CONSERVATION OF LARGE CARNIVORES IN A HUMAN DOMINATED LANDSCAPE: HABITAT MODELS AND POTENTIAL DISTRIBUTION

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AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Alessandra Falcucci, submitted for the degree of Doctor of Philosophy with a major in Natural Resources, and titled "CONSERVATION OF LARGE CARNIVORES IN A HUMAN DOMINATED LANDSCAPE: HABITAT MODELS AND POTENTIAL DISTRIBUTION", has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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ABSTRACT

Large carnivores are particularly sensitive to human-induced changes in their habitat, and this has been particularly evident in the Italian context. Historically, wolves, bears and lynx were widespread throughout the entire Italian peninsula but in the last century lynx went extinct and the other two species were limited to small mountainous areas.

However, the pattern of land use change currently occurring throughout the Mediterranean basin could favor the return of large carnivore populations. In this context there is a clear need for scientifically sound conservation tools that can be used to avoid conflicts between carnivore populations and human activities.

I measured land-use/land-cover change occurring in Italy during the last 40 years, finding that most of the mountainous regions are changing towards a more natural condition as rural populations move to urban areas, favoring the recovery of the populations of ungulates and carnivores. Thus I used a series of habitat suitability models to predict possible conservation scenarios for the wolf and the brown bears.

In particular, using deductive habitat suitability models and Markov-chain land-use change models, I simulated the future habitat suitability for the brown bear through 2020. Habitat availability is not going to be a problem for its conservation in the future.

However, there are clear indications that the bears are experiencing a population decline, mainly linked to human related mortality. Using ecological niche factor analyses, I produced a double-layer habitat suitability model that combines the probability of presence with the probability of human-related mortality. Using this approach produced a map that contrasts source-like habitat with mortality sinks that could be extremely useful for the management of the species and its environment.

The Italian wolf is naturally returning in the whole Italian peninsula, and is now spreading through the alpine range. This is creating problems with stockmen. To adrress this challenge I created a composite habitat suitability model, using deductive modeling techniques together with ecological niche factor analysis and partitioned Mahalanobis distance to predict the potential distribution of the wolf along the entire Italian peninsula and the Alpine range. This model provides a conservation tool that can be used for transboundary management plans.

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Chapter 1: GENERAL INTRODUCTION

During the past several thousand years the human population has had an increasingly important role in the modification of the environment (William and Turner 1992; Ojima et al. 1994; Vitousek et al. 1997; Sanderson et al. 2002). Forests covered about 50% of the earth's land area 8,000 years ago, as opposed to 30% today (Noble and Dirzo 1997), and human have expanded agriculture into forests, savannas, and steppes in all parts of the world (Matson et al. 1997). About half of the ice-free land surface has been converted or substantially modified by human activities over the last 10,000 years (Lambin et al. 2003). Landscape ecological processes, biogeochemical cycles, and biodiversity have been impacted, showing complex and usually unpredictable interactions with natural and human induced changes (Lambin et al. 2003; Vitousek et al. 1997).

Considering only the last century, the human population has increased from less than 2 billion people at the beginning of 1900 to more than 6 billion people in 2000 (Loh and Wakernagel 2004; United Nations Population Divisions 2004), corresponding to a threefold increase at least. At the same time, the Ecological Footprint – a measure of the environmental sustainability of human activities– has exceeded the Earth's ecological carrying capacity by 20% (Loh and Wakernagel 2004). As a result, the global carbon cycle has been deeply impacted (Houghton et al. 1999), the atmospheric concentration of CO_2 has increased by 25% (Ojima et al. 1994) and the climate cycles have been altered in unpredictable ways (DeFries et al. 1997).

The structure of the landscape has been altered also. Nearly a third of the earth surface has been fragmented and transformed from "unproductive" lands to agricultural areas (Reid et al. 2000). In particular, more than half of the cultivated areas have been cleared of natural vegetation in the last century (Houghton 1994).

Biodiversity is one of the components of world ecosystems that is deeply impacted by these human-induced changes, both globally and locally (Pimm et al. 1995; Dobson et al. 1997; Pimm et al. 2001). The Living Planet Index – a measure of the overall trends in populations of wild species around the world – dropped by about 40% from 1970 to 2000 (Loh and Wakernagel 2004) indicating a substantial decrease in the viability of the populations being monitored (555 terrestrial species, 323 freshwater species and 267 marine species). Many recent publications have documented or predicted extinction risks close to those that occurred during mass extinction events of the past (Jablonski 1985; Brook et al. 2003; Thomas et al. 2004; Cardillo et al. 2005), and numerous studies have pointed out that extinction risks seem to be far from random (McKinney 1997; Purvis et al. 2000a, 2000b; Cardillo et al. 2005).

McKinney (1997) provides a clear review of the species' attributes supposedly associated with high vulnerability to extinction risk: population size (small populations are more likely to go extinct that larger ones); endemism (small geographic range and hence small populations); trophic level (species at higher trophic levels are more vulnerable than species at lower trophic level); life history (species with small litters, slow growth rates, late sexual maturity, long gestation and long inter-birth periods are more exposed to extinction risks than others); social structure (complex social structure for mating, foraging, etc. makes a species more vulnerable); home range (species with large home ranges are particularly vulnerable to habitat loss); diurnal behavior (usually species with diurnal behavior have characteristics that make them more vulnerable, like large body size, sociality, larger home ranges, etc.); body size (large body size is correlated with many of the characteristics outlined above). Purvis et al. (2000a) tested the hypotheses outlined above and found that small geographic range, low density, higher trophic levels and low reproductive rates are the characteristics that more than others determine the extinction risk for a species. Moreover, Woodroffe and Ginseberg (1998) found that group size, activity pattern and home range size can play an important role in determining the extinction risk for a species.

All the characteristics considered above point out that top predators represent particularly vulnerable species. Different studies have demonstrated that large carnivores are particularly sensitive to habitat destruction (Doak 1995; Breitenmoser 1998; Duffy 2003), harvesting (Breitenmoser 1998; Jackson et al. 2001; Baum et al. 2003; Myers and Worm 2003; Treves and Karanth 2003; Ward and Myers 2005) and climate change (Petchey et al. 1999; Van Valkenburgh 1999; Voigt et al. 2003). Moreover, it has been demonstrated that top predators have a strong influence on their prey populations and on the ecosystems in which they live (Tardiff and Stanford 1998; Soulé et al. 2003; Williams et al. 2004; Croll et al. 2005) and many studies have documented that their extinction can have important consequences for the ecosystems in which they live (Berger et al. 2001; Terborgh et al. 2001; Ballard et al. 2003; Dulvy et al. 2004; Hebblewhite et al. 2005). In particular, it has long been recognized that extinction of top predators can cause a cascade of secondary extinctions (Paine 1966; Estes and Palmisano 1974; Borrvall et al. 2000; Ebenman et al. 2004; Ebenman and Jonsson 2005). Borrvall and Ebenman (2006) demonstrated that secondary extinction will be quicker if loss of species is caused by the extinction of a top predator compared to secondary extinction following the extinction of species in lower trophic levels.

A clear example of the importance of top predators for communities and ecosystem is provided by Soulé et al. (2003) with their proposal on "ecological effectiveness and interactive species". The authors reviewed a number of studies regarding sea otter and wolves. The influence of sea otters on coastal ecosystems have been studied contrasting places within the species' historical range where the species was present or absent, and also following in time areas being re-colonized by the species. All the studies found a strong limiting influence of sea otters on their most important prey, sea urchins, which control kelp. Thus, where sea otters are present there exist important kelp forests, and where sea otters are absent kelp forest are limited by overabundant sea urchins. Moreover, this trophic cascade impacts dozens of other coastal species. A similar situation has been described for the wolf: the species preys extensively on moose that, besides being lower in number, are displaced from willow stands with increasing densities of breeding birds.

