ISPRA), rather than only the main course and main tributaries as in the HS model.

Results

HS model results and validation

Of all the ten HS classes resulting from the HS model, only three held sufficient data for the validation analysis (Fig. 4). The Mann–Whitney U-tests revealed significant differences between positive and negative UTM cells for the HS classes with values of 0.75, 1 and 3 ($p < 0.05$ for all pairwise comparisons). HS classes 1 and 3 were found to be significantly associated with the presence of otters, while the 0.75 class was significantly associated with their absence. No significant difference was reported for the other HS categories, which is probably due to their small sample size.
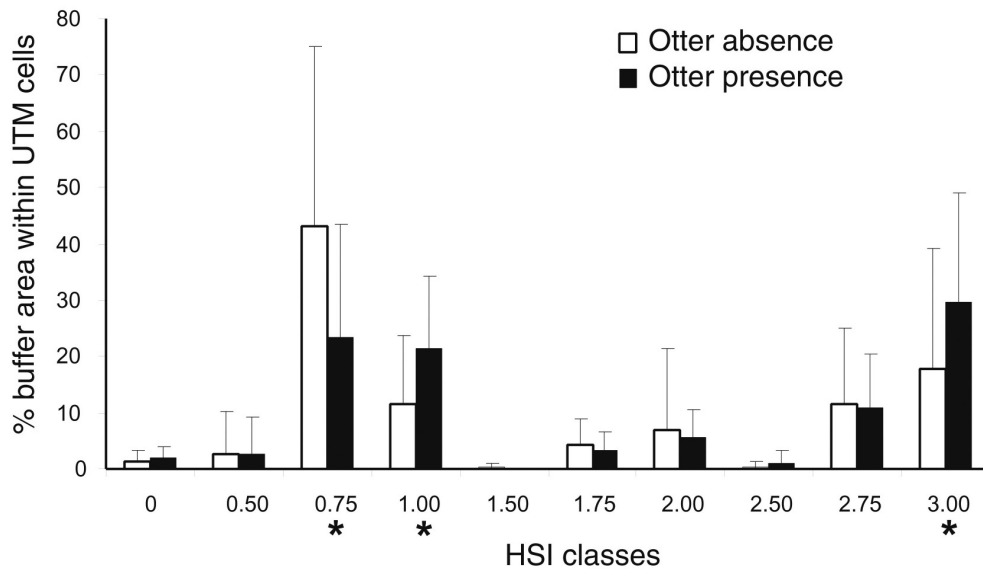
Fig. **4** - Mean and SD of suitable (filled bars) and unsuitable (empty bars) areas computed for HS classes within each UTM cell shown in Fig. 2. Asterisks indicate HS classes showing significant differences between presence-absenceUTM cells (Mann-Withney U, p < 0.05).

The three significant HS classes with values of 0.75, 1 and 3 were subjected to a sensitivity analysis using ROC curves. For HS class 1 and 3, the Area Under the ROC curve (AUC) had, respectively, the values of 0.74 and 0.69, suggesting that they were able to discriminate the presence of otters relatively well (Fig. 5A). The ROC plot to test for the sensitivity of the HS class 0.75 was used to evaluate its ability to predict otter absence, rather than presence (Fig. 5B). Also in this case, an AUC value of 0.68 suggested a good probability of a correct prediction.
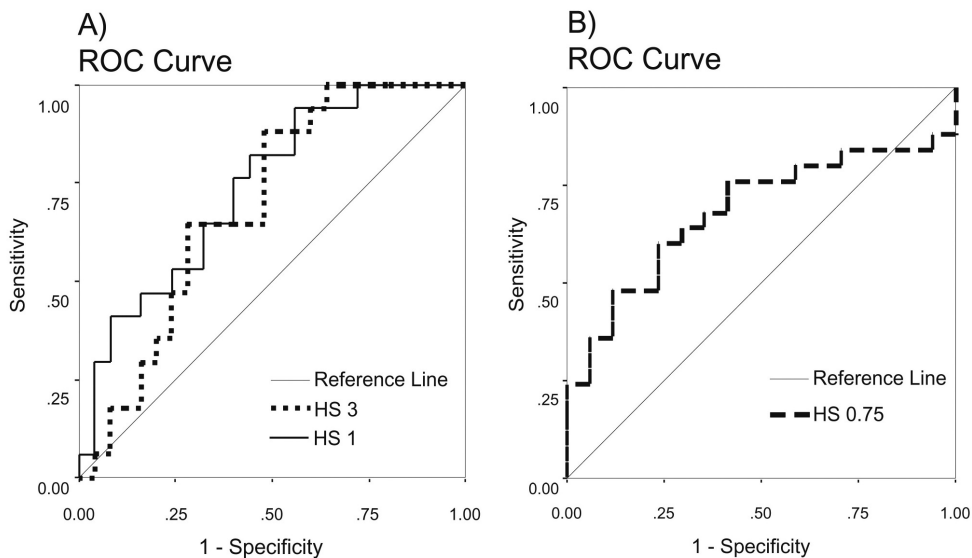

Fig. **5**. A – ROC plot for the HS values 1 and 3, testing the accuracy to predict the presence of otters. B – ROC plot for the HS value 0.75, testing the accuracy to predict the absence of otters.

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Based on the above results, we considered 0.75 as a threshold value and a new HS map was hence produced by reclassifying all 20 x 20 m cells as non-suitable or suitable, according to whether they were, respectively, above or below this HS value (Fig. 6).

The river Biferno, followed by the river Sangro, Trigno and Volturno were identified by the HS model as the ones with the highest suitability for otters (Figs. 6 and 7). Suitable areas were concentrated in the upper and medium course of the rivers, while the lower plains were generally unsuitable for otters. A small concentration of suitable areas was also found in the upper river Fortore, where scattered otter signs were found, whilst its lower course and the whole course of the rivers Sinarca and Saccione were classified as unsuitable for otters.
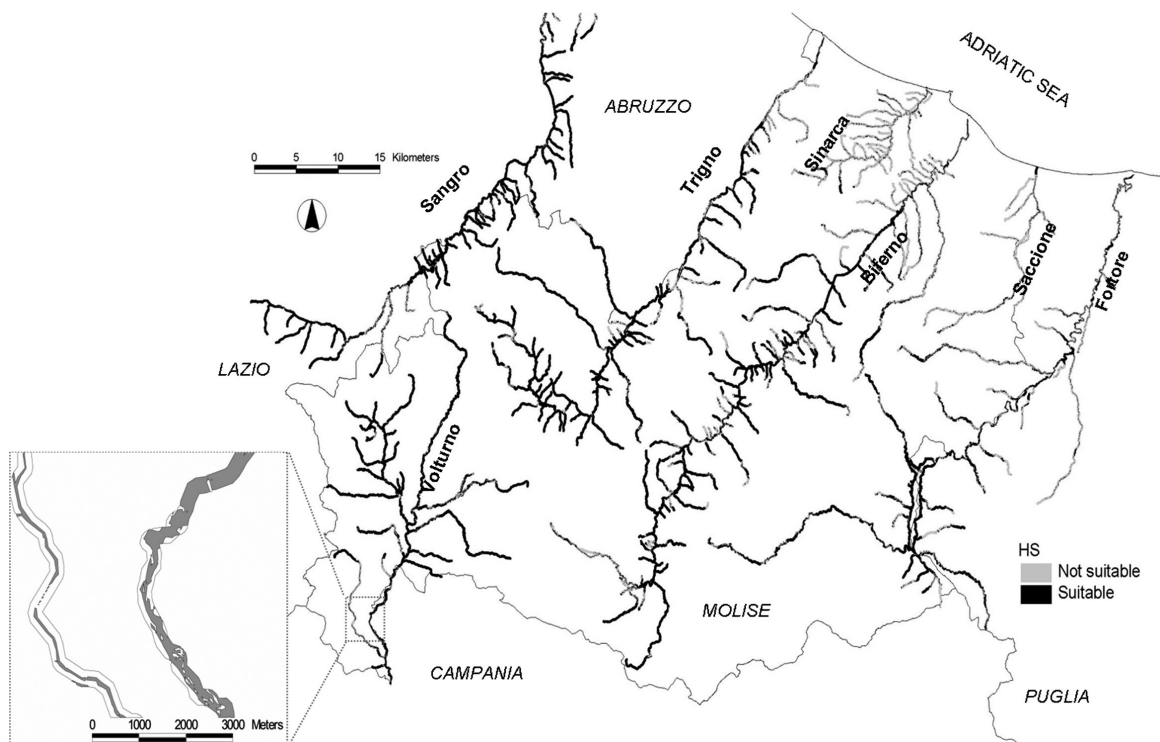

Fig. 6. Map showing the distribution of suitable (HS ≥1) and unsuitable (HS < 1) habitat patches for the seven river catchments of the study area.
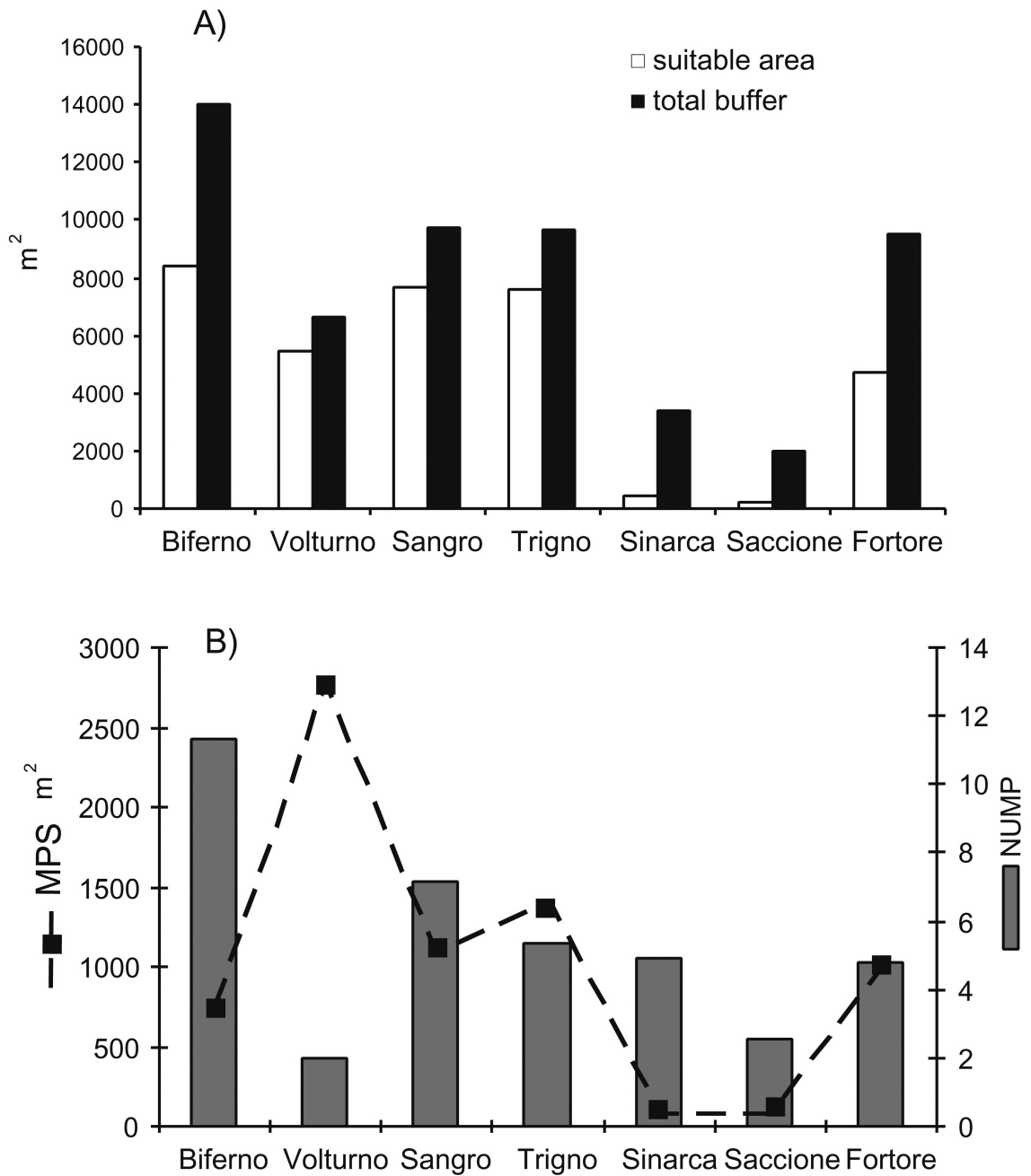
Fig. **7**. A – Comparison of the total buffer extension and total surface of suitable habitat for each river basin. B – Mean size (MPS) and number (NUMP) of suitable patches for the same river basins.
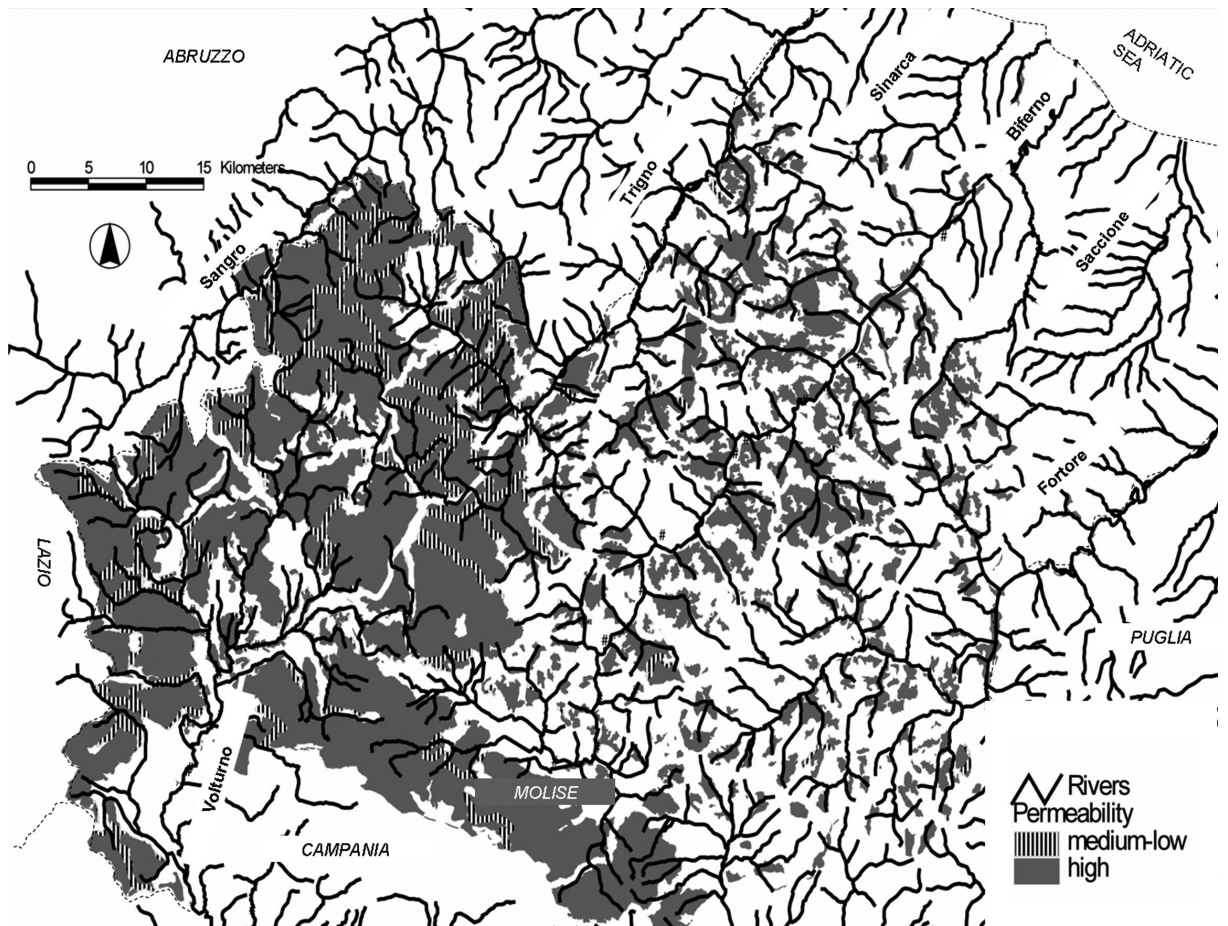
Fig. **8** - Results of the lateral connectivity analysis for the river catchments within the region Molise. Patches are shaded according to the degree of permeability to otter moving across the watersheds.

Connectivity analysis

The analysis of the distribution and extension of suitable patches along rivers (longitudinal connectivity) indicated that the river Volturno had the best connectivity having the largest extension of suitable patches and the most connected patches (Fig. 7). The rivers Biferno, Trigno and Sangro had also, overall, a relatively large extension of suitable patches, but their distribution was quite different from the suitable patches on the Volturno. Indeed, on these three rivers suitable patches tended to be numerous but highly fragmented.