All the considerations reported above clearly call for the conservation of highly interactive species (Soulé et al. 2003), and for top predators in particular (Borrvall and Ebenman 2006). This is extremely important in Italy and in the Mediterranean basin in general, areas where large carnivores struggle to survive in a human dominated landscape.

"A geological pivot between Africa and Eurasia, the crossroad of the great human migration over the past 2 millions years, the stage on which so many civilizations have come and gone, the Mediterranean has been loved, exploited and inhabited by human beings for longer than any other part of the world outside Africa. It is humans who have very largely made it what it is today, and the marks of this domination are visible everywhere." Peter H. Raven, with his elegant description of the Mediterranean basin (Blondel and Aronson 1999), summarizes the key characteristic of the area and of the Italian peninsula: human – biodiversity interactions. Apart from some remote areas and cliffs, every single square meter of Italy has been directly and repeatedly manipulated and, in many cases, redesigned by humans (Blondel and Aronson 1999). An extremely important part of the story has resulted from forest destruction and replacement by simpler systems, with a balance between agricultural and pastoral activities and with forests and woodlands being cleared and exploited as needed near farms and villages. From this system gradually evolved a remarkable structural and habitat diversity with the establishment of an "oecumene", defined by Blondel and Aronson (1999) as "a convivial and sustainable system of close and friendly interactions with their near environment".

However, the 19th and 20th centuries have seen an increasingly severe destruction of vegetation in many parts of the Mediterranean, destruction that is still continuing in the eastern Mediterranean as well as in northern Africa. In the last 40 years, a particular pattern of land-cover change has taken place in Mediterranean Europe: planes are being increasingly utilized, hilly and mountain areas are being abandoned by humans and naturally reforested (see Chapter 3 for further details). These new patterns are largely independent from planned conservation strategies and appear to have a substantial impact on landscape and biodiversity. However, most of the studies on land-cover change in the Mediterranean have concerned limited areas without analyzing the large scale effects of these patterns.

Animal species have obviously followed these patterns, with large mammals being particular sensitive to habitat changes (both natural and human caused) and direct persecution. Large carnivores, in particular, are those that more than others have been impacted from habitat loss and direct persecution because of conflicts with traditional human activities (Breitenmoser 1998). Important human caused extinctions among large carnivores date back to the upper Pleistocene: the spotted hyena (*Crocuta crocuta*) survived in Italy till 13,000 years ago, the cave bear (*Ursus spelaeus*) survived till 12,500 years ago, the lion (*Panthera leo*) survived till 10,600 years ago, and the same was true for most of the large herbivores (Masseti 2003).

Today only four species of large carnivores survive in Italy: the wolf, with the endemic Italian subspecies *Canis lupus italicus* (Nowak and Federoff 2002; Nowak 2003), the brown bear, with one population reintroduced in the northern part of Italy and with the endemic subspecies *Ursus arctos marsicanus* (Randi et al. 1994; Vigna Taglianti et al. 1984) surviving in central Italy, the European lynx (*Lynx lynx*), that is currently re-colonizing the Italian part of the Alpine range (but no stable population can be considered to be present; Molinari et al. 2001; Boitani et al. 2003), and the jackal (*Canis aureus*), that is colonizing Italy from eastern Europe (Lapini 2003). Very little is known of the ecology and distribution of the last two species in Italy, so I will concentrate on the first two.

Status and distribution of the brown bear in Italy

Originally, the brown bear (*Ursus arctos*) was widespread throughout the holarctic region. In Europe it could be found on the entire continent, except for Ireland, Iceland and the Mediterranean islands, but it was present in Sicily (Swenson et al. 2000; Zedrosser et al. 2001).

Due to diffuse direct persecution and habitat destruction, by 1850 the brown bear had seen a marked decline in its populations, and it is now present with important numbers only in the eastern and northern part of Europe (Servheen 1990; Swenson et al. 2000; Zedrosser et al. 2001), in the forested regions of the Carpathians, Balkans and Rhodope mountains (Fig. 1). In Western Europe, the species exhibits an extremely patchy geographic distribution (Fig. 1; Table 1), and several populations face the threat of extinction in the near future (Taberlet et al. 1995). The small populations (between 4-5 and 80-100 individuals at most) still living in this part of Europe are disconnected and located in the least accessible and disturbed areas of the Pyrenees (in Spain), of the Alps and of the Apennines. In the last decades, three projects of reintroduction have been realized: one in central Austria (1989-1993), one in the Pyrenees (1996-1997), and one in the central Alps (1996-2004).

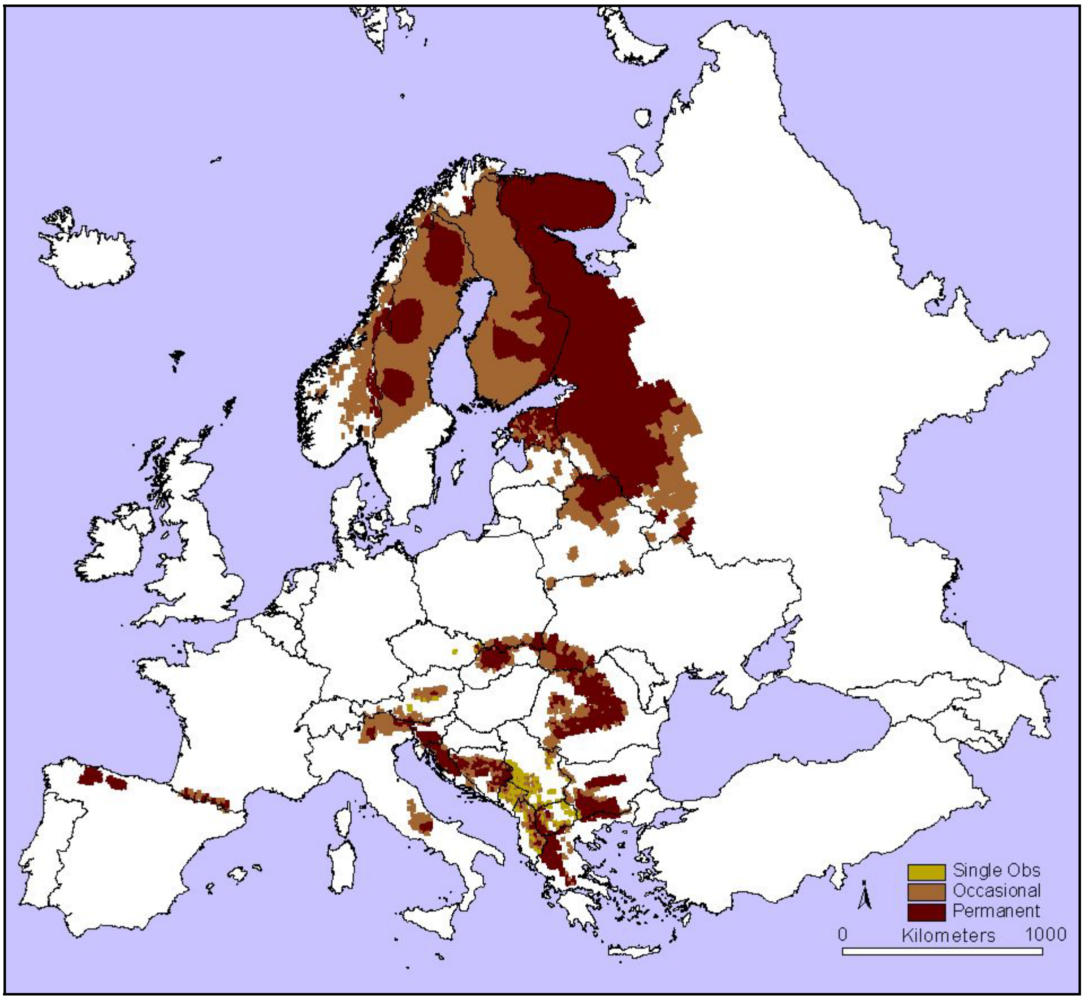


Figure 1. Present distribution of the brown bear in Europe (www.lcie.org).