The map in Fig. 8 reports the results for lateral connectivity and highlights a concentration of areas of the land matrix that are likely to be permeable to otter movements located between the upper river Volturno and the river Sangro, Trigno and Biferno, whilst permeable areas between the other catchments are less extended and more fragmented. The high permeability around the upper reaches of the Volturno probably allowed the recent

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otter expansion to the Sangro river basin (De Castro & Loy 2007), and will likely lead to the recolonization of the river Trigno in the short term.

Discussion

The fine scale HS model adopted in this study was well able to discriminate between areas with and without signs of otters for the subpopulation living in the northern portion of the Italian otter range, suggesting that riparian vegetation cover (fine scale land cover), bank slope, altitude, and human disturbance (human density and extra-riparian land use) can be useful factors for assessing the probability of otter presence or absence in an area.

Riparian vegetation may be important for otters for several different reasons: it provides resting and breeding dens, provides cover during movements, enhances filtering of pollutants, and promotes fish productivity (Jenkins & Burrows 1980, Green et al. 1984, Macdonald & Mason 1994, Rader 1997, Morrow & Fischenich 2000). It is possible that in Italy vegetation cover may play a particularly important role in protecting the animals from human and human-related disturbance. Indeed, human disturbance is likely to be particularly important in constraining the distribution of otters in southern and central Italy because otters are still illegally killed (Laura Bonesi, unpublished data), rivers are often surrounded by areas with a relatively high human population density, and feral dogs, that are known to be a threat to otters (Marjana Hönigsfeld, pers.obs.), are often present. While these threats are still also common in other Mediterranean countries (e.g. Robitaille & Laurance 2002), all or most of them are often absent from areas or countries, like for example the UK, where otters are known to live along rivers with scarce or absent riparian vegetation and which even frequent urban environments (Crawford 2003). Similarly to riparian vegetation, steep rocky banks, which are taken into account in the model with the variable "bank slope", may be important as they provide protection from disturbance because they are not easily accessible overland by both humans and dogs. Ruiz-Olmo et al. (2005) in their study of female otters with cubs in north-east Spain also found that otters, in particular older cubs, tended to be concentrated around areas which were well protected by steep rocky cliffs. Finally, altitude may play a role as usually the upper reaches of the streams that are found at higher altitudes tend to host a less diverse community of fish and fish biomass is less abundant (Ruiz-Olmo 1998). Compared to other HS models developed for otters (Ottino et al. 1995, Prigioni 1995, Prenda & Granado-Lorencio 1996, Antonucci 2000, Barbosa et al. 2001, Reggiani et al. 2001, Boitani et al. 2002), our model was based on a much finer scale as it considered habitat variables at a resolution of 20 x 20 m. We think that working at this fine scale resolution may provide a management tool that allows an accurate identification of specific sites along rivers which could benefit from special

protection or from specific improvements that may favour the otter. The model of matrix permeability was able to identify overland areas where corridors which would favour otter dispersal are more likely to occur within and between catchments, thus offering a tool for the management of the extra-riparian landscape for otter conservation. The identification of suitable habitat patches for otters within rivers, along with the assessment of the permeability of the land matrix to dispersal and the presence/absence data, provide a general framework to interpret the otter's movements within and between river basins and to make an assessment of each catchment in terms of its ability to host source or sink populations. Among all the seven catchment considered, one river in particular (the river Volturno), where otters are currently present, showed one of the largest extensions of suitable habitats and the best connectivity both within the river and between the river and the neighbouring catchments, suggesting that this river could play a strategic role in the survival and expansion of otters in the surrounding areas, and in the joining of the two isolated portions of otter range.

In fact, otters at present occur in two portions of this river basin, the upper Volturno in the south central range, and one of its tributary in the southern range. Thus the colonization of the medium course of this river will likely allow the joining of the two ranges in the short-medium term.

In spite of the ability of the HS model to predict relatively well presence and absence of otters at a 10 x 10 km resolution, there are, however, a number of limitations to our model. First of all, the model is based on the distribution of spraints and not on the distribution of the actual animals, but there are two factors that may mitigate this limitation. First, in otters, spraints are likely to be used to signal the use of resources such as food and dens, rather than reproductive status or aggressive encounters, at least when they live in groups such as on the Shetland coast (Kruuk 1992). In freshwater areas, otters live at lower densities than in coastal areas and tend to be more solitary, although their home ranges may still overlap, especially between males and females (Kruuk 2006). If in freshwater areas, spraints are also used to signal the use of resources, then the distribution of spraints may be considered as an acceptable surrogate for the distribution of otters in HS models which consider variables that are directly linked to the use of resources or disturbance, such as ours. Second, to validate the model, we considered a spatial scale of 10 x 10 km, which is in the order of magnitude of an otter's home range, i.e. 10-20 km (Antonucci 2000). Probably due to the fact that we considered relatively large validation cells of 10 x 10 km and a relatively large study area with enough variability, the use of spraints as surrogates for otter distribution was not particularly limiting because the

suitability of a relatively large area around the 600 m sites with signs of otters was considered.

Another limitation to our model was that we were unable to take into account one of the most important resources for otters: fish availability (Kruuk et al. 1993, Jeņdrzejewska et al. 2001, Lanszki & Sallai 2006). Reliable data on fish community composition and biomass are difficult to obtain over large areas. Moreover, translating these data into actual availability of fish for otters is a further obstacle. However, for five of the seven catchments considered in this study (Sangro, Biferno, Volturno, Fortore and Trigno) data on fish biomass collected at 54 sampling stations (Regione Molise 2004) were available (Loy et al. 2008). On average, a fish biomass of 13.08 gr/m^2 was registered across these five catchments (range: 0.01-98.60 gr/m^2, SD = 4.08, n = 54 sampling stations). Kruuk et al. (1993) demonstrated that otters could successfully exploit oligotrophic streams populated mainly by salmonids with fish biomass between 9 and 14 g/m^2, while Ruiz-Olmo (1998) noted that otters were present at sites with biomass values of 10–20 g/m^2. Taking all studies that relate otter distribution with fish biomass into consideration, Chanin (2003) proposed that, as a rule of thumb, otter populations can survive and breed where fish biomass exceeds 10 g/m^2. Therefore, the values that are reported for five of the seven catchments considered in this study would seem to be sufficient, on average, to support a population of otters. It was, however, not possible to incorporate these values into the model because of the relative scarcity of sampling stations for fish biomass relative to the whole study area.

The application of the HS model to the six catchments (the Trigno was excluded) resulted in only three of the ten HS classes being significantly related to the presence-absence of the species. This is probably due mainly to the fact that only these three classes were significantly represented in our sample, all the other classes being found at a relatively low frequency.

The planned extension of this approach to study the southern Italian subpopulation, together with the development of an inferential approach and the implementation of more sophisticated algorithms for longitudinal and lateral connectivity analysis, currently in progress, will probably help to improve the prediction ability of the HS and connectivity models and to offer better insights into the areas of potential range expansion of otters in Italy and into the likelihood that the two subpopulations will become connected in the future.

CHAPTER 3 - HABITAT SUITABILITY TO PREDICT THE RECOVERY OF THE OTTER

Do habitat suitability models reliably predict the recovery areas of threatened species?

Carmen Cianfrani[1,2 $][*], Gwenaëlle Le Lay[2,3 $], Alexandre H. Hirzel[2,4], Anna Loy[1]

[1] *Department of Science and Technology for the Environment, University of Molise, I-86090, Pesche, Italy*

[2] *Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland*

[3] *Landscape Modeling Research Group, Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*

[4] *Informatics' center, University of Lausanne, CH-1015 Lausanne, Switzerland*

Abstract

Identifying the areas suitable for the recolonization of threatened species is essential to support efficient conservation policies. Habitat suitability models (HSM) predict species' potential distributions, but the quality of their predictions should be carefully assessed when the species-environment equilibrium assumption is violated.

We studied the Eurasian otter (*Lutra lutra*), recovering in southern Italy. To produce results widely applicable, we chose standard HSM procedures and looked for the models' capacities in predicting the suitability of a recolonization area. We used two fieldwork datasets: presence-only data, used in the Ecological Niche Factor Analyses (ENFA), and presence-absence data, used in a Generalized Linear Model (GLM). In addition to cross-validation, we independently evaluated the models with data from a recolonization event, using presences on a previously unoccupied river.

Three of the models successfully predicted the suitability of the recolonization area, but the GLM built with data before the recolonization disagreed with these predictions, missing the recolonized river's suitability and badly describing the otter's niche. For modeling practices, our results revealed three points: 1) absences may unable the models to rightly identify the areas suitable for a species spread, 2) processes of variables' selection may lead to randomness in the predictions, and 3) the AUC, a commonly used validation index, was not well suited to evaluate the models' quality on the recolonization area, whereas the Boyce Index (CBI), based on presence data only, better highlighted the models' fit to the field observations.

For species with unstable spatial distributions, presence-only models may be preferred to the presence-absence methods to provide reliable predictions of the areas of potential expansion, essential sites for the threatened species preservation An iterative modeling process, using new occurrences from each step of the species spread, may also help in progressively reducing errors.

Conservation plans depend on reliable models of the species' suitable habitats. In non-equilibrium situations, as those of threatened or invasive species, models could be affected negatively by the inclusion of absence data when predicting the areas of potential expansion. Using presence-only methods would better engage wildlife conservation efforts in productive management practices.

Introduction

Sound wildlife management policies depend critically on our ability to predict the spatial distribution of species, both in their current situation and in the future. Threatened species and communities, invading alien species, species whose habitat will be altered by climate change, or recovering populations of rare species are all examples where the prediction of future species distributions is paramount. In the latter case, identifying the locations of habitats suitable for potential colonization is crucial to produce efficient and long term conservation strategies. In this context, habitat suitability models (HSM), which produce maps of the distribution of suitable habitats, are fundamental tools as they support the geographic perspective for conservation strategies (Barbosa, 2003; Rondinini et al., 2005; Pearce and Boyce, 2006).

HSMs have been used for several years and were applied to a wide range of species and issues. Many methods are available (e.g. Guisan and Zimmermann, 2000; Scott et al., 2002; Hirzel and Le Lay, 2008) but, as observed in the literature, some are more commonly used, in particular those using the species' presence and absence data. Some methods were developed earlier than others and their rapid and easy ways to be implemented probably contributed to their success. Several analyses compared HSMs' performances (Brotons et al., 2004; Tsoar et al., 2007; Elith and Graham, 2009) and some papers warned modelers to choose HSM methods carefully taking the input data and the application goals into account (e.g. Elith and Graham, 2009). HSMs are based on the species-environment equilibrium assumption (Guisan and Zimmermann, 2000) and its validation is essential to model the species' ecological niche accurately. It supposes that the species occupies all suitable habitats available. Conversely, absence data indicate areas unsuitable for the species. Absence data thus usefully help in restricting the habitat suitability (HS) prediction (Elith and Graham, 2009), making presence-absence methods suited in many situations. However, in the case of populations threatened by human perturbations (hunting, pollution, etc.) or subject to dispersal limitations (e.g., ecological barriers), the species does not occupy all the suitable areas. The significance of the observed absences should thus be carefully addressed (Pulliam, 2000; Gibson et al., 2007; Hirzel and Le Lay, 2008; Lobo et al., 2008), as using them in HSMs could produce unreliable predictions, as demonstrated with a virtual species dataset (Hirzel et al., 2001).

Although the species-environment equilibrium assumption of HSMs has been already questioned (Guisan and Thuiller, 2005; Hirzel and Le Lay, 2008), surprisingly, its consequences have never been thoroughly tested. Technical aspects could limit such tests. For instance, it is quite rare to get data of one species' expanding distribution. Surveys

have to be conducted on areas larger than the currently known distribution, during several years, and intensively enough to be sure that absences and presences are identified correctly. Modeling methods add some difficulties. Input data, models algorithms, types of results and validation methods are all parameters that make their comparison difficult. Nevertheless, as HSMs provide interesting information, managers have to rely on the available methods and data to build them. Identifying the domain of application of the models is of great importance at several stages of conservation plans, and researchers and managers still lack extensive tests (Elith and Graham, 2009), especially with data on real cases (Brotons et al., 2004). The availability of pre- and post-colonisation data from a threatened recovering species, the Eurasian otter (*Lutra lutra*) in Italy, gave us the opportunity to assess the efficiency of modeling methods in identifying the suitable areas for the recolonization.

The Eurasian otter is a semi-aquatic carnivore, once widespread in Europe. Its distribution has seen a sharp decline in the last few decades, but it recently locally recovered in several European countries (Kranz, 2000). In Italy the species was listed as a *critically endangered* in the Italian vertebrates red lists (Bulgarini et al., 1998). Before 1950, the species was distributed over the whole country (Cagnolaro et al., 1975), but by 2002, it was confined to a small part of southern Italy (Spagnesi et al., 2002). Causes for this decline include hunting, food shortages (mainly of fish), and the destruction of riparian vegetation (Mason, 1989). Presently, the otter's Italian population consists of two, apparently isolated, sub-populations (Fig. 1) showing a slow recovering process (Prigioni et al., 2007). The budding expansion process, the relatively small size of the otter Italian population and the presence of two disjoint sub-populations all stress the importance of the establishment of effective conservation strategies. Among conservation priorities are (i) the protection of the areas of potential otter recolonization, and (ii) a better understanding of the otter's habitat requirements.

Our goal was to test the capacity of HSMs in identifying the locations and characteristics of the areas potentially suitable for the recovery of the European otter in Italy. More generally, we expected the results to help in defining guidelines for a right use of the HSMs, especially in non-equilibrium situations, such as spreading species. We considered two species distribution datasets: the first was collected before, and the second after, a recolonization event. We assumed that the first situation was not at equilibrium, and that the second had reached a sub-equilibrium state. For HSMs, we used two common methods, one dealing with presence-only data, and the second using presence and absence data of the species. We computed and cross-validated models based on the pre-

colonization dataset and then externally validated them with the post-colonization dataset. The modeling methods were deliberately chosen among the commonly used methodologies, as we wanted our results to be useful to other researchers and conservation practitioners.

Materials and methods

Study area

The study area covers the northern sub-population of the Italian's otter range, mostly located in the Molise region (Fig. 1). This area comprises seven river catchments (Sangro, Biferno, Trigno, Fortore, Saccione, Sinarca, and the upper part of the Volturno River). We described the study area by variables related to the ecological requirements of the otter and to potential disturbances (Tab. 1). Variables were prepared as maps in a geographic information system (ArcGIS 9.3; ESRI, Redlands, USA).
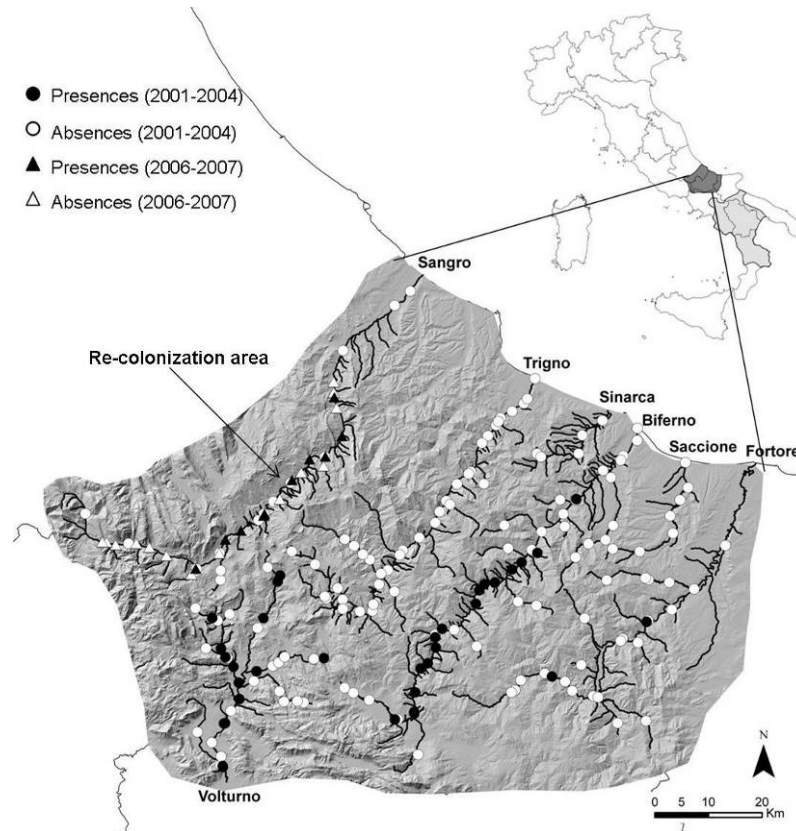
Fig. 1 - Sampling design and study area. Points refer to the fieldwork data, years of the surveys are indicated in brackets. Black lines and names refer to the rivers. The inset (top-right) shows the two Italian populations (grey areas).

Otters are attracted by the availability of food, breeding dens and low levels of human disturbance (Kruuk, 2006). Their diet consists mostly of fish (Ruiz-Olmo, 2001). Preliminary analyses (unpublished data) indicated that the otter's presence is probably

linked to high fish biodiversity. To obtain a continuous map of the fish biodiversity (F) for our study area, we fitted a Generalised Linear Models (GLM) model expressing F, from data of 59 electrofishing sites (Regione Molise, 2005), as a function of elevation E and slope S: $F \sim E + S$ (all coefficients were highly significant with adjusted deviance of 45.8). Slope and convexity are important descriptors influencing the hunting capacity of individuals (Kruuk, 2006). These variables were derived from a Digital Elevation Model of 20 m resolution. Convexity was computed in a moving circular window of 1 km diameter. Positive (negative) values indicate a convex (concave) terrain shape. Vegetation cover is needed to inform on potential resting sites. During the day, the otters rely on riparian vegetation for resting, reproduction and care to cubs (Beja, 1996). We considered the distances to cities, excavated surfaces and productive sites as the main metrics of disturbance (Prenda, 1996). We used a land-use map at scale 1:5000, derived through interpretation of the most recent high-resolution digital orthophotograph, rasterized at 20 m resolution (Loy et al., in press-b). Land-use classes were then transformed into frequency maps computed on a moving circular window of 5 km diameter. This diameter was chosen in relation to the otter's home range size, which has been estimated to be between 5 and 50 linear km (Kruuk, 2006).

Water availability is an important parameter (Beja, 1992). We calculated flow accumulation as the number of upslope cells that flow into each cell. To ensure their equal influence in the models despite various data units, all predictors were standardized.

The study area was restricted to a 150 m buffer around rivers, as otters are rarely found beyond 150 m from streams (Philcox et al., 1999; Kruuk, 2006). We only considered main courses and the first-order tributaries, as the presence of permanent water is an important factor for the otter (Prenda, 2001).

Category	Predictor name	Description
Resting site availability	FOREST	Frequency of deciduous forest in a *2.5* km radius
	SCLEROPH	Frequency of sclerophylous vegetation in a *2.5* km radius
	HERB-CROP	Frequency of dry herbaceous cropland in a *2.5* km radius
	ARBOR-CROP	Frequency of arboreal cropland in a *2.5* km radius
	AGR-HETER	Frequency of heterogeneous agricultural areas in a *2.5* km radius
Disturbance	CITIES	Distance from cities
	MINES	Distance from surface excavation
	INDUSTRIAL	Distance from productive areas
Water availability	FLOW-ACC	Flow accumulation
Food	CONVEX	Convexity (hunting efficiency)
	SLOPE	Slope (hunting capacity)
	FISH-BIOD	Fish biodiversity

Tab. 1- Environmental predictors used in habitat suitability models

Species data

In each UTM grid cell of 10x10 km, otter droppings (spraints) were searched at four random sites (Loy et al., in press-a). A site consisted of a 600 m segment of both banks of the river. The first survey was carried out from 2001 to 2004 (174 sites) and revealed that otter occurrence was restricted to the Biferno and the upper Volturno river basins, with only sporadic records for occurrence in the Fortore. The Trigno, Saccione, Sangro and Sinarca Rivers did not reveal any sign of otter presence (Fig. 1). The second survey, carried out in the Sangro river (24 sites) from 2006 to 2007, revealed that this river had been recently recolonized (Fig.1).

For our analyses, we distinguished three datasets (Fig. 2). The first dataset ("01-04") includes data from surveys carried out in 2001-2004, from which we excluded the absence data from the Sangro River. As shown by the 2006-2007 survey, these absences were not indices of unsuitable habitats. This pre-colonization dataset reflects non-equilibrium conditions. The second dataset ("01-07"), identified as post-recolonization, includes all survey data and reflects sub-equilibrium conditions. The third dataset ("rec") only contains data collected from the newly colonized Sangro River, in 2006-2007. This dataset was used to evaluate how the predictions of the HSMs performed in the recolonized river (Fig. 2).

We rejected as assumed inappropriated absences all absences recorded within 5 km of any presence, as measured along the river network (Janssens, 2006) (see Appendix S1 in Supplementary Material). These absences may be due to a non-detection of the species (MacKenzie et al., 2003).
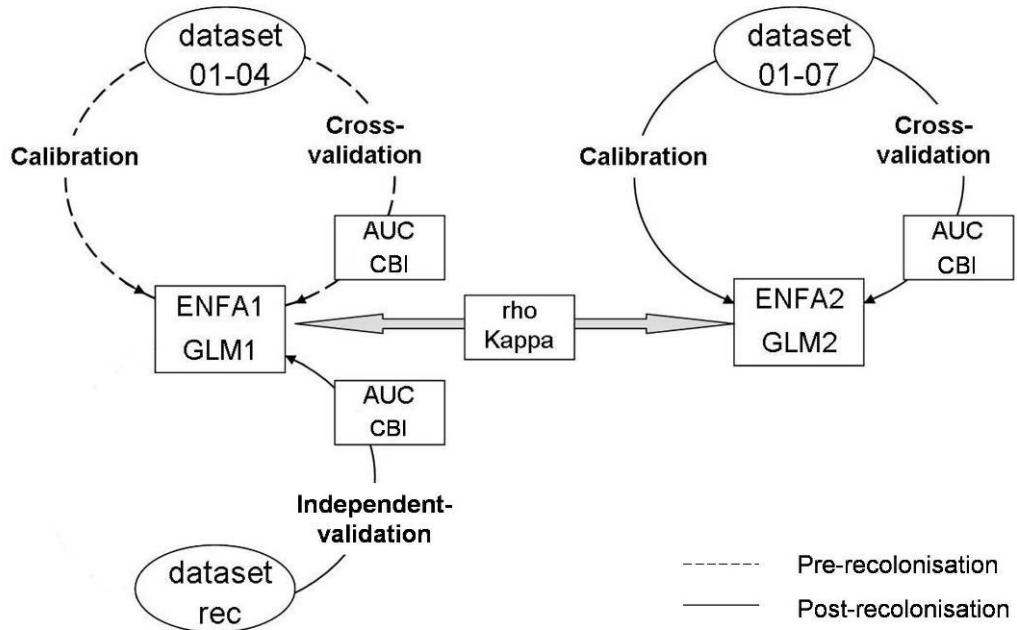
Fig. 2 - Modeling framework. Two species' datasets from fieldwork, indicating a pre-recolonization event (dataset 01-04) and a post-recolonization event (dataset 01-07), are used to calibrate and cross-evaluate ENFAs and GLMs, by two indices, the AUC and the Boyce index (CBI). Data of the recolonization event (dataset rec) are used to independently evaluate the pre-recolonization models. Models obtained before and after the recolonization event are compared with Spearman's rank correlation coefficient (rho) and Cohen's agreement coefficient (Kappa).

Habitat suitability modeling

We selected two standard methods of habitat suitability modeling: the Ecological Niche Factor Analysis (ENFA; Hirzel et al., 2002), using presence-only data, and the Generalized Linear Model (GLM; McCullagh and Nelder, 1989), using presence-absence data. Each approach was applied twice: first before the recolonization event, on the dataset "01-04" (ENFA1 and GLM1), and second after the recolonization event, on dataset "01-07" (ENFA2 and GLM2). We evaluated all four models by cross and independent validation (Fig. 2). The models were finally applied to geographic space in order to produce habitat suitability (HS) maps. Following the predicted-to-expected evaluation-point frequency curves (P/E curves; see Appendix S2), obtained during the validation process, HS predictions were reclassified into three classes: unsuitable, suitable or optimal. Thresholds were based on the mean μ and the standard deviation σ of the P/E curves. The "unsuitable" class corresponds to all HS values whose μ is below 1 and the "suitable" class to μ values ranging from 1 to σ. The "optimal" class corresponds to HS values whose μ is

above σ. All the modeling procedures were done in the Biomapper 4.0 software (Hirzel et al., 2008).

Ecological niche factor analysis

We applied ENFA to presence data according to the standard software procedures. The ENFA quantifies the species' ecological niche by comparing the environmental characteristics of the sites it occupies (''the species distribution'') with the environmental characteristics of the whole study area (the ''global distribution'') (Hirzel et al., 2002). To model habitat suitability, we chose a geometric-mean distance algorithm, as recommended by Hirzel and Arlettaz (2003). The environmental predictors are collated into a few uncorrelated ecological niche factors. The first factor explains all species' marginality, i.e., the difference between the species means and the global mean. Other factors explain specialization, i.e., the niche narrowness relative to the global variance. The inverse of the specialization indicates the tolerance of the species. From each environmental predictor, a score for marginality, specialization and tolerance (the weighted sum of the specialization coefficients) can be calculated. The importance of a predictor is given by the weighted sum of these scores.

Generalized Linear Model

We used GLM with a binomial variance and a logistic link function to relate the species presence-absence with the environmental variables. GLM were conducted in R (Development Core Team 2006), in conjunction with Biomapper. To select the most parsimonious model, we used an automatic forward stepwise model-selection procedure, based on the Akaike Information Criteria (Akaike, 1973). Although this selection criterion has been criticized in some papers (e.g. Johnson, 1981; Burnham and Anderson, 2002; Whittingham et al., 2006) it is still the standard method used in most studies (e.g. Elith and Graham, 2009; Roura-Pascual et al., 2009). Up to second-order polynomials (linear and quadratic terms) were allowed for each predictor. GLMs contain a formula where significant variables appear with their corresponding weighting coefficients. As the environmental predictors were standardized, we used these coefficients as indicators of their importance.

Evaluation of model predictions

Assessing the predictive ability of a model is a crucial step towards its application in conservation ecology (Fielding and Bell, 1997; Manel et al., 2001).

We made two types of evaluation: 1) an internal evaluation by means of cross-validation of all four models, and 2) an external evaluation of the ENFA1 and GLM1 by the "rec" dataset (Fig. 2).

For internal evaluation, we made a *k*-fold cross-validation (Fielding and Bell, 1997; Manel et al., 2001). It consists in partitioning the species dataset into *k* sets, building a model on the base of *k-1* sets and validating it with the remaining data set. The procedure is repeated *k* times, providing a mean and variance for the validation measure. In our case, we used *k*=4 (Huberty's rule; Huberty, 1994) (Fig. 3).
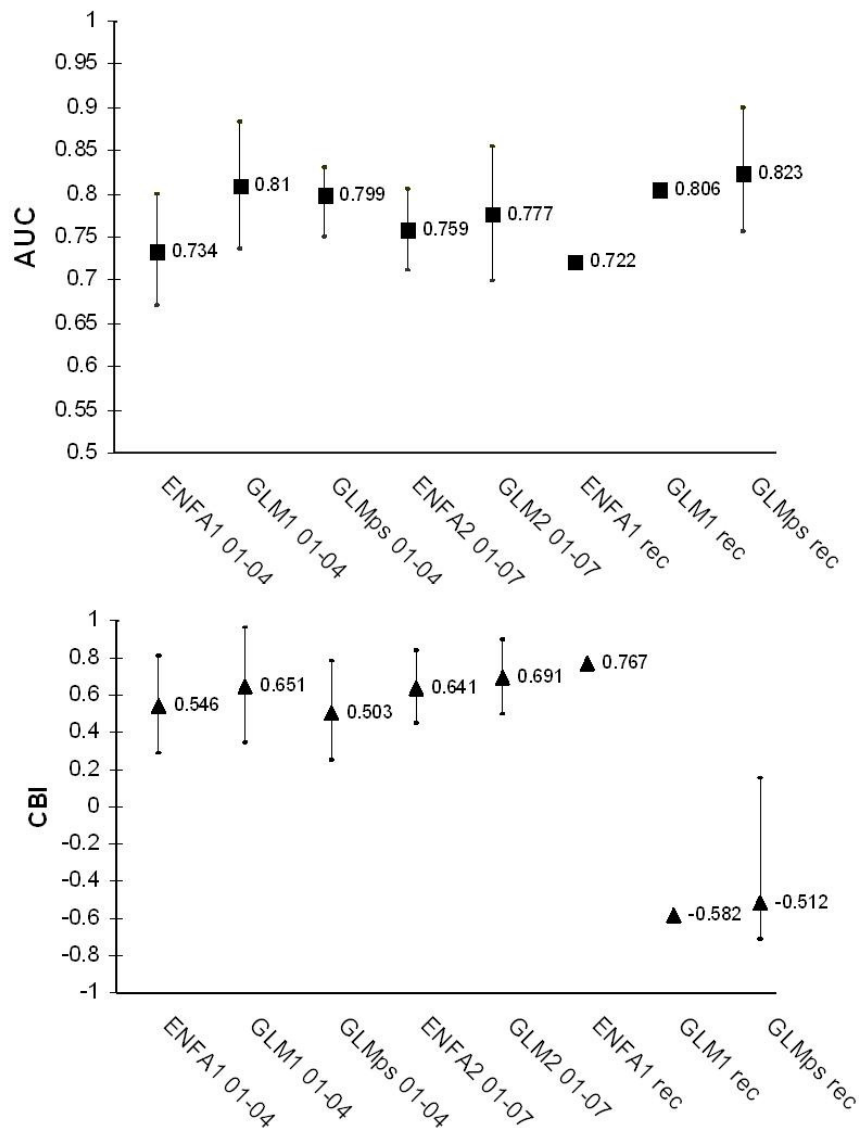

Fig. 3 - Mean values and standard deviation of the AUC and the Boyce index (CBI) are calculated for the six models. The names on the X axis refer first to the model type (GLM or ENFA), second to the dataset of calibration (1 for survey 01-04 and 2 for survey 01-07) and third to the dataset of validation (01-04, 01-07 or rec, i.e. dataset from the recolonized area).

For both internal and external validation, we used two measures to compare predictions with field observations: 1) the threshold-independent Receiver Operating Characteristic (ROC) approach (Fielding and Bell, 1997) by calculating the area under the ROC curve (AUC). It uses presence-absence data and ranges from 0 for an inverse model to 0.5 for a random model and to 1 for a perfect model. 2) The continuous Boyce index (CBI) (Boyce et al., 2002; Hirzel et al., 2006), a recently developed index particularly useful to assess the quality of the HSMs' predictions for the species' presence. This index can be used with presence data only. It is based on P/E curves. It consists in calculating the Spearman correlation between the suitability index and the predicted-to-expected ratio of the frequency of evaluation points, over a moving window (cf. Appendix S2). The continuous Boyce Index varies from −1 for an inverse model to 0 for a random model to 1 for a perfect model (Boyce et al., 2002; Hirzel et al., 2006).

To compare our results, we calculated correlations between the HS maps produced by the different models. We calculated Spearman coefficients on continuous HS values and Cohen's agreement coefficients (Kappa; Cohen, 1960) on the reclassified maps (with three HS classes). As GLM and ENFA produces HS values that distributes differently, these two measures allow to evaluate the models similarity in two cases: one independent from the HS reclassification threshold, but potentially disturbed by the different HS distributions, and the second based on reclassified HS values, supposed to improve the comparability between predictions, but that depend on reclassification threshold. Note, however, that this latter factor is minimized here, as we chose the same information (i.e. P/E curves) to reclassify the models. Both measures range from -1 (negative correlation) to +1 (positive correlation).

Complementary assessments

Our main hypothesis was that the predictions of GLM1 and ENFA1 may differ, mainly because GLM1 had information on the species' absence, whereas ENFA1 not. Nevertheless, we addressed the effects of two complementary factors of the modeling procedures. The first one concerns the type of the species absences. GLM1 used absences recorded in the field. When such data are available, they should be preferred, as demonstrated in previous studies (Engler et al., 2004; Lobo et al., 2008). However, assuming that field data may bring fallacious absences (Hirzel and Le Lay, 2008), we produced GLM for the pre-colonization stage with pseudo-absence data. We generated ten sets of randomly selected pseudo-absences, defined as the absences of the "01-04" dataset, i.e. as numerous as in the "01-04" dataset and located on all the rivers except the Sangro

river. Using our standard modeling procedure, we made ten GLMs with these pseudo-absences, cross validated them and independently validated them with the "rec" dataset. These ten values provide ranges for AUC and CBI.

The second factor we assessed was the influence of the environmental variables selection on the final HS predictions. Using the stepwise procedure, the final GLM results from a selection of a set of variables, whereas the ENFA can keep all the environmental variables in the model. To increase the models' comparability, we thus cross-used the sets of variables: we produced GLMs with the six best variables of the ENFAs, as ranked by their global scores (Tab. 2), allowing linear and quadratic terms for each predictor. Inversely, we made ENFAs with the variables selected in the GLMs (see Appendix S3).