POPULATION	**LOCATION**
North-eastern population (37,000 bears)	Latvia, Estonia, European Russia, Finland and northern Norway
Scandinavian population (1,000 bears)	Sweden, now expanding into central and southern Norway
Carpathian population (8,100 bears)	From Romania, through Ukraine, Poland and Slovakia, almost to the Czech Republic
Dinaric-Eastern Alps population (2,800 bears)	From Austria, through Slovenia, Croatia, Bosnia and Herzegovina, the Yugoslavia Federation, and the Republic of Macedonia to northwest Greece
Rila-Rhodope Mountains (520 bears)	On the Greece-Bulgaria border
Stara Planina Mountains (200 bears)	In central Bulgaria
Central Apennines (40-50 bears) and Central Alps (8 bears)	Italy
Pyrenees (total of 12 bears)	Two discrete locations in the French-Spanish border
Cantabrian Mountains (2 populations 50-60 and 20 bears)	Spain

Table 1. Details on the history and the status of these populations are summarised in Swenson et al. (2000) and Servheen et al. (1999).

In Italy, bears were once widely distributed throughout the forested zones; by the 16th century the species had been exterminated from most of the country, due to deforestation, hunting, and habitat degradation (Fabbri et al. 1983; Bologna and Vigna Taglianti 1992; Febbo and Pellegrini 1990). Today, the bear is present in only three areas (Fig. 1; Boitani et al. 2003):

- Central Alps (Adamello-Brenta Regional Park): approximately 15-17 individuals live in the area after the reintroduction of 1999-2000 and the birth of some cubs (http://www.parcoadamellobrenta.tn.it/lifeursus/lifeursus.htm);
- Eastern Alps (Tarvisio, Alpi Carniche, Dolomiti Bellunesi): an important, but unstable and numerically reduced, population is present in the area, probably because of the natural recolonization from the Dinaric-Eastern Alps population;
- Central Apennines: an undefined number of animals (guesses range from 30 to 50 individuals) live in the area, and there is a possible expansion of the population from Abruzzo National Park.

I will focus on the central Apennines populations, the last surviving individuals of the subspecies *Ursus arctos marsicanus* (Altobello 1921) that is endemic of Italy. This population (hereafter called Abruzzo brown bear) has seen a progressive reduction in its range starting from 1700s (Fig. 2), due essentially to legal hunting (before the XXth century), poaching and habitat destruction (Boscagli 1990; Bologna and Vigna Taglianti 1992; Boscagli 1999).

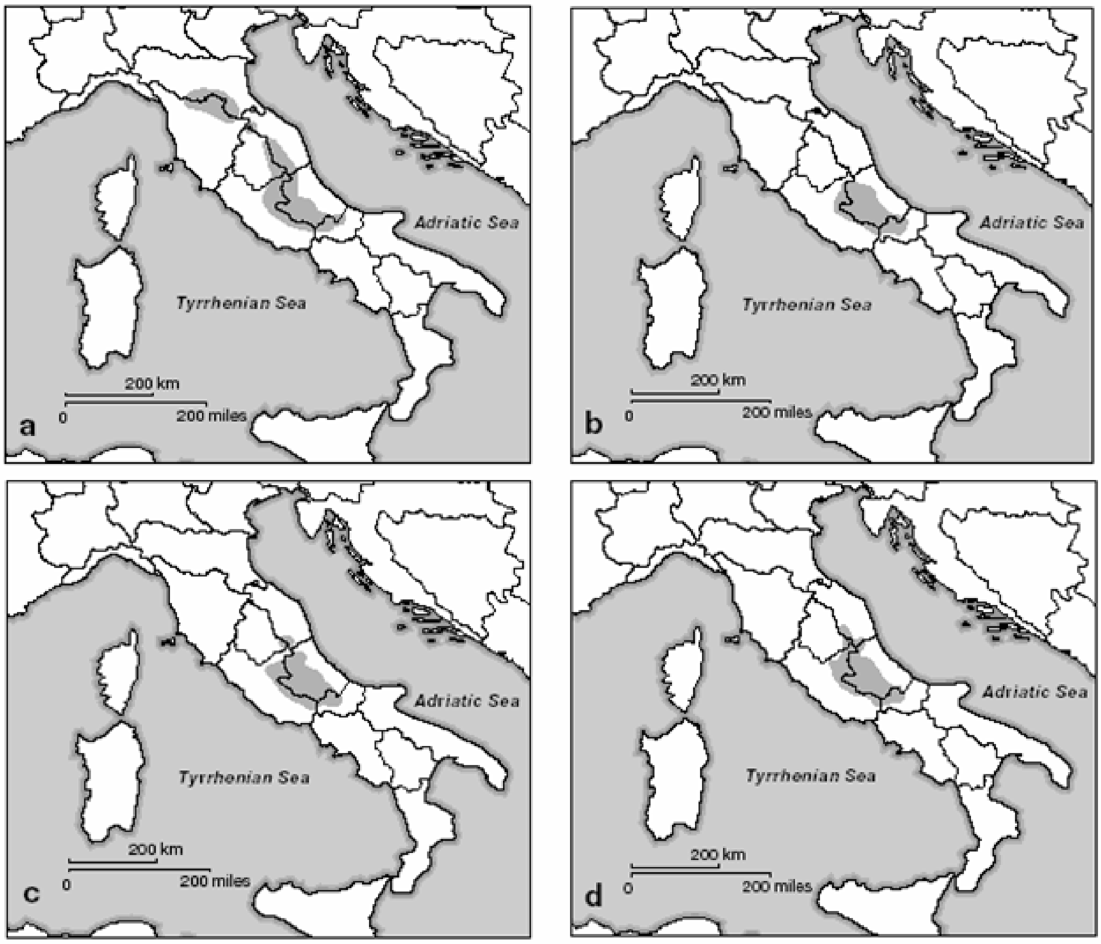


Figure 2. Distribution of the Abruzzo brown bear in 1800s (a), 1900 (b), 1993 (c) and 2000 (d). Modified from Boscagli 1999.

Today, Abruzzo brown bears exists in central Italy as a remnant, isolated population, restricted principally to the mountain zone of Abruzzo National Park (Bologna and Vigna Taglianti 1992; Posillico et al. 2004) in an area of 1,500 km^2. Other 4,000 km^2 of the Apennine region are rarely frequented by individuals or with very low density (Fabbri et al. 1983). No *ad hoc* individual count has been done, so no-one knows the exact number of animals present in the region. However, different authors have estimated a population size between 40 and 100 individuals (Boitani et al. 2003).

The population in central Italy is still impacted by consistent human caused mortality. In the last 30 years, inside the boundaries of Abruzzo National Park alone, 56 bears have been found dead (Abruzzo National Park pers comm.): for 37 of them it has been possible to find the cause of death, and in almost all cases it was poaching (with poisoned lures, with guns, etc.). Moreover, more than 14 bears have been trapped and examined by veterinarians. Four of them were affected by brucellosis, 13 were affected by cimurro and 8 by hepatitis (Leonardo Gentili pers comm.). It is clear that conservation of the Abruzzo brown bear requires an important effort from all the conservation community.