Biological interpretation	Predictors	ENFA1 Marginality[1]	Sum[2]	ENFA2 Marginality[1]	Sum[2]	GLM1 Coefficient[3]	GLM2 Coefficient[3]
Food	FISH-BIOD	+	(1) 20.60	+	(2) 11.30	-	-
	SLOPE	-	(3) 15.39	-	(5) 7.42	(4) 0.91	(4) 0.87
	CONVEXITY	-	(5) 13.45	-	(1) 11.71	-	(3) 0.89
Resting sites	HERB-CROP	-	(2) 17.76	-	(4) 7.56	(6) 0.59	(7) 0.08
	FOREST	+	(4) 14.41	+	(3) 9.84	(1) 1.46	(1) 1.32
	ARB-CROP	+	(9) 6.11	0	(8) 5.27	-	(2) 1.24
	SCLEROPH	0	(10) 5.96	0	(6) 7.23	-	-
	AGR-ETER	+	(11) 5.81	+	(10) 4.39	-	(6) 0.39
Disturbance	MINES	-	(6) 8.50	-	(7) 6.29	(2) 1.20	-
	CITIES	-	(7) 6.81	-	(11) 4.26	(3) 1.15	(5) 0.61
	INDUSTRIAL	0	(12) 3.93	-	(9) 4.47	(5) 0.90	-
Water	FLOW-ACC	+	(8) 6.14	+	(12) 3.58	-	-

Tab. 2 - Ranking of environmental predictors by the four habitat-suitability models. Numbers in bracket indicate the predictor's rank of importance.

[1] + and - mean that otters are found, on average, in areas with higher (respectively lower) values than the study area mean. Values around 0 means that the otters' habitats do not differ from the common areas of the study area.
[2] Sum of the scores over all ENFA factors..
[3] Coefficients in the GLM formula. Predictors were standardized.

Results

Ecological niche descriptors

The four models do not rank the importance of the various predictors similarly (Tab. 2). The two ENFA models agree that the most important environmental predictors are related to food (FISH-BIOD, SLOPE, CONVEXITY) and resting site availability (HERB-CROP, FOREST). By contrast, the two GLMs differ. While GLM1 ranks resting site availability (FOREST) and disturbance (MINES, INDUSTRIAL) first, GLM2 finds resting sites availability (FOREST, ARB-CROP) and food (CONVEXITY, SLOPE) more important (Tab. 2). In short, ENFA2 and GLM2 agree, ENFA1 agrees with both ENFA2 and GLM2, and GLM1 differs from the other models. When doing GLM as GLM1 with

pseudo-absence data (ten GLMps), the selection and the order of the predictors differ. Resting sites availability (HERB-CROP, FOREST) were still the most selected variables, but here food information (FISH-BIOD) ranked just before the disturbance variables (MINES, INDUSTRIAL).

Comparing the niche statistics provided by the two ENFA models showed that, while the global marginality coefficients were similar (0.59 for ENFA1 and 0.60 for ENFA2), the tolerance (i.e., the inverse of specialization) coefficients differed (0.50 for ENFA1 *vs*. 0.63 for ENFA2).

Spatial predictions comparison

The comparison of the HS values of the map showed that ENFA1, ENFA2 and GLM2 were highly correlated (Spearman $\rho \cong 0.7$, Kappa $\cong 0.55$), while GLM1 was less correlated to the others ($0.37 \leq \rho \leq 0.59$, $0.18 \leq$ Kappa ≤ 0.35) (Tab. 3). The HS map predicted by GLM1 is indeed quite different from that predicted by ENFA1, ENFA2 or GLM2, particularly on the Sangro River recolonization area (Fig. 4).
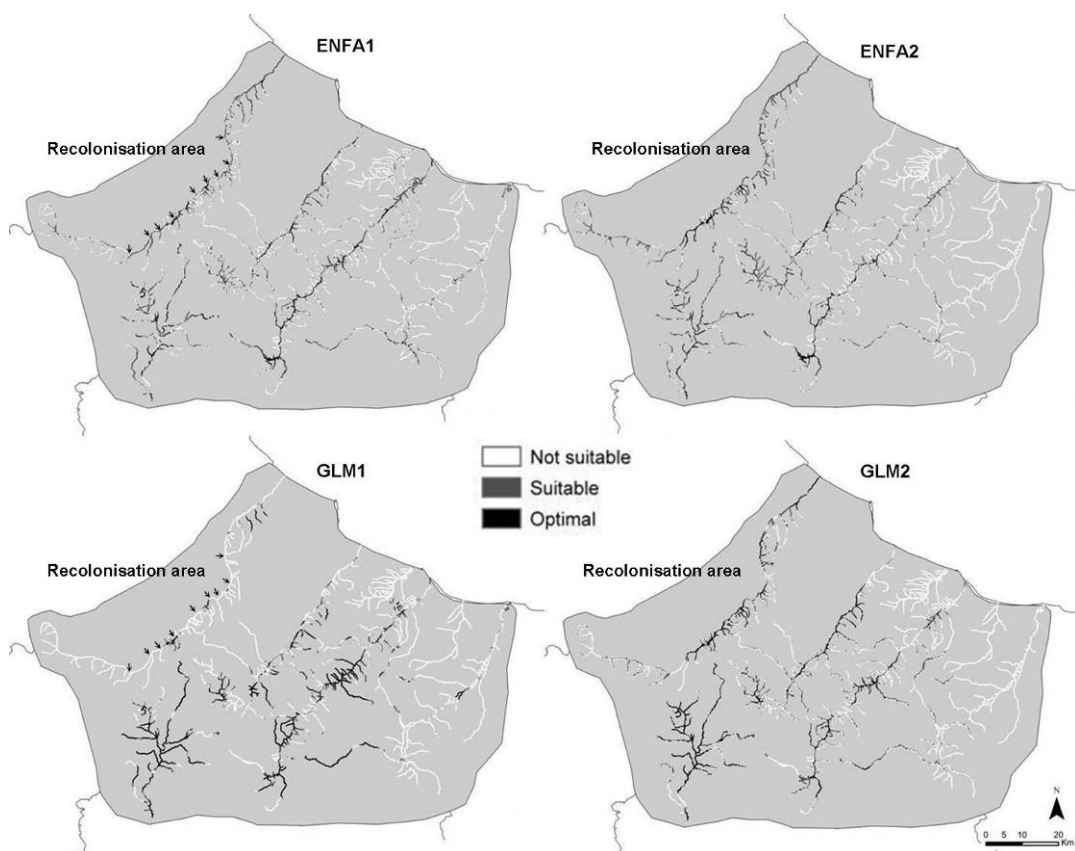

Fig. 4 - Habitat suitability maps (ENFA1, GLM1, ENFA2 and GLM2) reclassified by binning the predicted/expected (P/E) curves in three classes of suitability: unsuitable,

suitable and optimal. The arrows on the recolonized area indicate the recolonization data ("rec").

	ENFA1	ENFA2	GLM1	GLM2
ENFA1	1.00 (1.00)			
ENFA2	0.73 (0.47)	1.00 (1.00)		
GLM1	0.45 (0.23)	0.37 (0.18)	1.00 (1.00)	
GLM2	0.68 (0.63)	0.70 (0.44)	0.59 (0.35)	1.00 (1.00)

Tab. 3 - Spearman rank correlation and kappa index, in brackets, calculated between pairs of habitat-suitability maps. The Spearman correlations were calculated on continuous HS values of the maps and the Kappa index on the reclassified maps (three HS classes).

Model validation

Cross-validation and external validation procedures gave conflicting results on the relative predictive power of the ENFA and GLM models (Fig. 3). The cross-validation results identified that the GLM had a non significant tendency to provide better results than ENFA models, with both the "01-04" and "01-07" datasets, and the pseudo-absence data. The external validation of the models built with the "01-04" dataset or with pseudo-absence data provided contradictory results: AUC were slightly better for the GLMs than the ENFA (0.81 and 0.799 *vs* 0.722), while the CBI values suggested that the GLM predictions in the recolonized area were unable to predict the species' presence (-0.582 and -0.512), whereas the ENFA achieved a good performance (0.767)

When exchanging the variables sets from ENFA to GLM and respectively (Appendix S3), our results are generally worse, both for cross and independent validation. For the GLM1 using the ENFA1 variables (GLM1$_{varENFA1}$), the model returned a similar AUC value (0.78) than the GLM1 for cross-validation, but better values for the cross-validation CBI (0.75 *vs* 0.651) and the independent-validation AUC (0.889 *vs* 0.806). Concerning the CBI index with the independent validation, while a bit better than the GLM1 (-0.492 vs -0.582), the GLM1$_{varENFA1}$ still predicts the habitat suitability of the recolonized areas poorly.

Discussion

Habitat suitability models can be usefully used to assess the species' distribution and to provide guidelines for their management. However, evaluations of the prediction quality are generally driven in simple ways and rely on commonly used methods, without comprehensive assessments. Studies addressing HSMs comparison also rarely provide

guidelines on the conditions of their application, despite the fact that some could lead to wrong conclusions, as in the case of species that are not at equilibrium with their environment. By testing the ability of HSM in predicting the locations of a species recolonization, our results highlight some important points.

Success in predicting the recolonization area

The predictions from the presence-only approach applied to the non-equilibrium situation (ENFA1) agreed with both models applied to the sub-equilibrium situation (ENFA2, GLM2), while it disagreed with the presence-absence approach applied to the non-equilibrium situation (GLM1) (Tab. 3). This difference is particularly evident in the recolonization area (Sangro river), where ENFA1 rightly predicts its suitability whereas not the GLM1 (Fig. 4). When a species is in a non-equilibrium situation, absence data used in HSM can thus lead to bad predictions on the future recolonization areas. Four results support this conclusion: 1) when fed with pseudo-absence data, the GLMps give poorer predictions on the colonization area (CBI value, Fig. 3) than the GLM1, 2) when fed with ENFA1 variables, the GLM still badly predict (CBI_rec=-0.492; Appendix S3), 3) when fed with post-colonization data, i.e. in the sub-equilibrium situation, the GLM makes predictions highly similar to those of ENFA, i.e. good ones, 4) in the recolonized area, ENFA1 correctly identifies the suitability of the recolonization areas, while GLM1 does not (Fig. 4). ENFA has sometimes been suspected to over-predict habitat suitability (Zaniewski et al., 2002; Brotons et al., 2004), but here it appears that many of the supposedly "over-predicted" areas were actually later recolonized by the otter (Fig. 4).

Description of the species' ecological niche

Regarding ecological niche trends (Tab. 2), GLM1 is the model the most influenced by disturbance variables. By contrast, ENFA1 gives more importance to food and resting-site variables, consistent with the models of the sub-equilibrium condition (GLM2 and ENFA2) (Tab. 2). The otter's distribution may then essentially depend on resource factors. Under strong environmental disturbance the species has a reduced distribution, as in the case of the non equilibrium situation ("01-04" dataset). However, including the disturbance variables in the ecological niche description obviously leads to a misidentification of the potential areas for the species' spread, as shown by the independent validation of the $ENFA1_{GLM1}$ and the $ENFA2_{GLM2}$ (Appendix S3). The relative habitat tolerance of the otter, which may support high capacities for spreading, is also highlighted by the ENFA niche

statistics, which show that the overall tolerance was higher in the sub-equilibrium than the non-equilibrium situation.

From our results, the ENFA shows a better generalization power (or transferability; Peterson, 2006) than the GLM, i.e. a better ability to provide correct predictions in an area different from the one on which the model has been calibrated (Vaughan, 2005). ENFA was able to predict the suitability on the Sangro river, without data from this particular river. This capacity is crucial to predict the distribution of spreading species. This property of the ENFA models may come from three factors: 1) its reliance on presence data only, i.e., no influence from unreliable absence data, 2) comparison of the environmental characteristics of the sites occupied by the species to the whole study area and not only comparison of selected sites, i.e. locations of the presence or absence data, as with the GLM model, and 3) capacity in taking into account many predictors, without requiring a selection process, as in the stepwise/AIC procedure. However, a good model can only be produced when fed with the right predictors and accurate species data. Indeed, when presence data corresponds to almost all of the environmental situations the species can use, i.e. covering the whole ecological niche of the species, the model can predict the species distribution outside the calibration area. For the GLM1, some absences contained in the species dataset of the non-equilibrium situation (dataset "01-04") may correspond to environmental situations similar to those found in the Sangro River, i.e., the colonized area, which brings troubles in the predictions. ENFA1, not influenced by these unreliable absences, predicts a larger ecological niche, which is better matched to the real ecological niche of the species. Similarly, ENFA2 and GLM2, taking into account all the available data (here the "01-07" dataset), provide better predictions. The problem is that it is difficult to know *a priori* which absences are unreliable. The species distribution is often a snapshot of a dynamic system. It is probable, therefore, that the species will further recolonize more suitable areas, e.g. on the Trigno river (Fig. 4), and that the supposed sub-equilibrium situation would still contain some unreliable absences (Fig. 5).
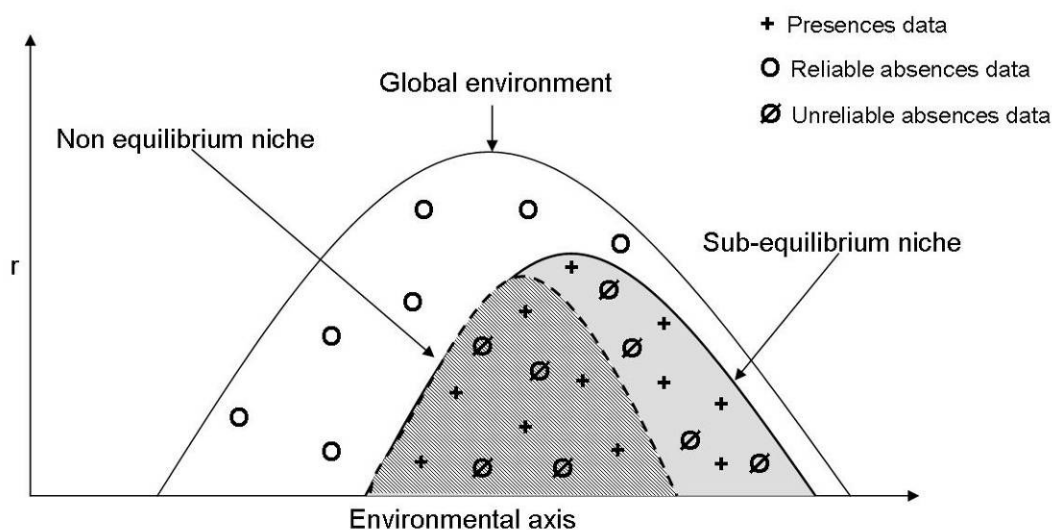
Fig. 5 - Theoretical representations of the otters' ecological niche and the global environment of a study area, along one environmental gradient. Two cases are represented: first, a non-equilibrium distribution (dark grey) with pre-recolonization presences and absences data ("01-04") and, second, a sub-equilibrium distribution (light grey) with post-colonization presences and absences data ("01-07"). The species absences are reliable for the models only when they fall outside the species' niche.

Methodological contributions

We observed that, in the non-equilibrium situation, presence-only data lead models to describe the species' niche correctly, thus predicting potentially suitable areas for the species spread. On the contrary, we observed that models using either fieldwork absences or pseudo-absences produced bad predictions for the recolonization area. In non-equilibrium situations, presence-only models should thus probably be preferred. However, as observed through our results, the strength of the presence-absence models' failure depends on the considered stage of the species' spread, i.e. how much the ecological niche is already rightly occupied or not. It may also depend on the species characteristics, such as its capacities of adaptation and the spatial and temporal variation of the environment. In order to test this issue further, models should be run in different environmental conditions, for other species, and with other modeling methods (e.g. minimizing the weight of absences, models including autocorrelation, pseudo-absences based on an ENFA as Engler et al., 2004) to thoroughly identify the importance of the influence of absences in HSM and provide alternative solutions.

The selection of the predictors during the stepwise procedure, in the GLM, may also lead to randomness. Indeed, the ten GLMs built with pseudo-absence data differed slightly in their selection and ordering of the predictors, and also showed high variability in their

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quality (see AUC and CBI for the recolonization area, Fig. 3). The GLM1$_{ENFA1}$ returns bad predictions (CBI_rec, Appendix S3), but slightly better than those of the GLM1, fed with the twelve environmental variables. This result suggests that, even when using the same "fallacious" absence data, the GLM can perform a bit better when it uses the "right" predictors. Nevertheless, the selection of the variables is closely related with the information on the presence-absence and it is thus difficult to improve the models. Although the stepwise/AIC procedure has been criticized in some papers, it is still the standard method used in most studies; we found it as the method used in 22 out of 23 recent papers which used GLM. More research on that issue should be conducted, to provide modelers with better methods in the process of the variables' selection than the stepwise.

Finally, in all situations but one, the AUC and CBI evaluation indices agree about the quality of the models. In the case of the GLM1, evaluations disagree: the AUC (0.81) indicates a good model, while the CBI (-0.58) indicates a bad one. As the maps also revealed that GLM1 was a poor model for the recolonization area, we are led to conclude that the AUC was misleading. More specifically, AUC did not provide an appropriate assessment for our goal: using presence-absence data, it looked for the overall quality of the predictions, i.e. presences and absences, although we wanted to focus on the models' ability in predicting the areas suitability, i.e. presences. Although the AUC is commonly used to estimate the accuracy of species distribution models (Pearce and Ferrier, 2000; Manel et al., 2001; Gibson et al., 2007), some recent papers criticized its use as a standard measurement (Hirzel et al., 2006; Austin, 2007; Lobo et al., 2008; Elith and Graham, 2009). Another weakness of AUC is the equal weights assigned to omission and commission errors. In many applications of distribution modeling, omission and commission errors may not have the same importance (Peterson, 2006).

As a conclusion, in the case of modeling the distribution of spreading species, the accuracy of the models should not be assessed by AUC. The CBI is more suited for such assessment goals and, as previously shown (Hirzel et al., 2006), it is more efficient in highlighting errors in modeling patterns.

Implication for conservation

Fitting habitat suitability models to predict recolonization areas of a recovering species is a challenging issue for applied ecology. In the important case of recovering or invasive species, which are not yet at equilibrium with their environment, modelers have to face with the problem of limited datasets, potentially unable to capture the whole

ecological niche of the species. In our study case, using ENFA1 to establish conservation management strategies would have rightly led to a protection on the Sangro River, thus supporting the species recovery. Using the GLM1 would not have produced the same efficient management. The problems caused by the use of unreliable absences are real, and, if ignored, will damage conservation efforts.

In such cases of non-equilibrium situation, models should thus more efficiently concentrate on presence data. The evaluation of the predictions should also be cautious and be done through several methods. To progressively improve the quality of the predictions, the modeling process should also be considered as a dynamic process and planned as an iterative framework, i.e. doing a new model at each step of the species' spread.

Supplementary materials

Appendix S1 **Discarding false absences**

To correct false absences due to high species mobility, we used a distance function from sites where the presence of the species was detected. From all spraint observations, a probability of occurrence was calculated as the probability that the species occurs given each distance, i.e., as the probability of a union of independent events. The distance was calculated along the river network (Janssens, 2006). The probability that the species occurs at a given distance from an observed presence was described by a normal distribution (Ricklefs & Miller, 2000). The variance of the distribution was fixed to 15 in order to obtain a probability of otter occurrence lower than 0.01 for a distance more than 50 km, i.e., the maximal otter home-range size (Chanin, 2003). In this way, we identified the stretches with a probability of occurrence of 95% or greater (stretching 5 km from the detection point). We thus finally considered as false absences the absences located in these stretches and delete them from the fieldwork datasets.

Appendix S2 **The continuous Boyce index**

Given a moving window size $2w$ (here, we used $2w=20$) and a number of evaluation points (i.e. species' presence data) N, for all suitability values i from w to $100\text{-}w$, we calculate two frequencies: 1) P_i, the *predicted frequency* of evaluation points in the interval $[i\text{-}w, i+w]$:

$$P_i = \frac{n_i}{N} \tag{1.1}$$

where n_i is the number of evaluation points predicted by the model to be in cells with a suitability in the interval $[i\text{-}w, i+w]$; and 2) E_i, the *expected frequency* of evaluation points, i.e., the frequency expected from a random distribution across the study area, given by the relative area covered by the suitability interval $[i\text{-}w, i+w]$:

$$E_i = \frac{a_i}{A} \tag{1.2}$$

where a_i is the number of grid cells whose suitability belongs to $[i\text{-}w, i+w]$, and   is the cell number in the whole study area.

Finally, for each interval $[i\text{-}w, i+w]$, the *Predicted-to-Expected* (P/E) ratio F_i is given by:

$$F_i = \frac{P_i}{E_i} \tag{1.3}$$

When the model predicts fewer presences than expected by chance, F_i is less than 1, and vice versa. Therefore, if the habitat model properly delineates suitable areas for the species, F_i should increase monotonically. This is measured by the Spearman rank correlation coefficient between

F_i and i. This coefficient varies from -1 for an inverse model to 0 for a random model and to 1 for a perfect model. See Hirzel *et al.* (2006) for further details.

Appendix S3 **Cross-use of the models' predictors**

From the set of the available predictors, the stepwise process of the GLM leads to a final model with a reduced set of variables. At the opposite, ENFA do not exclude any predictor. To test the effect of this variables selection on the final HS predictions, we crossed-used the sets of variables between models: we produced GLMs with the six best variables of ENFAs and inversely made ENFAs with the variables selected in GLMs. The six best variables of the ENFA were selected according to their ranking scores on all the ENFA factors (results of Tab. 2). We chose six variables, as the GLM only retained six variables.

We thus produced a $GLM1_{ENFA1}$ using the six first variables of the ENFA1 (FISH-BIOD, HERB-CROP, SLOPE, FOREST, CONVEXITY, MINES), an $ENFA1_{GLM1}$ using the six variables selected by the GLM1 (SLOPE, HERB-CROP, FOREST, MINES, CITES, INDUSTRIAL), a $GLM2_{ENFA2}$ using the six first variables of the ENFA2 (CONVEXITY, FISH-BIOD, FOREST, HERB-CROP, SLOPE, SCLEROPH), and an $ENFA2_{GLM2}$ using the six variables selected by the GLM2 (SLOPE, CONVEXITY, HERB-CROP, FOREST, ARBOR-CROP, AGR-ETER, CITIES).

	AUC_CV	CBI_CV	AUC_rec	CBI_rec
$ENFA1_{GLM1}$	0.731	0.247	0.672	-0.0429
$ENFA2_{GLM2}$	0.682	0.068	0.711	-0.201
$GLM1_{ENFA1}$	0.78	0.75	0.889	-0.492
$GLM2_{ENFA2}$	0.75	0.82	0.739	0.773

Table S1 - Validation values using AUC and CBI measures obtained through cross validation (AUC_CV and CBI_CV) and independent validation, with the "rec" dataset (AUC_rec and AUC_rec).

CHAPTER 4 - IMPACTS OF CLIMATE CHANGE ON THE EUROPEAN OTTER DISTRIBUTION

Adapting conservation to climate change: the case of the European otter

Carmen Cianfrani[1,2]*, Gwenaëlle Le Lay[2,3] , Anna Loy[1], Luigi Maiorano[2], Antoine Guisan[2]

[1] *Department of Science and Technology for the Environment, University of Molise, I-86090, Pesche, Italy*

[2] *Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland*

[3] *Landscape Modeling Research Group, Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland*

Abstract

In the last five decades the Eurasian otter *Lutra lutra*, has declined dramatically throughout all of Europe. Nowadays, the otter seems to be thriving in some European countries, but populations are still fragmented and the species is almost absent of central Europe. Promoting population expansion and reconnection is crucial to ensure the long-term maintenance of genetic diversity and the long-term persistence of the species. In this regard, habitat suitability models (HSM) represent powerful tools to evaluate habitat quality and produce maps of potential distribution and natural dispersion of the specie. This study aims at determining which factors influence the otter distribution and use them to predict the potential distribution of the species in Europe, under current and future climate. The environmental variables used are related to water availability, food supply, resting site and human disturbance using six different modelling approaches. Future projections are derived by running the CCM3 climate model under a 2 x CO_2 increase scenario. At the European scale, the otter is mostly influenced by water availability. The current potential distribution reveals large gaps of unsuitable habitats limiting connectivity between otter populations in Europe. Climate change would have different effects on otter habitat suitability in Europe. In the Western part, the model predicts losses of suitable habitats, whereas gains are predicted in central Europe and Eastern Europe shows equal rates of losses and increases of suitable habitat. Our results are important in helping setting up conservation actions and promote otter recovery in Europe.

Introduction

Following the predictions of the atmospheric CO_2 increase over the next century, several studies warned that climate change (CC) will probably become the first or second greatest driver of global biodiversity loss (Sala et al., 2000; Thomas et al., 2004; MAE, 2005). Due to these effects, there is now compelling evidence that species are already shifting their distribution range (Erasmus et al., 2002; Parmesan & Yohe, 2003; Lavergne, Molina & Debussche, 2006), altering their phenology (Zavaleta et al., 2003), suffering from increases of extinction risk, or having already been extinct (Parmesan, 2006; Pounds et al., 2006; Foden et al., 2007). To efficiently □□□□□□□□□□□□□□□□□□□□□ß□□□re is a need of robust estimates of the impacts of CC on species, since it is likely that many species, if not disappearing, will move out of the current locations of reserves network and designated conservation areas (Coetzee et al., 2009). Considering CC as a reality, conservationist should embrace the problems instead of delaying actions or ignoring uncertainties, to identify practical strategies that could help to limits the effects of CC (Mawdsley, O'Malley & Ojima, 2009), Proactive conservation strategies should especially take into account the potential shifts of the species distribution.

Species distribution models (SDM) are used for several years to predict the species distribution (e.g. Guisan & Zimmermann, 2000) and are now often used as supports for conservation plans. Using data from species occurrences and from their environment, they model the species ecological niche and project it on the geographical space to highlight where the species are more likely to occur (Hirzel & Le Lay, 2008). Incorporating climate change forecasts as environmental variables, many studies already produced predictions of the future species distribution (e.g.Thuiller et al., 2008). Substantial challenges still remain in their use and application. A technical limit often comes from the difficulties in interpreting between-model differences for the same species under different CC scenario and under different modelling methods. Instead of trying to identify the best method, an alternative way to reduce the predictions' uncertainties is to use an ensemble forecasting framework (Thuiller, 2004; Araujo & New, 2007), which combines models from various methods. This approach rely on the idea that the different predictions could represent different situations of the species distribution (Marmion et al., 2009). Although this method will not avoid uncertainties in the predictions, it will certainly decrease the risk of proposing conservation strategies on the only base of one wrong model (Araujo & New, 2007) and will help taking into account these various possible scenarios.

Conservation measures already exist throughout Europe to protect species and habitats. They are of different types, are established at different spatial scales and under various protection rules. Nevertheless, some similar protections, i.e. protections established under similar criteria, or areas of similar biodiversity importance, could be considered as a European network in which species can migrate as on stepping stones to face shifts of habitat suitability due to CC. Under this assumption, it is thus particularly relevant to assess overlays between these protected areas and 1) the potential distribution of species in the current situation, to evaluate their ability in protecting the species now and, 2) the potential distribution of species under CC in the future, to evaluate their ability in protecting the species in the future. If protected areas match the two species distribution cases, these areas could then be considered as key areas for the conservation of the focus species. This mixed approach, combining species distribution models and conservation areas is certainly an essential tool to support conservation accounting for species distribution shift.

Using such approach could be done for species pool (Coetzee et al., 2009), to assess the global efficiency of protected areas in preserving various species. However, although providing interesting assessments, such approach may have limited possibilities for direct conservation applications, as the study species may require too different ecological conditions to support efficient conservation efforts on specific systems. To use the mixed approach for suggesting conservation guidelines, we focused on an umbrella species of freshwater systems, the European

otter (*Lutra lutra*). Due to CC, freshwater systems may soon suffer from strong perturbations due to changes in precipitation characteristics. Precipitations are predicted to increase in some regions or shift to more common droughts (e.g. in the Mediterranean basin), fluctuate more through time, or occur with more frequent heavy precipitation events, increasing risks of floods in temperate-cold regions (e.g. in central Europe) (Hall, Stuntz & Abrams, 2008). Despite these predictions of strong effects of CC, studies on freshwater systems are quite rare (Mulholland et al., 1997; Wrona et al., 2006).

In this study, our goal was to assess the efficiency of a mixed approach, combining predictions of a species distribution by an ensemble forecasting modelling and the network of the current European protected areas, for providing guidelines for conservation plans at a European scale. Predictions are done for the current environmental situation and in the future, according to a scenario of climate change. Results provided for the study species, the European otter, are considered as important general guidelines for a global conservation of the freshwater systems in a near future. By taking into account the species distribution shift due to climate change, we identify the priority areas for long term conservation and discuss the efficiency of the current protected areas network (Protected areas and Natura 2000 network) in protecting these priority areas.

Materials and methods

Otter distribution in Europe

The European distribution of the otter is currently divided into three distinct sub-distributions (Fig. 1 - a): 1) a western distribution, including Portugal, Spain and France, 2) an eastern distribution, including most Eastern European countries and the Balkans, and 3) a small southern distribution limited to southern Italy. In a wide area covering the central part of Europe, from southern Denmark to north-central Italy, and from eastern France to western Austria and Germany, the otter is not present anymore (Ruiz-Olmo & Delibes, 1998; Kranz, 2000; Mason, 2004; Reuther & Krekemeyer, 2004). This absence is mainly due to the population decreases during the years 1970-1990, due to habitat destruction, pollution, and direct persecution (Reuther et al., 2000). We studied the otter distribution over the whole Europe, but we excluded British Islands and Scandinavia as these areas are spatially disconnected from the rest of Europe, disabling them as useful steps for otter's natural spread.

We merged data of the species occurrence on the study area coming from the *Information System for Otter Survey* (ISOS) database (Reuther & Krekemeyer, 2004) and from a specific Italian survey (Loy et al., 2007). The records were then linked to 12100 UTM 10x10km grid cells, as recommended by the *European standard* for otter surveys (Reuther et al., 2000).
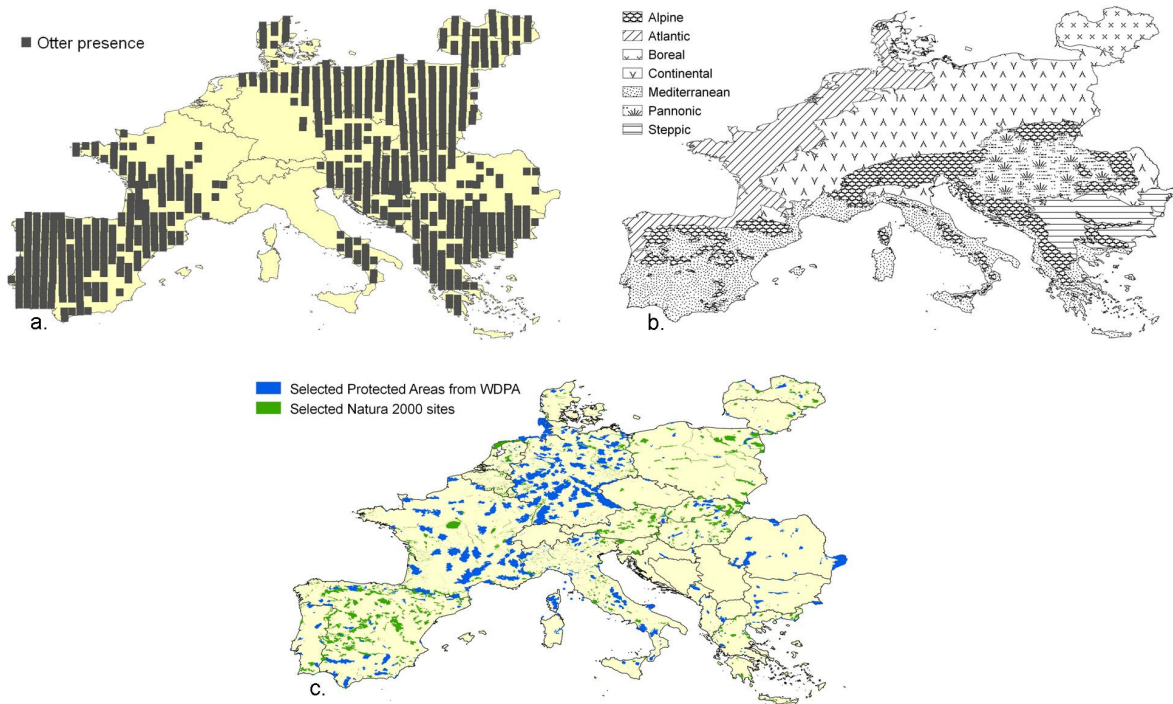
Fig. 1 - a) Distribution range of the otter in continental Europe (source: EIONET). b) Bioregions. c) Protected Areas and Natura 2000 network.

Environmental data

Following the results of previous otter studies at large extents (Robitaille & Laurence, 2002; Barbosa, 2003; Reuther & Krekemeyer, 2004), we described the study area by 13 variables related to the otter's ecological requirements or to potential disturbances (Tab. 1). As water availability is a crucial parameter (Beja, 1992), we used data of annual precipitation, mean precipitation of the wettest quarter and the driest quarter of the year, percentage of small rivers, medium rivers, big rivers and lakes. As otters need vegetation cover on river edges as potential resting sites, we considered the percentage of forest. Otter's diet consists mostly of fish (Ruiz-Olmo, 2001). We did not have these data at the European scale but we used altitude as a surrogate, as elevation influences both the diversity of fish assemblages and abundance, as well as the otter distribution (Remonti, Balestrieri & Prigioni, 2009). We considered the distance from cities containing more than 100 000 inhabitants, distance from roads, percentage of industrial areas and population density as the main indices of environmental disturbance (Prenda, 1996).