Legally the brown bear has been protected by Italian law since 1938 and many reserves and national parks have been instituted in the area to secure its conservation. Moreover, the State can require the party guilty of poaching a bear to repay the full economic value of a bear, which has been estimated at $1,280,000 (Boscagli 1999). The subspecies is also protected at the international level: the IUCN Red List classifies *Ursus arctos marsicanus* as threatened (L. Boitani pers com.); also CITES includes the subspecies in its Appendix II, and the European Community considers the bear in the Bern convention (1979), where it is defined as a species strictly protected, in need of particular attention; lastly the Habitat Directive (1992) considers the bear an endangered species.

Status and distribution of the wolf in Italy

The original distribution of the wolf encompassed the entire northern hemisphere north of roughly 13°N-20°N of latitude (Boitani 2003). In this short review, I will focus on the distribution of the species in Europe and in particular in Italy (Fig. 3).

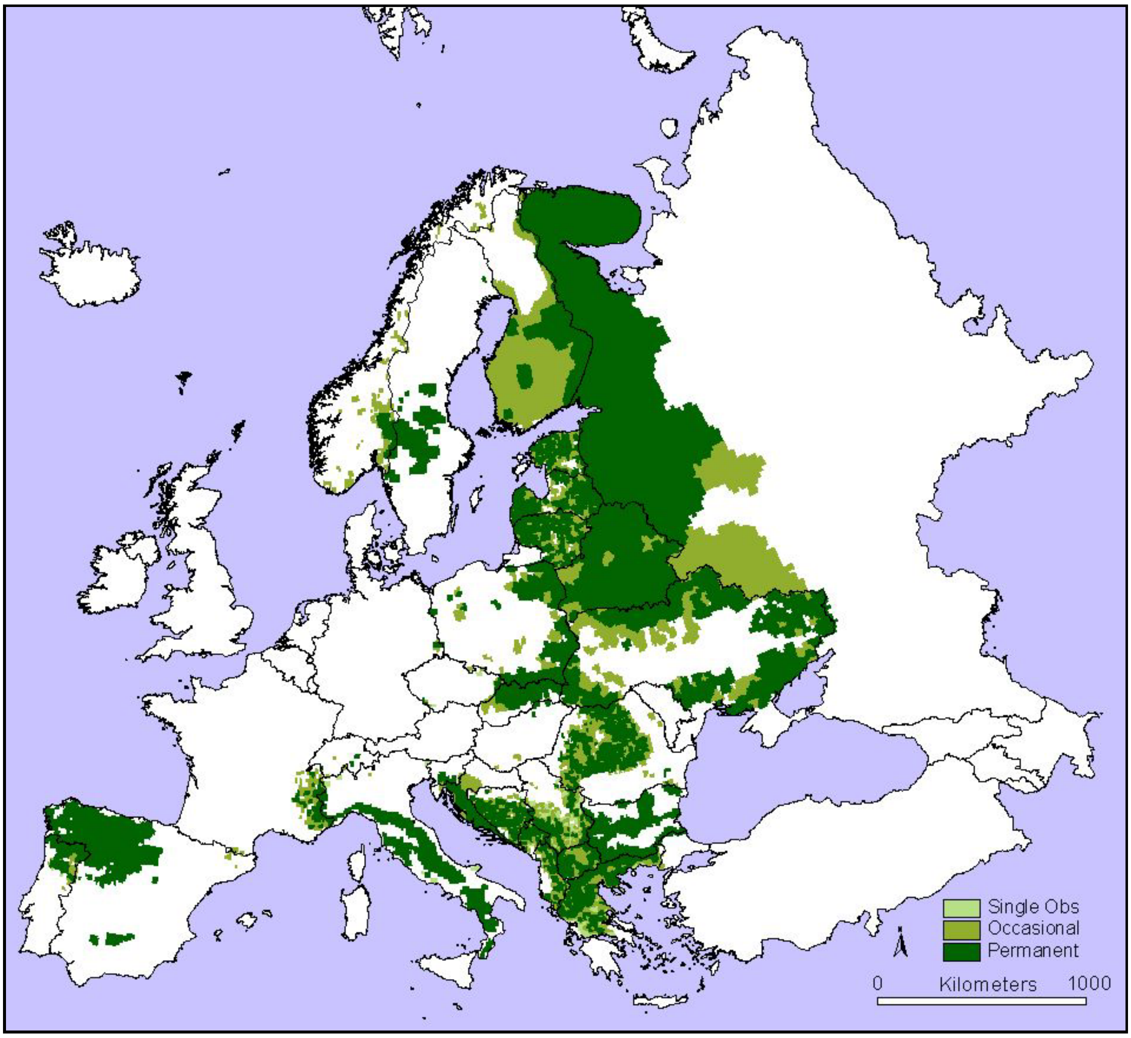


Figure 3. Present distribution of the wolf in Europe (www.lcie.org).

The species has always been actively persecuted by man, and the first bounty paid to kill wolves dates to the 6th century B.C. (Boitani 2003). However, it was in the medieval period that wolf persecution became an organized effort. In 800 A.D. Charle Magne established a special corps of wolf hunters, and about in the same period the species was actively persecuted throughout all of Europe. The British islands were the first place where the species was exterminated: England's last wolf was killed in the early 1500s, Scotland burned up all its forests with the aim of eradicating wolves (the last group was killed in 1684), while in Ireland the extinction of the species dates back to 1770. In the 1700s the wolf was also drastically reduced in central Europe and by the end of the 1800s the species was extinct. In northern Europe the species survived till

1973, when the last wolf was killed in Norway and legal protection was accorded to the species. In Eastern Europe the socio-economic situation coupled with the vastness and diversity of the region and with the contiguity with Asia prevented wolf extermination, but the species was reduced to extremely low numbers (Boitani 2003).

Southern Europe clearly represents a unique situation, since the attitude of people towards wolves was (and partly is) completely different from that of central and North Europe (Boitani 2003). As a result, persecution of the species in Spain and Italy was not comparable to what occurred in the rest of Europe. Although, wolves were actively hunted in Spain throughout the history of the region, in 1800 the species still occupied its original range, and by 1900 the species was still present in more than half of the original range (Boitani 2003).

In Italy wolf bounties have been paid at least from 1100 to 1950, but wolf hunting was mainly carried out by farmers, without a great organization or persistence and rarely far from inhabited places (Boitani 2003). The first scientific investigations on the distribution of the species at the national level dates back to the beginning of the 1900s (Ghigi 1911), but a systematic series of studies was carried out only in the 1970s or later (Ciucci and Boitani 1998; Boitani et al. 2003). The species was present on the entire Italian peninsula until the second half of 1800s, it was exterminated in the Alps in the 1920s and in Sicily in the 1940s. In 1950 the species was still present throughout the entire Apennine range, but in 1970 it was limited to less than 100 individuals distributed in some small and fragmented areas in the central and southern Apennines (Ciucci and Boitani 1998; Boitani et al. 2003; Fig. 4).

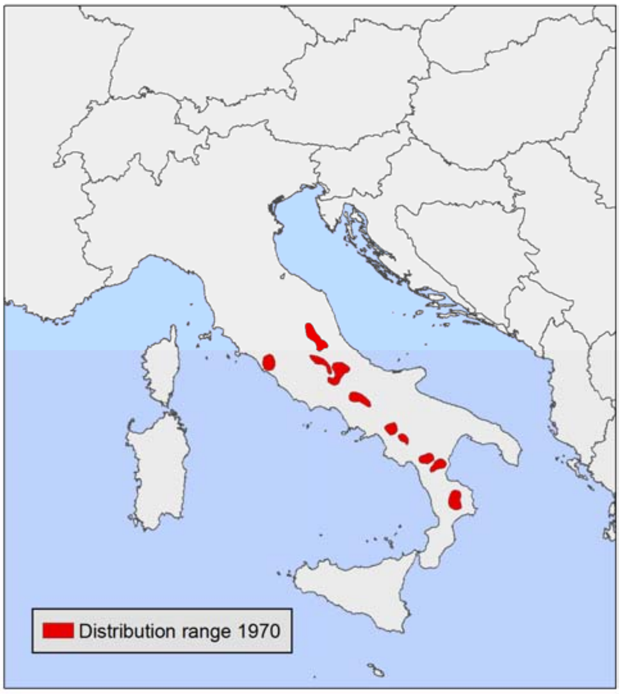


Figure 4. Distribution range of the wolf in Italy in 1970s (modified from Boitani et al. 2003).

From the 1970s the species gradually increased in number and distribution and now more than 500 individuals occupy the entire Apennine range together with the French Alps (Parc National du Mercantour) and the eastern part of the Alpine range (Italy and Switzerland).

The species is considered vulnerable by the IUCN red list and CITES includes the wolf in Appendix II (Appendix I for some countries); the species is also listed in Appendix II of the Bern Convention as well as in the Habitat Directive. In Italy the species was legally hunted till 1971, when any type of wolf hunting was prohibited.

Even though the species is protected, human caused mortality in Italy is still high (Ciucci and Boitani 1998). Analyzing 60 animals found dead between 1984 and 1990 it was concluded that 78% of the animals were killed (rifle, poison, trap), 13% died in car accidents and only 8% died because of a disease (Ciucci and Boitani 1998).

Objectives

The main objective of this thesis is to provide a spatially explicit conservation framework for the two large carnivores currently present in Italy: the wolf and the brown bear. To accomplish this goal I will rely on habitat modeling techniques. I will organize the chapters of this thesis as 4 independent papers plus this general introduction (Chapter 1) and a short review on habitat modeling techniques (Chapter 2).

Chapter 3 titled "Changes in Land Cover Patterns in Italy and Their Implications for Biodiversity Conservation" (published by Landscape Ecology) provides the first large scale evaluation of the patterns of land use change occurring in Mediterranean Europe and in Italy in particular. The chapter also provides a discussion of the potential benefits and problems of biodiversity in response to the patterns measured.

Chapter 4 titled "Land-cover Change and the Future of the Abruzzo Brown Bear: a Perspective from the Past" provides a new perspective on the conservation of the subspecies in central Italy using historical data and projection of future distribution. The chapter has been submitted to Oryx.

Chapter 5 is a two-dimensional model combining mortality and suitability to provide a model of the source areas and sinks for the Abruzzo brown bear.

Chapter 6 provides a spatially explicit model of the potential expansion of the wolf over the alpine range.

References

Altobello, G. 1921. Fauna dell'Abruzzo e del Molise. Vertebrati, Mammiferi. IV. I Carnivori (Carnivora). Colitti, Campobasso.

Ballard W.B., L.N. Carbyn and D.W. Smith. 2003. Wolf interactions with non-prey. In Mech L.D. and L. Boitani (eds). Wolves: behavior, ecology and evolution. The University of Chicago Press, Chicago, US, pp. 259-271.

Baum J.K., R.A. Myers, D.G. Kehler, B. Worm, S.J. Harley and P.A. Doherty. 2003. Collapse and conservation of shark populations in the northwest Atlantic. Science 299:389-392.

Berger J., P.B. Stacey, L. Bellis and M.P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affects avian neotropical migrants. Ecological Applications 11:947-960.

Blondel J. and J. Aronson. 1999. Biology and wildlife of the Mediterranean region. Oxford University Press, Oxford, UK.

Boitani L. 2003. Wolf conservation and recovery. In Mech D.L. and L. Boitani (eds). Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, USA, pp. 317-340.

Boitani L., S. Lovari and A. Vigna Taglianti (eds). 2003. Fauna d’Italia. Mammalia III: Carnivora – Artiodactyla. Calderini Ed, Bologna, Italy.

Bologna M.A. and A. Vigna Taglianti. 1992. Osservazioni sull’areale dell’orso marsicano con particolare riferimento al Gran Sasso e ai Monti della Laga. Hystrix – Italian Journal of Mammalogy 5:75-80.

Borrvall C. and B. Ebenman. 2006. Early onset of secondary extinctions in ecological communities following the loss of top predators. Ecology Letters 9:435-442.

Borrvall C., B. Ebenman and T. Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. Ecology Letters 3:131-136.

Boscagli G. 1990. Marsican brown bear population in central Italy: status report 1985. Aquilo (Serie Zoologica) 27:81-83.

Boscagli G. 1999. Status and management of the brown bear in central Italy (Abruzzo). In Servheen C., S. Herrero and B. Peyton (eds). Bears: status, survey and conservation action plan. IUCN SSC, Gland, Switzerland, pp. 81-84.

Breitenmoser U. 1998. Large predators in the Alps: the fall and rise of man’s competitors. Biological Conservation 83:279-289.

Brook B.W., N.S. Sodhi and P.K.L Ng. 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424:420-423.

Cardillo M., G.M. Mace, K.E. Jones, J. Bielby, O.R.P. Bininda-Emonds, W. Sechrest, C.D.L. Orme and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239-1241.

Ciucci P. and L. Boitani. 1998. Il lupo: elementi di biologia, gestione e ricerca. Documenti Tecnici 23.

Croll D.A., J.L. Maron, J.A. Estes, E.M. Danner and G.V. Byrd. 2005. Introduced predators transform subartic islands from grassland to tundra. Science 307:1959-1961.

DeFries R.S., J.R. Townshend and S.O. Los. 1997. Scaling land cover heterogeneity for global atmosphere-biosphere models. Pp. 231-246 in Quattrochi D.A. and M.F. Goodchild (eds). Scale in remote sensing and GIS. CRC Press, Lewis Publisher, New York, USA.

Doak D.F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conservation Biology 9:1370-1379.

Dobson A.P., A.D. Bradshaw and A.J.M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. Science 277:515-522.

Duffy J.E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680-687.

Dulvy N.K., R.P. Freckleton and N.V.C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. Ecology Letters 7:410-416.

Ebenman B. and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. Trends in Ecology and Evolution 20:568-575.

Ebenman B., R. Law and C. Borrvall. 2004. Community viability analysis: the response of ecological communities to species loss. Ecology 85:2591-2600.

Estes J.A. and J. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058-1060.

Fabbri M., G. Boscagli and S. Lovari. 1983. The brown bear population of Abruzzo. Acta Zoologica Fennica 174:163-164.

Febbo D. and M. Pellegrini. 1990. The historical presence of the brown bear on the Apennines. Aquilo (Serie Zoologica) 27:85-88.

Ghigi A. 1911. Ricerche faunistiche e sistematiche sui mammiferi d'Italia che formano oggetto di caccia. Natura II.

Hebblewhite M., C.A. White, C.G. Nietvelt, J.A. McKenzie, T.E. Hurd, J.M. Fryxell, S.E. Bayley and P.C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135-2144.

Houghton R.A. 1994. The worldwide extent of land-use change. Bioscience 44:305-309.