Biological interpretation	Predictors name	Description	Data source	Resolution/scale of original data	Up-scale at 10km method
Water	p_driest*	Mean precipitation driest quarter	Worldclim	1km	Mean
	p_wettest*	Mean precipitation wettest quarter	Worldclim	1km	Mean

	an_prec*	Annual precipitation	Worldclim	1km	Mean
	smal_riv	Rivers 1,2 Strahler order	CCM Rivers and catchment Database	1:250.000	Percentage
	med_riv	Rivers 3-5 Strahler order	CCM Rivers and catchment Database	1:250.000	Percentage
	big_riv	Rivers 6-9 Strahler order	CCM Rivers and catchment Database	1:250.000	Percentage
	perc_lake	Lake	CCM Rivers and catchment Database	1:250.000	Percentage
Disturbance	dist_road	Distance from main roads	Edit Geoplatform	1:250.000	Mean
	dist_town	Distance from cities comprising more than 100.000 inhabitants	ESRI Dataset Database	1:250.000	Mean
	perc_indus	Industrial areas	Corine Land Cover 2000	100m	Percentage
	pop_dens	Human population density	Gridded population of the world (2000)	1km	Mean
Resting sites	perc_forest	Forest	Corine Land Cover 2000	100m	Percentage
Food supply	elev	Altitude	Shuttle Radar Topography Mission	100m	Mean

Tab. 1 – Environmental predictors used in the habitat suitability models. The predictors are related to the ecological requirements and to potential disturbance influencing the global distribution of the otter.

To describe environmental conditions in future, under CC, we modified the current annual precipitation, mean precipitation of the wettest quarter, mean precipitation of driest quarter with anomalies derived from simulation produced by the CCM3 model run in a scenario of 2xCO2 in the atmosphere predicted to occur in the 2100 and with an increase of 2 °C of temperature (Govindasamy, Duffy & Conquard, 2003a).

Variables were prepared in a geographic information system using ArcGIS 9.3 (ESRI, Redlands, USA). All data were developed at a spatial resolution of 10x10 km grid cells to fit species data (see tab. 1 for the up-scale method). To obtain percentage values of landcover elements initially described as vector data (i.e. rivers, lakes, forest, cities, roads, industrial areas), we firstly converted vector data to raster at a resolution depending on the scale of the original data (100m or 250m, see Tab. 1) and then calculated the proportion of these pixels contained in a 10 x 10 km raster cell.

Species distribution models

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Preliminary test: consistency of the species' habitat requirements

As the otter's European distribution is split into three disconnected sub-distributions, we wanted to verify the consistency of the otter's habitat characteristics before modelling the distribution. This parameter is essential to support the merge of occurrence data in a same model (Osborn & Suerez-Seoane, 2002), but it is also important from a conservation perspective, to justify actions to promote reconnections between the three European sub-distributions. We tested it by mean of a Principal component analysis (PCA), run by the "ade4" library in the R software. As done by Broennimann et al (2007), we compared the position of the three clouds of occurrences in the PCA, fed with the species occurrences and our environmental variables. The magnitude and the statistical significance of the distance between the three clouds were assessed using a between-class analysis, yielding a between class inertia percentage (Doledec, Chessel & Gimaret-Carpentier, 2000). We further tested this ratio with 99 Monte-Carlo randomizations (Romesburg, 1985).

Ensemble forecasting approach

The whole set of the species presences (12100 grid cells) was randomly split into 11 sub-datasets, each one containing 1100 presences. To limit data clustering, we split the sets of occurrence by choosing points separated at least by 30 km, which distance corresponds to the average size of the otter's home range (Kruuk, 2006). To completely cover the study area with absence data, we generated 3300 random pseudo-absences, also under the criteria of a minimum distance of 30km, both between the absence points and between the presence and absence points. We used these pseudo absences in each model, in combination of each of the 11 subsets of presences. To reduce the impact of these pseudo-absences towards presences, we used a case weighting method (Gibson, Barrett & Burbidge, 2007), weighting each absence with the value n_presence/n_pseudo-absence (i.e. 0.33).

To produce species distribution maps, we used an ensemble forecasting approach (fig 2), which was applied twice, firstly with environmental data of the current situation, and secondly with the environmental data under CC combined. The modelling framework comprises six modelling methods: Artificial Neural Network (ANN), Generalised Additive Models (GAM), Generalised Boosting Models (GBM), Generalised Linear Models (GLM), Multivariate Adaptive Regression Splines (MARS) and Maximum Entropy (MAXENT). The five first methods use presence and absence data, and were implemented through the BIOMOD R package (version 2008.06.01) (Thuiller, 2003). The last modelling method uses only presence data and was modelled with MAXENT software (Phillips, Anderson & Schapire, 2006).

The six methods were applied to each of the 11 datasets (i.e. one presence sub-dataset and the pseudo absences dataset, for presence-absence models), leading to 66 models, providing predictions with a continuous index of suitability, ranging from 0 to 1. Each model was evaluated independently, using the 10 other sub-datasets. Using the ROC approach (Fielding & Bell, 1997), we obtained 10 independent evaluation measures for each model.

We used the results of the 66 models to analyse the importance of our environmental variables in defining the suitable areas for the otter at the European scale. For that, we proceed to a randomization process of the variables in the models. For each modelling method, we considered 1) the prediction made with all the variables (as described above) and 2) the predictions made by deleting one focused variable. For each variable, the correlation score computed between the two predictions provides an estimation of the importance of this variable in the model. For instance, a good correlation score indicates that the two predictions only slightly differ, meaning that the studied variable do not influence a lot the model in its predictions. This procedure was repeated 100 times for each variable independently and for each modelling method, using the function "VarImport" in BIOMOD (Thuiller et al. 2009).

Finally, to obtain a prediction of the species distribution, both in the current situation and in the future, we proceed to the combination of the 66 models (Fig 2) for each case. We firstly combined models in each modelling method (i.e. 11 models for each method), leading to six predictions (ANNtot, GAMtot, GBMtot, GLMtot, MARStot, MAXENTtot), ranging from 0 to 1. We evaluated these models with the ROC approach (Fielding & Bell, 1997), using the full European database (internal validation). Secondly, maps of these six predictions were reclassified into 2 classes (i.e. 0 and 1). We chose the reclassification threshold as the suitability value corresponding to an equal predicted and observed prevalence (Freeman & Moisen, 2008), when the full species occurences. Finally, we combined these six binary maps into a final prediction map (Fig 2), which predicts the species distribution by three habitat suitability classes: the highly suitable habitat, where the six models had a value of 1, the suitable habitat, where at least of the six models had a value of 1, and the unsuitable habitat, where the six models had a value of 0.
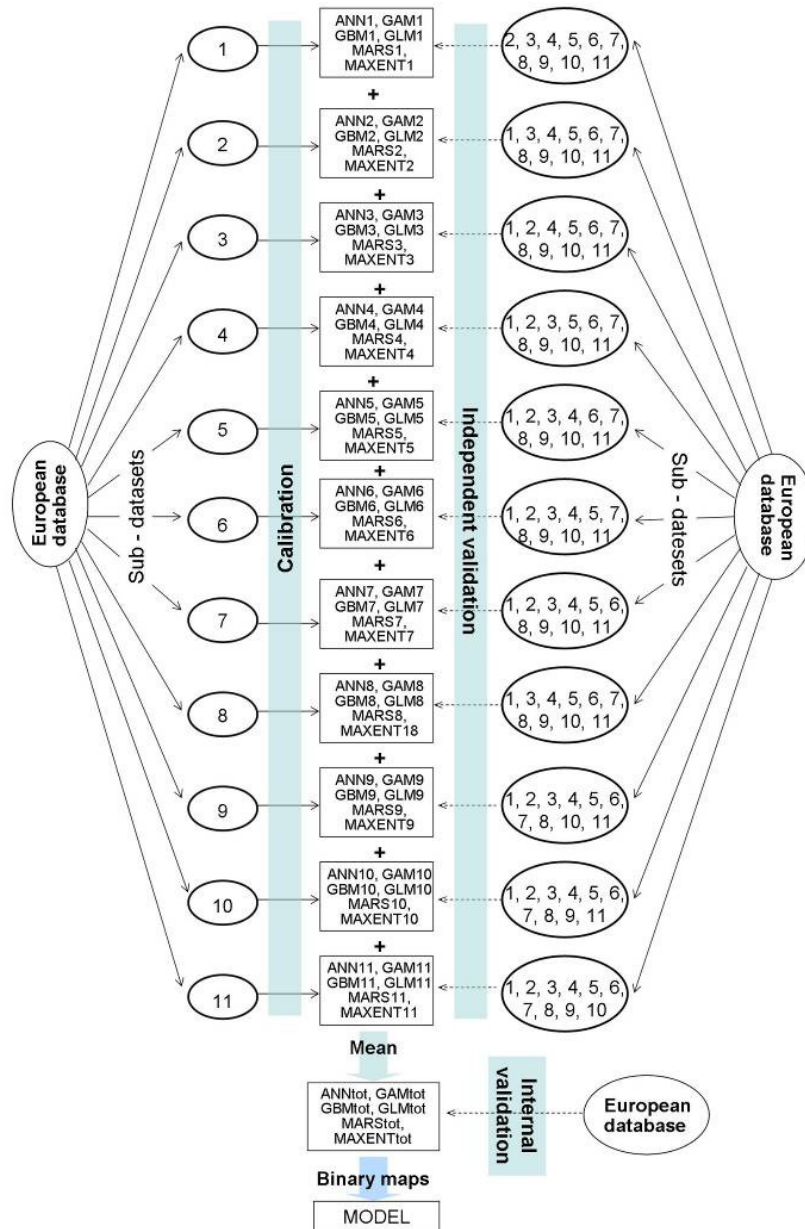
Fig. 2 – Ensemble forecasting used to produce the otter's distribution models.

Assessment of the species distribution shift

To assess the shift of the otter's distribution under CC, we overlaid the two final prediction maps, provided for the current environmental conditions and, in the future, under CC. We then calculated the proportions of pixels of the three habitat suitability classes (highly suitable, suitable and unsuitable) that remain the same or differ in the two predictions. We did this calculation 1) over the whole study area, 2) for each European sub-distribution and the central Europe, 3) for each European bioregion, and 4) for each European country. The map of the bioregions was created by us and were derived from WWF Ecoregions grouped using the EEA's Biogeografic regions (downloadable from http://www.eea.europa.eu) (Fig. 1 - b).

Species' conservation assessments

From the results of the otter's distribution shift done for the whole study area, we identified the areas that present highly suitable environmental conditions both currently and in the future, under CC. These areas were defined as priority areas for the otter's conservation, that should urgently be considered. The areas predicted as highly suitable only in the future were defined as opportunities for the otter's conservation in the future.

We overlapped the otter's priority areas with the areas with important conservation goals at the European scale, i.e. the national and international Protected Areas with a high enforcement level, that we called the protected areas, and the Special areas of conservation (SAC) and the Special protection areas (SPA) designated under the Natura2000 network specifically for aquatic and semi-aquatic birds and mammals (EU Habitat Directive 92/43/EEC). This information was obtained from the World Database on Protected Areas (WDPA, 2009). Note that for Switzerland, Croatia, Bosnia-Herzegovina, Montenegro, Albania, Serbia, Macedonia, Romania, and Bulgaria no Natura 2000 sites is designated. Overlaps were done both for the species distribution under the current environmental conditions and for the future conditions, under CC.

From that overlap, we calculated the proportion of highly suitable areas that belong to these conservation areas. We provide the results for each European country.

Results

Otter's habitat requirements

A scatter plot of the first two PCA components (Fig. 3) clearly reveals an overlap of the occurrences belonging to the three otter sub-distributions. Centroids of the three clouds are also very close (between class inertia percentage ranging between 0.015 and 0.0045, *P*-value=0.001), suggesting strong similarities in the habitat characteristics of the otters present in each of the three European sub-distributions.

The analysis of the importance of the environmental variables (Fig. 4) reveals that the most relevant one over all the approaches is the mean amount of precipitation in the driest quarter of the year. Annual precipitation and precipitation of the wettest quarter of the year are very important for ANN, GAM, GLM and MARS, but less important for GBM and MAXENT. Human population density is the most important variable linked to disturbance. This predictor is quite important for whole approaches. Distance from large towns is relevant only for ANN. Percentage of forest and elevation, respectively related to availability of resting site and food supply, are quite important for whole approaches. Specifically, elevation is important for ANN (Fig. 4).

Models' evaluation

The models show a good predictive power of the species distribution (Fig 5), with a mean AUC of 0.759 estimated with the independent evaluation procedure and 0.791 with the internal validation. As expected, the internal validation showed larger AUC values if compared to the independent validation For the independent validation, the minimum accuracy value is 0.703, recorded for MAXENT, and the maximum accuracy value is 0.807, recorded for the ANN. For the internal validation, the minimum value is 0.747, recorded for the GLM, and the maximum is 0.848, recorded for the ANN.

Shifts of the otter's distribution under CC scenario

Climate change has effects on the spatial distribution of the three habitat suitability classes (Fig. 5-b, c). These effects are unevenly distributed in the study area (Fig. 5, Tab. 2).
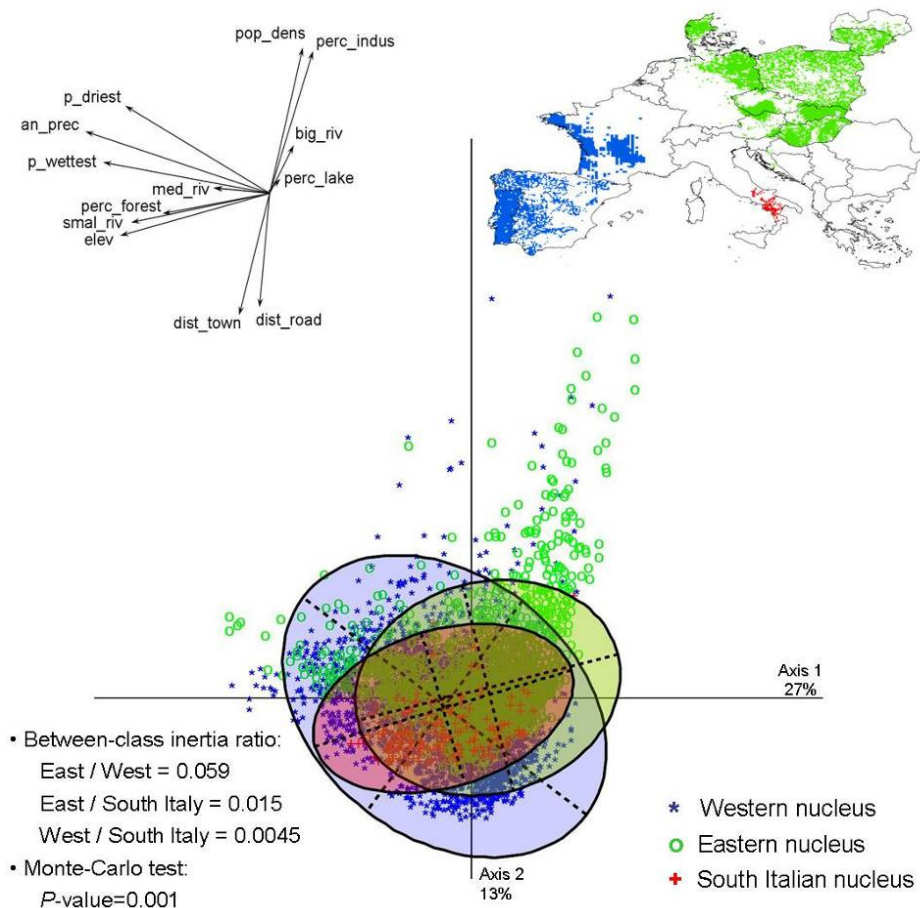

Fig. 3 – Environmental space with the positions of the otter's occurrences in the three European sub-distributions (i.e. eastern European, western European and southern Italian) along the two first axes of the PCA. The map on the top right shows the otter's occurrence data referred to the UTM 10x10km grid. Colors refer to the three sub-distributions. The enclosed correlation graph indicates the importance of each environmental variable on the two significant axes of the PCA.

Overall, future climate warming has little effects on the amount of highly suitable areas: this category decreases from 39% in current conditions to 36% in CC scenario. Inversely, a 16% increase of the suitable areas is noted. Unsuitable habitats decrease from 23% to 20% (Tab. 2). However, when considering the three sub-distributions, changes are more important (Tab. 2).