Houghton R.A., J.L. Hackler and K.T. Lawrence. 1999. The U.S. carbon budget: contribution from land use change. Science 285:574-578.

Jablonski D. 1985. Extinctions in the fossil record. Pp. 25-44 in Lawton J.H. and R.M. May (eds). Extinction rates. Oxford University Press, Oxford, UK.

Jackson J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Borsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner and R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629-638.

Lambin E.F., H.J. Geist and E. Lepers. 2003. Dynamics of land-use and land-cover change in tropical regions. Annual Review of Environment and Resources 28:205-241.

Lapini L. 2003. *Canis aureus* (Linnaeus, 1758). In Boitani L., Lovari S. and A. Vigna-Taglianti (eds). Fauna d’Italia. Mammalia III: Carnivora – Artiodactyla. Calderina Ed., Bologna, Italia pp. 47-58.

Loh J. and M. Wackernagel (eds). 2004. Living Planet Report 2004. WWF, UNEP-WCMC, Global Footprint Network.

Masseti M. 2003. Estinzione dei carnivore e degli ungulati italiani nell’Olocene. In Boitani L., S. Lovari and A. Vigna-Taglianti (eds). Fauna d’Italia. Mammalia III: Carnivora – Artiodactyla. Calderini Ed., Bologna, Italy, pp. 1-16.

Matson P.A., W.J. Parton, A.G. Power and M.J. Swift. 1997. Agricultural intensification and ecosystem properties. Science 277:504-509.

McKinney M.L. 1997. Extinction, vulnerability and selectivity: combining ecological and paleontological views. Annual Reviews of Ecology and Systematics 28:495-516.

Molinari P., L. Rotelli and M. Catello. 2001. Present status and distribution of the Eurasian lynx (*Lynx lynx*) in the Italian Alps. Hystrix – Italian Journal of Mammalogy 12:3-9.

Myers R.A. and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423:280-283.

Noble I.R. and R. Dirzo. 1997. Forests as human dominated ecosystems. Science 277:522-525.

Nowak R.M. 2003. Wolf evolution and taxonomy. In Mech D.L. and L. Boitani (eds). Wolves: behavior, ecology and conservation. University of Chicago Press, Chicago, USA, pp. 239-258.

Nowak R.M. and N.E. Federoff. 2002. The systematic status of the Italian wolf *Canis lupus*. Acta Theriologica 47:333-338.

Ojima D.S., K.A. Galvin and B.L. Turner II. 1994. The global impact of land-use change. BioScience 44:300-305.

Paine R.T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

Petchey O.L., P.T. McPhearson, T.M. Casey and P.J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402:69-72.

Pimm S.L., G.J. Russell, J.L. Gittleman and T.M. Brooks. 1995. The future of biodiversity. Science 269:347-350.

Pimm S.L., M. Ayres, A. Balmford, G. Branch, K. Brandon, T. Brooks, R. Bustamante, R. Costanza, R. Cowling, L.M. Curran, A. Dobson, S. Faber, G.A.B. da Fonseca, C. Gascon, R. Kitching, J. McNeely, T. Lovejoy, R.A. Mittermeier, N. Myers, J.A. Patz, B. Raffle, D. Rapport, P. Raven, C. Roberts, J.P. Rodriguez, A.B. Rylands, C. Tucker, C. Safina, C. Samper, M.L.J. Stiassny, J. Supriatna, D.H. Wall and D. Wilcove. 2001. Can we defy nature's end? Science 293:2207-2208.

Posillico M., A. Meriggi, E. Pagnin, S. Lovari and L. Russo. 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. Biological Conservation 118:141-150.

Purvis A., J.L. Gittleman, G. Cowlishaw and G.M. Mace. 2000a. Predicting extinction risk in declining species. Proceedings of the Royal Society of London Series B 267:1974-1952.

Purvis A. P.M. Agapow, J.L. Gittleman and G.M. Mace. 2000b. Non-random extinction and the loss of evolutionary history. Science 288:328-330.

Randi E., L. Gentile, G. Boscagli, D. Huber and H.U. Roth. 1994. Mitochondrial DNA sequence divergence among some west European brown bear (*Ursus arctos*) populations: lessons for conservation. Heredity 73:480-489.

Reid R.S., R.L. Kruska, N. Muthui, A. Taye, S. Wotton, C.J. Wilson and W. Mulatu. 2000. Land-use and land-cover dynamics in response to changes in climatic, biological and socio-political forces: the case of south-western Ethiopia. Landscape Ecology 15:339-355.

Sanderson E.W., M. Jaiteh, M.A. Levy, K.H. Redford, A.V. Wannebo and G. Woolmer. 2002. The human footprint and the last of the wild. BioScience 52: 891-904.

Servheen C., S. Herrero and B. Peyton. 1999. Bears: status, survey and conservation action plan. IUCN SSC, Gland, Switzerland.

Servhenn C. 1990. The status and conservation of the bears of the world. International Conference on Bear Research and Management 2.

Soulé M.E., J.A. Estes, J. Berger and C. Martinez del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology 17:1238-1250.

Swenson J.E., N. Gerstl, B. Dahle and A. Zedrosser. 2000. Action plan for the conservation of the brown bear (Ursus arctos) in Europe. Nature and Environment 114. Strasbourg, Council of Europe Publishing.

Taberlet P., J.E. Swenson, F. Sandegren and A. Bjärvall. 1995. Localization of a contact zone between two highly divergent mitochondrial DNA lineages of the brown bear *Ursus arctos* in Scandinavia. Conservation Biology 9:1255-1261.

Tardiff S.E. and J.A. Stanford. 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology 79:2219-2228.

Terborgh J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G.H. Adler, T.D. Lambert and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923-1926.

Thomas C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beumont, Y.C. Collingham, B.F.N. Erasmus, M.F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A. Townsend Peterson, O.L. Phillips and S.E. William. 2004. Extinction risk from climate change. Nature 427:145-148.

Treves A. and K.U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491-1499.

United Nation Population Division. 2004. World Population Monitoring 2003. United Nations, New York. http://www.un.org/esa/population/unpop.htm.

Van Valkenburgh B. 1999. Major patterns in the history of carnivorous mammals. Annual Review of Earth and Planetary Sciences 27:463-493.

Vigna Taglianti A., G. Iacobone and A. Loy. 1984. Osservazioni sistematiche e zoogeografiche sull'orso bruno nell'Appennino centrale. Bollettino di Zoologia 51:113.

Vitousek P.M., H.A. Mooney, J. Lubchenco and J.M. Melillo. 1997. Human domination of earth's ecosystems. Science 277:494-499.

Voigt W., J. Perner, A.J. Davis, T. Eggers, J. Schumacher, R. Bährmann, B. Fabian, W. Heinrich, G. Köhler, D. Lichter, R. Marstaller and F.W. Sander. 2003. Trophic levels are differentially sensitive to climate. Ecology 84:2444-2453.

Ward P. and R.A. Myers. 2005. Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86:835-847.

William B.M. and B.L. Turner II. 1992. Human population growth and global land-use/cover change. Annual Review of Ecology and Systematic 23: 39-61.

Williams T.M., J.A. Estes, D.F. Doak and A.M. Springer. 2004. Killer appetites: assessing the role of predators in ecological communities. Ecology 85:3373-3384.

Woodroffe R. and J.R. Ginsberg. 1998. Edge effects and the extinction of population inside protected areas. Science 280:2126-2128.

Zedrosser A., B. Dahle, J.E. Swenson and N. Gerstl. 2001. Status and management of the brown bear in Europe. Ursus 12:9-20.