In the western European sub-distribution, highly suitable areas decreases by 35% and unsuitable areas increases by 56%. The central part of Europe, where the species is currently absent, will experience a significant increase of highly suitable areas (10%) and suitable areas (24%), and a decrease of unsuitable areas (22%). The eastern and the southern sub-distributions remain quite stable in their amount of highly suitable areas, manifest an increase of the suitable areas, and a decrease of the unsuitable ones.
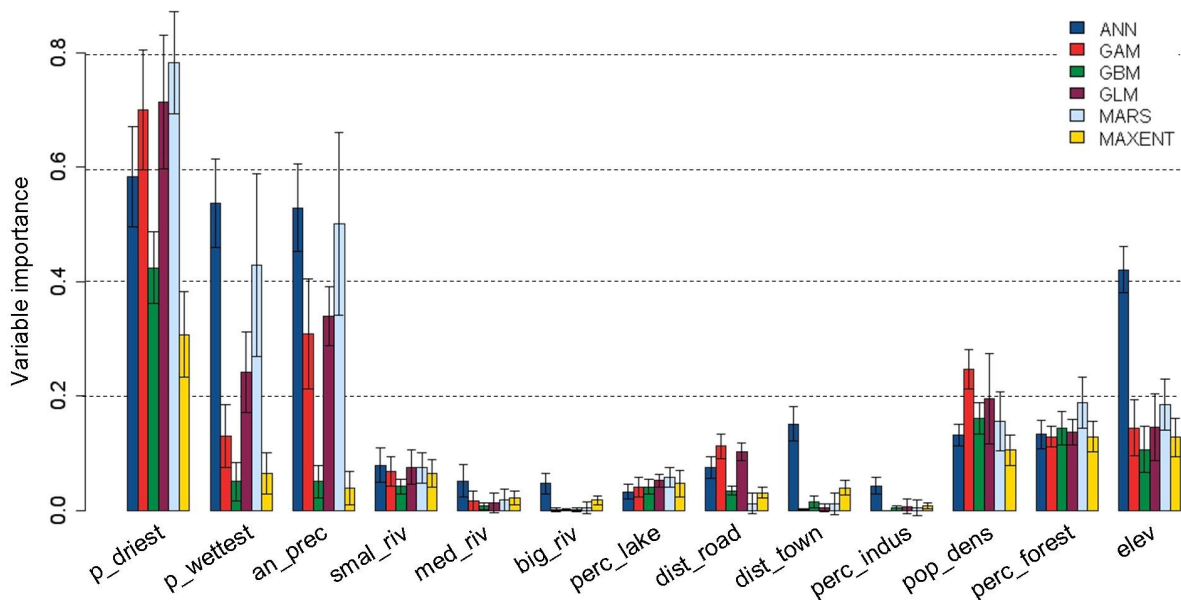

Fig. 4 – Importance of each environmental variable in each modelling method used in the ensemble forecasting. Values are calculated as one minus the correlation score between the prediction map using all the variables and the prediction maps made with permutated variables. Standard deviations of the values result from the set of 100 permutation runs. The first three variables (prec_driest, prec_wettest, annual_prec) refer to climatic parameters, i.e. precipitations, the four next variables (small_riv, med_riv, big_riv, perc_lake) refer to the freshwater system, the four next variables refer to the potential disturbances, and the final two variables, i.e. perc_forest and elevation, are indicators of potential resting sites and fish availability, respectively.

Considering the bioregions (Tab. 2), the Mediterranean one is the most negatively influenced by CC, with a 28% decrease in highly suitable areas and an increase of 17% of the unsuitable areas. The Atlantic and the alpine bioregions also show a decrease of their highly suitable areas (25%).

When focusing on the countries, highly suitable areas in Spain will decrease from 43% to 26%, in Portugal from 93% to 84%, in France from 24% to 17%. These countries are important as they contain a large proportion of the current presence of the species.

The areas ranging from Central Italy up to Southern France will also lose most of their highly suitable habitats (Fig. 5 - c). These changes might therefore compromise the northward expansion of the Italian population and its reconnection with the western population through southern France.

North-central France, central Germany and Pre-Alps will gain suitable and highly suitable areas. These changes could enforce the expansion of the species from the western part of France, the expansion from Austria and from Slovenia, and eventually the reconnection of the eastern and western populations.
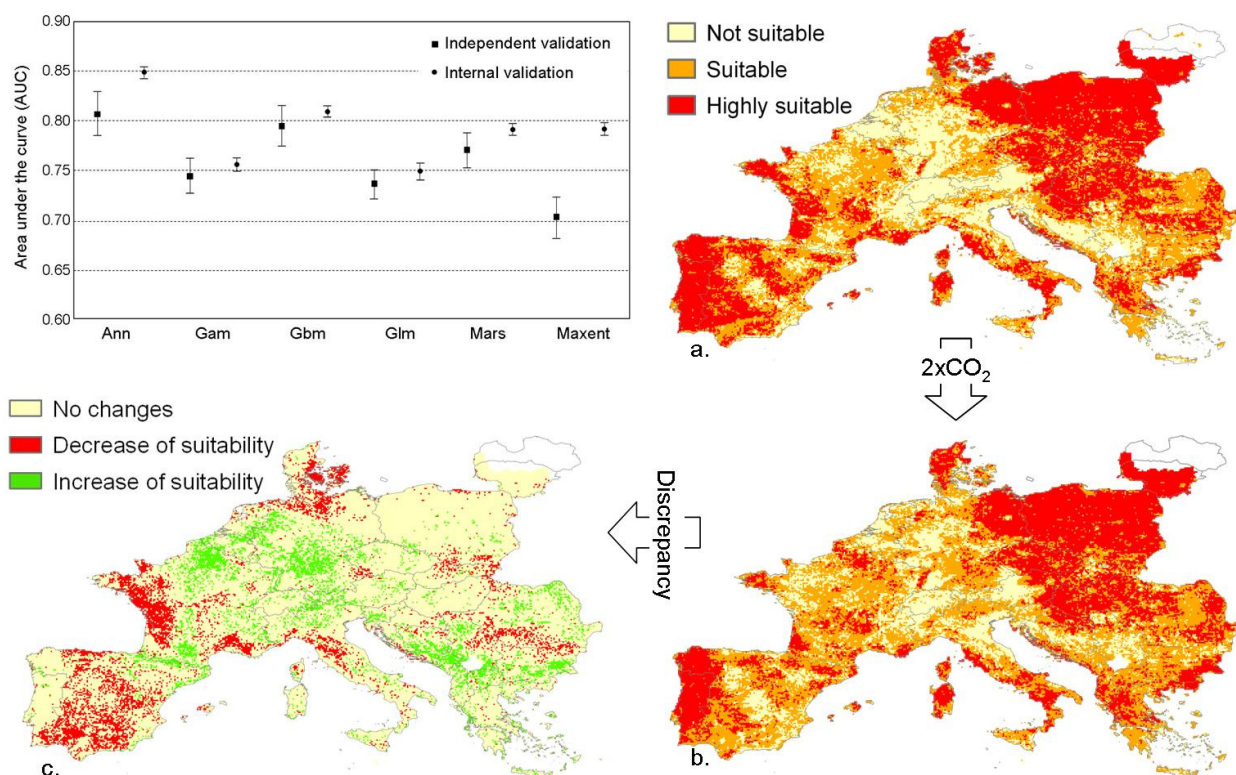

Fig. 5 – a) otter's distribution map for the current environmental conditions. b) otter's distribution map predicted for the future environmental conditions, under cliamate change. c) Discrepancies between the maps a) and b). In the graph Models performance evaluated through independent and internal validation using the Area Under the Curve (AUC).

Priority areas for conservation

The priority areas to successfully preserve the species are identified in Figure 6. In the western sub-distribution, highly suitable areas, both now and under CC scenario, are mainly located all over Portugal, northern western Spain (Galicia), northern western France (Brittany),

southern western France and the Massif Central. In the eastern and southern-Italian sub distributions, these areas are quite extensive. In the central part of Europe, where the otter is not currently present, highly suitable areas are mainly located in central Italy and southern France. Under CC scenarios highly suitable areas are mostly located in northern eastern France (Alsace) and in central Germany (Fig. 6).

	Highly suitable areas			Suitable areas			Unsuitable areass		
	Pres	Fut	Change	Pres	Fut	Change	Pres	Fut	Change
Study area	0.39	0.36	- 8%	0.37	0.43	16%	0.23	0.2	- 13%
Western	0.55	0.36	- 35%	0.36	0.5	39%	0.09	0.14	56%
Eastern	0.56	0.56	0%	0.3	0.33	10%	0.13	0.11	- 15%
South-Italian	0.61	0.59	- 3%	0.37	0.39	5%	0.02	0.01	- 50%
Center Europe	0.1	0.11	10%	0.41	0.51	24%	0.49	0.38	- 22%
Mediterranean	0.39	0.28	- 28%	0.43	0.51	19%	0.18	0.21	17%
Alpine	0.23	0.21	- 9%	0.39	0.53	36%	0.38	0.26	- 32%
Atlantic	0.32	0.24	- 25%	0.39	0.5	28%	0.29	0.27	- 7%
Boreal	0.97	0.96	- 1%	0.03	0.04	33%	0	0	0%
Continental	0.48	0.49	2%	0.29	0.33	14%	0.23	0.18	- 22%
Pannonic	0.58	0.58	0%	0.34	0.34	0%	0.08	0.08	0%
Steppic	0.22	0.22	0%	0.52	0.56	8%	0.26	0.22	- 15%
Albania	0.26	0.38	46%	0.56	0.55	- 2%	0.19	0.06	- 68%
Austria	0.25	0.27	8%	0.2	0.29	45%	0.55	0.44	- 20%
Belgium	0	0	0%	0.22	0.48	118%	0.78	0.52	- 33%
Bosnia Herz	0.09	0.1	11%	0.29	0.5	72%	0.62	0.4	- 35%
Bulgaria	0.18	0.26	44%	0.65	0.6	- 8%	0.16	0.14	- 13%
Croatia	0.41	0.4	- 2%	0.38	0.43	13%	0.21	0.18	- 14%
Denmark	0.77	0.53	- 31%	0.22	0.36	64%	0.01	0.12	1100%
France	0.24	0.17	- 29%	0.49	0.58	18%	0.27	0.25	- 7%
Germany	0.26	0.26	0%	0.34	0.45	32%	0.4	0.29	- 28%
Greece	0.26	0.3	15%	0.54	0.57	6%	0.19	0.13	- 32%
Italy	0.24	0.21	- 13%	0.42	0.48	14%	0.34	0.31	- 9%
Lithuania	0.98	0.96	- 2%	0.02	0.03	50%	0	0	0%
Luxembourg	0.08	0.08	0%	0.49	0.62	27%	0.44	0.3	- 32%
Macedonia	0.14	0.2	43%	0.51	0.73	43%	0.34	0.07	- 79%
Montenegro	0.02	0.09	350%	0.31	0.77	148%	0.67	0.13	- 81%
Netherlands	0	0.01	0%	0.4	0.45	13%	0.6	0.54	- 10%
Poland	0.89	0.87	- 2%	0.11	0.12	9%	0.01	0.01	0%
Portugal	0.93	0.84	- 10%	0.07	0.15	114%	0.01	0.01	0%
Czech Republic	0.65	0.72	11%	0.32	0.25	- 22%	0.04	0.03	- 25%
Romania	0.37	0.39	5%	0.54	0.53	-2%	0.09	0.09	0%
Serbia	0.06	0.08	33%	0.41	0.48	17%	0.53	0.45	- 15%
Slovakia	0.57	0.51	- 11%	0.37	0.35	- 5%	0.06	0.13	117%
Slovenia	0.11	0.12	9%	0.41	0.57	39%	0.48	0.31	- 35%
Spain	0.43	0.26	- 40%	0.41	0.53	29%	0.16	0.22	38%
Switzerland	0	0	0%	0.06	0.21	250%	0.94	0.79	- 16%
Hungary	0.77	0.77	0%	0.21	0.22	5%	0.01	0.01	0%

Tab. 2 - Frequencies of the highly suitable, suitable and unsuitable areas under the current conditions (present) and under climate change (future), and proportions of changes for the whole study area, the three otter sub-distributions, the European bioregions and the European countries.
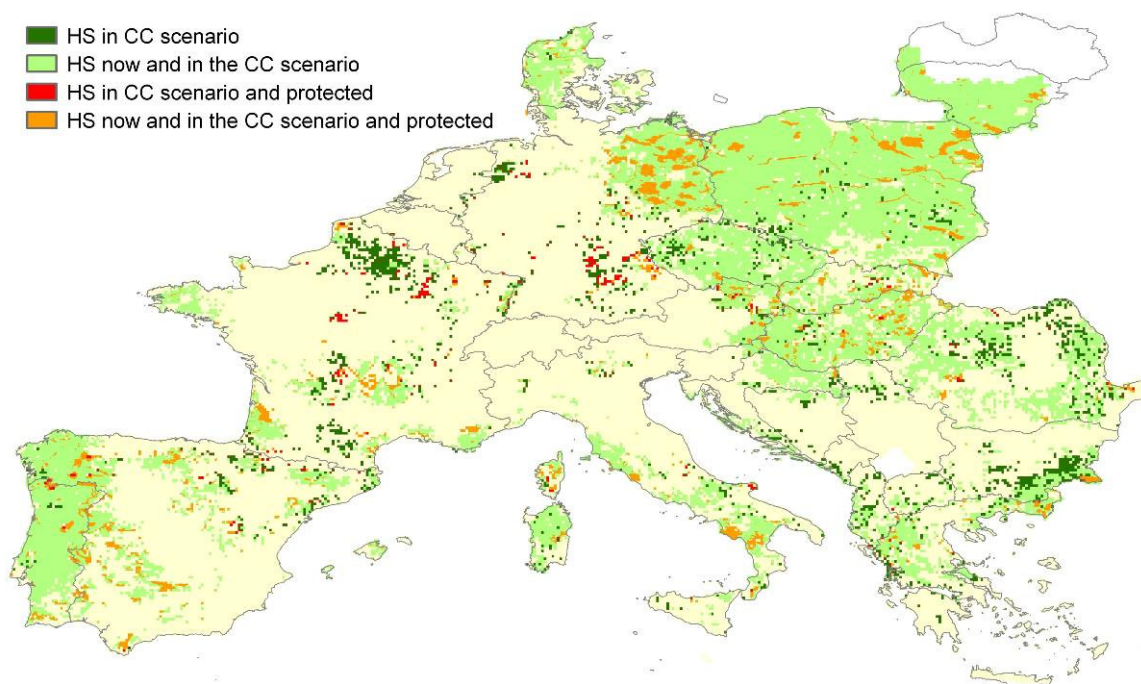
Fig. 6 – Map of priority areas for the conservation of the otter and overlapping with Protected Areas-Natura 2000 sites.

These areas, important for the otter conservation, are unevenly protected in the European countries by the existing protected areas systems (Tab. 3). Considering the whole study area, the 4% of the highly suitable now and under CC are protected by protected areas (PA). This value raises to 10% considering the Natura 2000 network. The 8% of highly suitable habitats under CC is protected by PA, the percentage of protection increase to 12% adding the Natura 2000 sites.

	Frequency of protection	
	Highly suitable areas for current and future conditions	Highly suitable areas in future conditions
Albania*	0.02	0.03
Austria	0.14	0.29
Belgium	0.55	0.16
Bosnia Herz*	0.00	0.00
Bulgaria*	0.07	0.01
Croatia*	0.02	0.01
Denmark	0.06	0.00
France	0.20	0.17
Germany	0.27	0.29
Greece	0.11	0.06
Italy	0.13	0.11
Lithuania	0.05	0.00

Luxembourg*	0.13	0.15
Macedonia	0.02	0.04
Montenegro*	0.00	0.00
Netherlands	0.36	0.10
Poland	0.07	0.02
Portugal	0.09	0.30
Czech Republic	0.02	0.02
Romania*	0.03	0.05
Serbia*	0.01	0.00
Slovakia	0.17	0.28
Slovenia	0.05	0.06
Spain	0.18	0.22
Switzerland*	0.00	0.00
Hungary	0.13	0.20

*Natura 2000 sites were not available

Tab. 3 – Frequency of priority areas for conservation protected by the current network of protected areas or included in the Natura2000, calculated by country.

Discussion

Effects of climate change

The ROC analysis showed that the model performs significantly better than a random model (Fig. 5). Because of the good performance of the model we can consider it reliable and use it as a tool to establish effective conservation strategies. The combination of different approaches and calibration dataset using an ensemble forecasting approach is of crucial importance when planning for climate change to efficiently support conservation decisions (Araujo & New 2007; Marmion et al 2009).

The strong importance of the climatic variables, namely mean precipitation of the driest quarter of the year, mean precipitation of the wettest quarter of the year and the mean annual precipitation, demonstrate the sensibility of the species to CC. Considering the species as the umbrella species for the freshwater ecosystems (Barbosa et al 2003), these results showed the sensibility of the freshwater ecosystems to climate change.

Our results evidenced that under climate change scenario associated with a doubling in CO_2 levels, the effects on the distribution of otter's suitable habitats are unevenly distributed in continental Europe (Fig. 5, Tab. 2).

The Mediterranean bioregion is the most affected by climate change (Tab. 2). Here the warming climate could cause an increase of drought with a disappearing of the rivers in some cases. In the Atlantic bioregion is predicted a decrease of highly suitable habitats, maybe caused by an increase of flood events (Hall, Stuntz & Abrams, 2008). The increase of these extreme and

periodic events may play an important role in modifying the freshwater ecosystem (Hannah, Midgley & Millar, 2001).