Chapter 2: SPECIES HABITAT/DISTRIBUTION MODELING

"Why are organisms of a particular species present in some places and absent from others?". Krebs (2001) presents this as the simplest question that can be asked in ecology and Guisan and Thuiller (2005) as one of the most important. Indeed, there are a number of theoretical and practical reasons to quantify species distribution, for both plant and animals (Brown et al. 1996; Gaston 2003; Fortin et al. 2005). In particular, the quantification of the spatial structure of species' ranges is critical for making management decisions, planning conservation efforts, assessing the potential impact of climate change, assessing the impact of habitat loss (Lawton 1993; Boitani et al. 1999; Robertson et al. 2001; Cardillo et al. 1999; Gaston 2003; Rodrigues et al. 2003; Baillie et al. 2004; Higgins et al. 2004; Rodrigues et al. 2004; Fortin et al. 2005; Holt et al. 2005).

To answer all the above questions and many others (see Brown et al. 1996; Gaston 2003; Fortin et al. 2005 for a review) we need maps that accurately delineate the geographical distribution of the species considered. But this is not an easy task. Direct inventories and surveys of species presence are expensive and time-consuming (Mack et al. 1997; Ferrier et al. 2004) and are therefore impractical to conduct in remote regions of the world or over large landscapes (Cardillo et al. 1999; Vaughan and Ormerod 2003; but see Boitani et al. 1999; Rodrigues et al. 2003; IUCN et al. 2004; The SouthEast Asia Mammal Databank - http://www.ieaitaly.org/samd/index.htm for regional and global datasets on species distribution).

Moreover, geographic ranges are dynamic entities, which evolve following the evolution of the species (Krebs 2001; Gaston 2003; Zunino and Zullini 2004), and which have an internal structure with large variations in abundance (Pulliam 1988). Hence the quantification of range' borders as well as of their internal structure is complicated by ecological, practical and statistical problems (Fortin et al. 2005). Thus we need a device to produce distribution maps quickly and cheaply, using easily accessible surrogate variables (Cardillo et al. 1999; Brotons et al. 2004).

The production of species' distribution maps is an exercise that has been relatively common in biogeography and conservation biology (Rapoport 1982; Scott et al. 2002; Zunino and Zullini 2004) and many different methods have been adopted to solve the problems above. In the following paragraphs I will provide a formal definition of a geographic range with a short review of the main methods that have been adopted, mainly with reference to conservation biology and habitat modeling.

Species distribution range

The distribution range of a species is usually defined as the portion of the geographical space where the species has a stable interaction with its environment (Gaston 2003). Its size, shape and internal structure are the result of complex interactions between the physiology, ecology and behavior of the species and the characteristics of the environment in which it lives (Brown et al. 1996; Gaston 2003; Fortin et al. 2005).

The first step in the description of the distribution range of a species implies finding the location of its boundaries on a paper or digital map (Fortin et al. 2005). Usually a range map is interpolated or extrapolated from sparsely distributed field observations, obtained mainly from museum specimens, field survey and check lists (Brown and Lomolino 1998; Henebry and Merchant 2002; Fortin et al. 2005).

These data on species distribution have potentially many different problems, going from the sampling method that has been used (Margules and Austin 1994; Williams et al. 1996, 2002; Freitag et al. 1996; Lawes and Piper 1998; van Jaarsveld et al. 1998; Maddock and du Plessis 1999; Reddy and Davalos 2003), to sampling effort in space and time (Williams et al. 2002). Moreover, field data have inevitably some degree of uncertainty due to measurement errors that, in our case, could be species misidentification, incorrect abundance estimates, incorrect location information (Fortin et al. 2005).

To these considerations should be added the fact that most of the times the point data available are too few to accurately depict the spatial distribution of a species and lumping more than one year of data (a solution that is often adopted with many important advantages) can potentially introduce sampling errors even when none is present at the level of the original data (Fortin et al. 2005).

Besides measurement errors, many ecological factors complicate even more the situation. Animal species can move and are subject to demographic and environmental variability; thus abundance within their range fluctuates from year to year (Guo et al. 2005). All these consideration make clear that species' ranges are probabilistic entities (at least from our point of view) and thus it is important to devise a method that correctly depicts this complexity.

Mapping distribution ranges

Usually, the starting point in the delineation of a distribution map is a cloud of points indicating the localities where the species has been found; from this, the boundaries of the species range can be defined using a more or less objective method. A number of strategies have been developed for this purpose. Some of them, the "by eye" or the "minimum circle", are commonly used to obtain a rough picture of the distribution of the species (Rapoport 1982), others, like the minimum convex polygon, are explicitly recommended for deciding conservation strategies (like for the IUCN Red Lists, [IUCN 2001]).

The most widely used technique is the cartographic method (Zunino and Zullini 2004). It has been widely used in the compilation of regional, national or continental atlases throughout the world, mainly for plants, vertebrates, and for some groups of invertebrates (see Mitchell-Jones et al. 2002; Sindaco et al. 2006 as examples). The cartographic method is based on a fishnet with square cells (usually in the European context the cells are 10X10km on a UTM fishnet): if a species is found in a single location inside a cell, then the entire cell is considered occupied (Fig. 1).

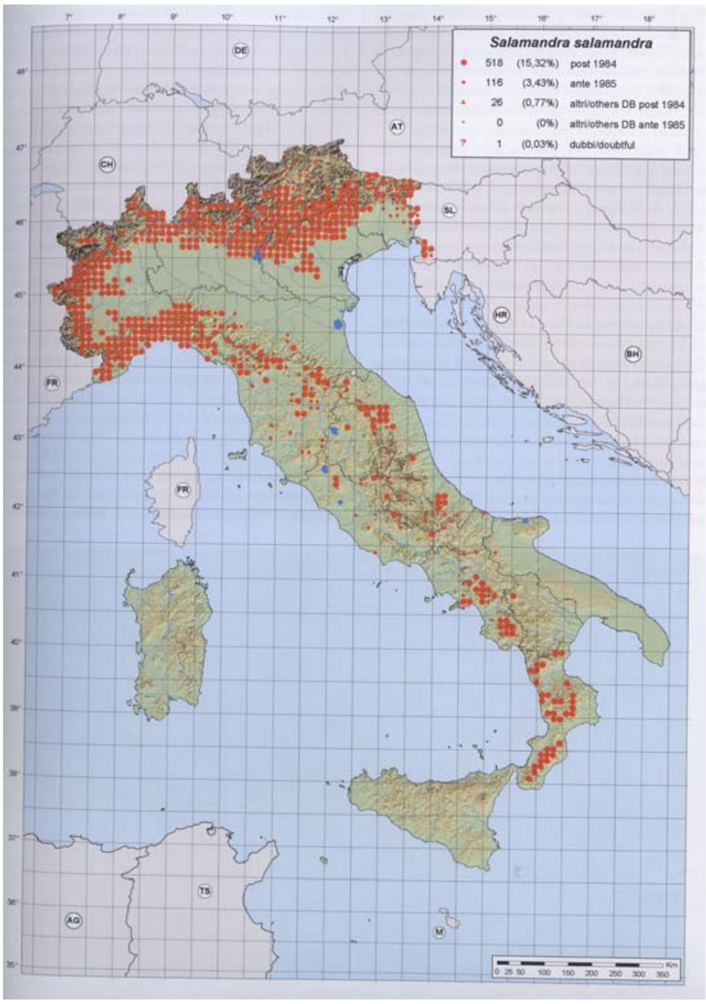


Figure 1. Distribution of the fire salamander (*Salamandra salamandra*) in Italy. Each red dot represents a 10X10km fishnet cell where the species has been found. Cells where the species has not been found are not shown. From Sindaco et al. 2006.