Considering the current otter distribution, the more evident changes in habitat suitability distribution appear in the western sub-distribution. Here the climate change causes a strong loss of highly suitable areas (Fig. 5, Tab. 2), in particular in Spain, southern Portugal and western France (Tab. 2) and an increase of unsuitable areas (Fig. 5, Tab. 2). On the contrary, in central part of Europe where the otter is nowadays absent, the scenario showed an increase of highly suitable habitats (Tab 2). The eastern and the southern sub-distributions remain stable in their amount of highly suitable habitats, manifest an increase in suitable habitat and a decrease the unsuitable one (Tab. 2, Fig. 5). The reduction of the highly suitable habitats and the increase of the unsuitable habitat in the western sub-distribution could lead to the contraction of the western population of otters. Thus a decrease in range size could result in a decline in population size, and consequently extinction rates could increase for the usual small population reasons, susceptibility to stochastic variation being amongst the most important (Lawton & May, 1995; Erasmus et al., 2002). A decrease in range size could imply that the species become more sensitive to catastrophic events (such as drought), or to increase of land transformation by humans (Lawton & May, 1995). Moreover the range contraction could mean that smaller catastrophic events affect a larger proportion of species total population. If a species is restricted to just a small area, then a local catastrophic event could easily caused the extinction of that species.

A further strong contraction of highly suitable habitats appears in the areas going from Central Italy up to Southern France (Fig. 5). This is also the case of the southern-Italian sub-distribution. In fact the reduction of highly suitable habitats in the areas going from Central Italy up to Southern France will cause a reduction of the connection between the southern-Italian and the western populations leaving the Italian population isolated and more sensitive to catastrophic events.

Nevertheless the increase of suitability in central Europe could favour the eastwards and westwards expansion of the otter allowing the re-conjunction of the two populations. But an extensive contraction of suitable habitats in the western nucleus could create large gaps within the current range, limiting the potential dispersal of the species (Erasmus et al., 2002).

Climate change affects such as freshwater fish and crustaceans and eutrophication caused by increase water temperature could easily drive to extinction some species, or some species will likely benefit from temperature increase and will colonise new areas (Hall, Stuntz & Abrams, 2008). These effects on freshwater ecosystem probably could be reflected by the habitat suitability shift of the otter

Several studies have attempted to assess the potential effects of climate change on biodiversity, for example a lot of studies have been carried out terrestrial and marine ecosystem, on birds (e.g. Ohlemuller et al., 2006; Pounds et al., 2006; Foden et al., 2007; Levinsky et al., 2007; Cheung et al., 2009; Coetzee et al., 2009; Li et al., 2009). Despite it is noted that the effects of climate change on species living in freshwater ecosystems will be strong because of strong perturbations due to changes in precipitations (Hall, Stuntz & Abrams, 2008), the assessments of the impact of climate change on biodiversity freshwater ecosystems are very few (Mulholland PJ et al, 1997, Prowse TD et al, 2009, Wrona FJ et al, 2006, Lassalle & Rochard, 2009) especially at large scales due to ecosystem complexity including the water bodies and the riparian communities.

The role of the otter as umbrella species for the freshwater ecosystems (Barbosa, 2003), make important our study to have knowledge on the effect of CC on the biological side of the freshwater ecosystems, moreover protecting this species we are going to protect the whole ecosystem.

Effectiveness of the existing PA to protect priority areas for conservation
The identification of the critical areas in face to climate change is crucial to maintain species and ecosystems (Vos et al., 2008). We identified critical areas for the long-term conservation of the otter as the areas that are highly suitable now and under CC scenario and areas will be highly suitable under CC scenario. These areas are dispersedly distributed in the study area (Fig. 6). The highly suitable habitats now and under CC scenario located in the currently distribution range are important to maintain the populations, as they could be "source" population. Instead where the species is not present it is important to support the re-colonization or the reintroduction in these areas. The highly suitable habitats under CC assure good habitats for the species in the future.

The overlapping of these critical areas with the existing protected areas and Natura 2000 network shows a heterogeneous distribution of the protection (Fig. 6; Tab. 3). This evidenced that protected areas should be supplemented with additional coverage to allow for the effects of climate change (Hannah, Midgley & Millar, 2001; Araujo et al., 2004). In particular improving the protection in highly suitable habitat now and in the future.

Knowing that climate change is a reality, conservation responses to climate change have to be anticipatory and systematic (Hannah, Midgley & Millar, 2001) and they have to consider the need of a compromise with the human development and the limiting resources for the biodiversity conservation (Joseph, Maloney & Possingham, 2009).

Adjustments for climate change can be made at different stages of conservation planning. Conservation goals can explicitly include maintaining suitable habitats for species expansion in the face of climate change (Cowling, 1999). Conservation strategies integrated with climate change should include mechanisms for coordinating conservation actions at the regional level across political boundaries and agency jurisdictions. Regional coordination is necessary for conservation goals and management to be coherent on the same scale at which climate change impacts will operate.

Our study could be considered also in view of the European water Framework Directive (WFD, CEE 60/2000). The objectives of the WFD, that concerns the whole river basins, including the water bodies and the riparian communities, are the prevention of deterioration of the status of all water bodies, protection, enhancement and restoring of all bodies of surface water, with the aim of achieving good surface water status at the latest 15 years (2015), protection and enhancement of all artificial and heavily modified bodies of water, with the aim of achieving good ecological potential and good surface water chemical status, reduction of pollution.

Conclusions

The use of ensemble modelling methods in this study provides in improvement in increasing prediction accuracy. We have identified priority areas for the conservation considering CC and we assessed the efficacy of the existing conservation tool to protect these areas and reiterate that conservation areas should be planned considering CC. Our conclusions are expected will occur in 2100 (with an increase of 2 °C) following the CCM3 model (Govindasamy, Duffy & Conquard, 2003b). But recent data suggest this values might underestimate the CC future scenario, as several studies evidenced that climate is warming faster than expected (van Oldenborgh et al., 2009). Recent studies reveals that the CO2 emissions from fossil-fuel burning and a global scale have been accelerating at a global scale (Canadell et al., 2007; Raupach et al., 2007), and new projections estimated a 5.2 °C increase of temperature in 2090-2100 (median surface) (Sokolov et al., 2009) following these estimation the 2 °C increase will occur faster that expected by the predictions made in the 2003. considering that the effects of climate change on the potential distribution of the species will be worst, we need to act urgently and more rapid.

Consequently CC is not the only factor changing and influencing distribution, we have to consider land use change too. It could be useful consider these changes in the future (usefulness for conservationists) at a more detailed scale influent parameters could be eutrophication, poisoning that helped freshwater conservation it would be possible to insert them in the model.

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On the way toward the comeback of the otter in Switzerland? - Using niche models to evaluate the potential suitability of habitats for successfully reintroducing a species

Carmen Cianfrani[1,2], Antoine Guisan[2]

[1] *Department of Science and Technology for the Environment, University of Molise, I-86090, Pesche, Italy*

[2] *Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland*

Introduction

The Eurasian otter (*Lutra lutra* L., 1758) is a semi-aquatic carnivore species whose habitat is usually linked to the existence of freshwater, available shelter (riparian vegetation, rocky structures and others) and abundant prey (Ruiz-Olmo & Delibes, 1998). Until the late 19th century the species was widespread throughout Switzerland, but became then extinct during the 20th century. Despite extensive research, the causes of its extinction have not been unambiguously identified, but likely results from a combination of riparian vegetation destruction, hunting, poisonous substances in the environment and a decrease of the fish stocks have led to its gradual disappearance (Weber, 1990).

At the European scale, the otter is currently included in the List of Rare and Threatened Mammals of the Council of Europe, in Appendix II of the Berne Convention, in Appendices II and IV of the Habitat Directive of the European Union, and in Appendix I of the CITES. Until 2007 the species was classified as *vulnerable* in the IUCN Red List of Threatened Species (Hilton-Taylor, 2000), but since 2007 the species' status degraded to *near threatened* (IUCN, 2007), and its status could degrade further if causal factors are not urgently remediated (IUCN, 2007).

The role of the otter as *umbrella* and *emblematic* species in conservation of freshwater ecosystems makes it a challenging project to attempt promoting its reintroduction in Switzerland, be it by mean of natural recolonization from natural populations in neighbouring countries, or eventually through active reintroduction programs. Moreover its geographic position in the middle of Europe, Switzerland may play a crucial role in reconnecting western and eastern European otter populations In this regard, habitat suitability models represent powerful tools to assess habitat quality for species of conservation interest, and produce maps of potential distribution and natural dispersion of the species (Barbosa, 2003). This is because, in order to re-establish viable otter populations and ensure their long term persistence, it is of crucial importance to evaluate the potential aptitude of Swiss habitats to sustain them. Moreover, it is not only important to identify locally suitable habitats, but also unsuitable habitats, as the mosaic of suitable and unsuitable habitats in the landscape will determine how connected will be the reintroduced populations, and how gene flux will be allowed between them to ensure long-term viability of meta-population. This certainly explains why these tools play a role of increasing importance to design efficient conservation actions (Côté & Reynolds, 2002; Robitaille & Laurence, 2002).

This project aims at evaluating the potential of Swiss landscapes to sustain the reintroduction of otter populations through the development and application of a habitat

suitability model, calibrated at the European scale, projected and refined with local environmental predictors at the fine scale over Switzerland using an Italian case study, and finally verified in the field. Its objectives are more specifically to:

- Identify suitable areas to receive otter populations and ensure their long-term viability.

- Identify partially suitable areas that would require a restoration action - like freshwater revitalization and/or local riparian vegetation restoration - to ensure population establishment and persistence.

- Identify areas not suitable now to receive otter population and where restoration and revitalization actions would not allow any future successfully reintroduction, because these areas lie outside the environmental niche of the species.

- Use the previous steps to develop a landscape suitability map, indicating how suitable, partially suitable and unsuitable habitats are arranged in the landscape.

Materials and methods

The general study design of the project is organized in three successive phases:

1) Calibrating a habitat suitability model for otter at the European scale.

2) Projecting the otter niche and model at a finer scale over Switzerland using local environmental predictors calibrating the model in Italy.

3) Verifying the predictions in the field.

The first two steps consist in the development of the habitat suitability map. The model integrates environmental characteristics into a correlative climatic model in a multi-scale-dependent hierarchical manner (Pearson, Dawson & Liu, 2004) (Fig. 1). We capture the entire climatic niche of the species calibrating the model at European scale, to then capture the environmental habitats requirements calibrating the model in Italy and considering in this step the downscaled climatic niche (Fig. 1). Once produced, the habitat suitability map can be used to identify, in the landscape, those sites that have a good potential for successfully reintroducing the otter. However, before it can be used in practice, such map needs to be verified in the field. . To do this, we will follow a model-based sampling strategy as already proposed for inventorying rare species in the landscape (Guisan et al. 2006). It consists in using the reclassified habitat suitability map (say in ten classes) to stratify field sampling. A same number of sites is then chosen randomly in each

strata and each site is then visited in the field to check whether the habitat is truly suitable for the long-term persistence of the otter. Field evaluation of habitat suitability will be based on expertise from Swiss and foreign Otter specialists (see below) and will also be important for eventually detecting colonizing individuals in areas of high habitat suitability and close to other otter nucleus in neighbouring countries (actual or potential, as revealed by the model). Completing this step is a crucial prerequisite for conducting any active reintroduction program.

The collaboration with the Swiss non-governmental organization 'Pro Lutra' and other partners in Switzerland (see 'Collaborations' below) will be of outmost importance if the final prediction is to be used effectively in practice for designing prioritization strategies and for supporting Otter reintroduction plans.
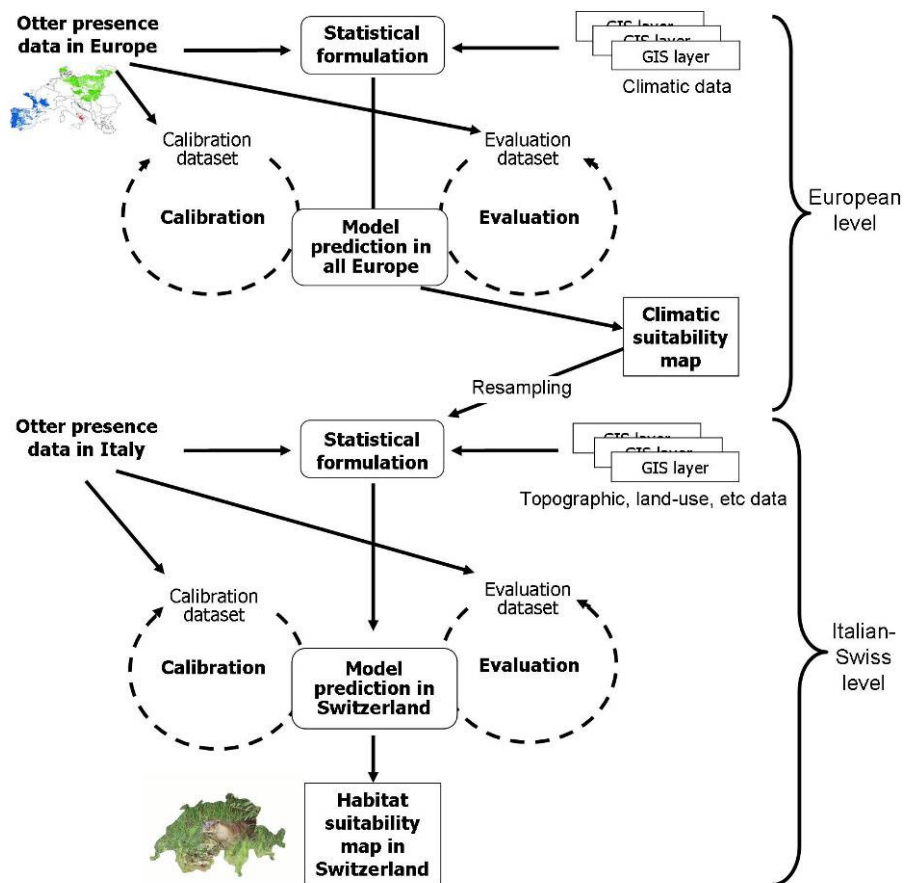
Fig. 1 – Schematic of the hierarchical modelling process

Post-project follow-up

Despite extensive research (Weber, 1990, Weber, 2004), the causes of the otter's extinction in Switzerland have been identified likely as the result from a combination of the direct

persecutions, riparian vegetation destruction and river canalization, poisonous substances in the environment, especially PCB (polychlorinated biphenyls), and a decrease of the fish stocks (Weber, 1990). Even if in the 1952 the species became protected in Switzerland with a federal law, the extinction of the species occurred in Switzerland,

Suitable habitats to receive the species exist in Switzerland, and with this project we will be able to identify them, but in these areas it will be crucial to assess the presence of the factors that caused the decline of the species. In particular the presence of PCB, an estimation of the food supply (mainly fish) and information about canalization of the rivers. In this view a follow step to improve the project could be the collection of the all data available in Switzerland on PCB, fish and river canalization and to geo-reference them. The inclusion of these data in the modeling process is very difficult because of the difficulties to interpolate them to produce continuous map, but a superposition of this information on the habitat suitability map is necessary to identifying the critical areas.

Another improvements of the project could be the use of the suitability map as a 'friction map' to identify potential dispersion corridors using software that simulate dispersal of the species in fragmented landscape (e.g. MigClim Engler & Guisan, 2009). The dispersal could be simulated from the nearest natural source populations outside Switzerland or for instance from the areas in which the species is recently found in Switzerland.

CONCLUSIONS

My thesis provides an important contribution on many aspects and concepts for the development of robust modelling frameworks and an important contribution for the conservation of the otter at the local and European scale.

Critical issues have been examined in depth including (i), the use of absence data when the species is not at equilibrium with its environment, (ii) the relationship between niche and species distribution, (iii) the development of a dispersal model along and across river basins, (iv) the use of an ensemble forecasting approach when assessing the impacts of climate change, (v) the incorporation of climate change effects when planning conservation areas.

Amongst the most important outputs provided by this thesis are the identification of crucial factors that influence the otter's preferred habitat. At a local scale these are represented by fish supply, features that influence the hunting ability of the otter (such as the slope of the river) and the riparian vegetation cover. At a large scale the most important factors are the climatic variables, especially precipitation as well as human density, forest cover and altitude.

This study also came to the fundamental conclusion that when the species is not at equilibrium with its environment because does not occupy the entire suitable habitat available, models should be calibrated and validated with presence data only. The models we developed were considered reliable enough to establish critical areas to preserve the species, gaps and corridors for dispersal.

Considering the separation of the three sub-distributions in Europe and the effects of climate change on the distribution of suitable habitat, an important contribution for the conservation of the species could be the identification of potential areas for dispersal. The suitability maps built considering the change in climate could be used as 'friction maps' to identify potential dispersal corridors using software that simulates dispersal of the species in fragmented landscapes (e.g. MigClim Engler & Guisan, 2009).

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