The cartographic method is a simple and practical way of standardizing the available information on species distribution. However, it heavily depends on the grain of the fishnet that is used and on the origin of the fishnet (and thus on the particular coordinate system that is chosen).

Most of the options described above give biased results (Burgman and Fox 2003) and many of them produce maps that usually are overly simplified, because they do not depict either holes within the range boundaries – representing areas where a species does not occur - or islands outside the boundaries – representing areas where isolated populations are found.

To overcome some of these problems Burgman and Fox (2003) have proposed the α-hull algorithms (Fig. 2), a modification of the classical aerographic methods (Rapoport 1982; Zunino and Zullini 2004). The steps necessary to build an α-hull are the following: 1) build a Delauney triangulation for the points in the sample (i.e. draw lines that join the points constrained so that no lines intersect between points); 2) measure the length of all the lines and calculate the average line length; 3) delete all lines that are longer than a multiple (α) of the average line length (the value of α determines the level of resolution: the smaller the value the finer the resolution; $\alpha = 0$ indicates the maximum possible resolution, $\alpha = \infty$ corresponds to the classical minimum convex polygon); 4) calculate the area of habitat by summing the areas of all remaining triangles.

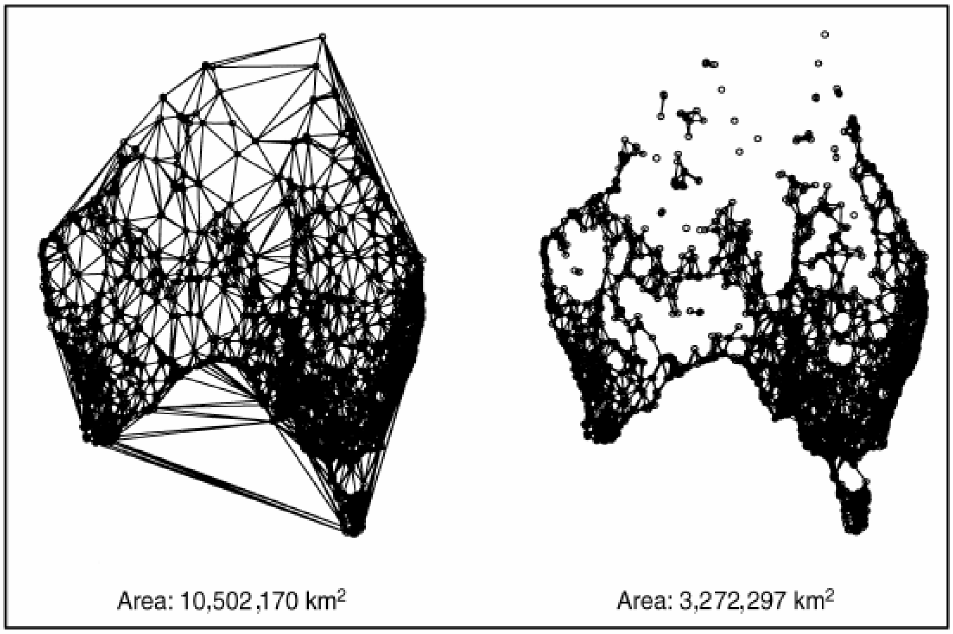


Figure 2. Convex polygon (left) and α-hull (right) with their areas obtained from atlas records in Australia. From Burgman and Fox 2003.

The α-hull algorithm seems to be more robust to the kind of sampling characteristics of traditional species atlases with the possibilities of generating estimates of ranges and inferences on their trends more reliably if compared to other traditional techniques (Burgman and Fox 2003).

Fortin et al. (2005) provide a brief review of other methods that are used to build range boundaries. Whichever method is used, the resulting distribution range encloses the area in which the species is considered likely to occur, but the likelihood level is seldom specified (see Figs. 1, 3 in Chapter 1) and/or known and the reliability of the distribution being mapped is never considered. The accuracy of these maps relies mainly on the location of specimens and on the empirical knowledge of specialists (Brown and Lomolino 1998; Corsi et al. 2000; Williams et al. 2002; Fortin et al. 2005).

Extent of Occurrence vs Area of Occupancy

The methods mentioned above can be valuable tools for the definition of the boundary of species' distribution ranges, but they usually cannot help in delineating how the range is occupied (Brown et al. 1996). In fact, a distribution range can be less or more densely inhabited, and it will never be homogeneously occupied because of the natural anisotropy of the environment and because of the population dynamics of the species (Guo et al. 2005). The internal pattern of a distribution range is of interest not only for theoretical ecology and biogeography, but also for conservation. In fact, the size and the changes in size and location of the distribution ranges are often used, for example, as criteria to prioritize species or areas for conservation (Baillie et al. 2004).

To this end, the World Conservation Union (IUCN) has adopted the definitions of Extent of Occurrence (EO) and Area of Occupancy (AO) that were first proposed by Gaston (1991, 1994). The EO is defined as the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon, excluding cases of vagrancy. This measure may exclude major discontinuities or disjunctions within the overall distributions of taxa. EOs are often measured using a minimum convex polygon (Fig. 3; Baillie et al. 2004).

The AO is defined as the area within the EO which is effectively occupied by a taxon, excluding cases of vagrancy. The measure reflects the fact that a taxon will not usually occur throughout the area of its EO, which may contain unsuitable or unoccupied habitats. The AO can be thought of as the smallest area essential at any stage to the survival of existing populations of a taxon. The size of the AO will be a function of the scale at which it is measured, and should be at a scale appropriate to relevant biological aspects of the taxon, the nature of threats and the available data (Fig. 3; Baillie et al. 2004).

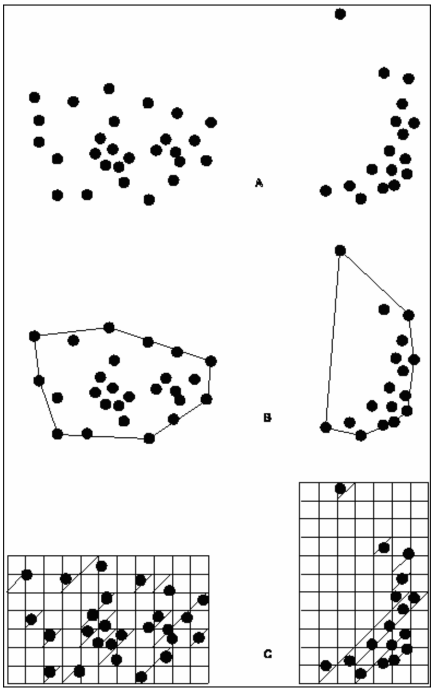


Figure 3. Two examples of the distinction between extent of occurrence and area of occupancy. (A) is the spatial distribution of known, inferred or projected sites of present occurrence. (B) shows one possible boundary to the extent of occurrence, which is the measured area within this boundary. (C) shows one measure of area of occupancy which can be achieved by the sum of the occupied grid squares. From IUCN (2001).

The EO represents in reality one end of a continuum that on the other end has the AO. In fact, the EO encompasses also areas that are not occupied by the species because unsuitable or because of historical reasons; while the AO is the part of the EO that is effectively occupied by the species. Following these definition it is clear that EOs are often of limited utility in a conservation context (Rondinini et al. 2005; Wilson et al. 2005). For example, a species that has an extremely large EO can be rare and endangered (this is usually the case with large carnivores in human dominated landscapes); while an endemic species can be limited to a given region, but locally extremely abundant (as in the case of some species of small mammals). AOs can be much more useful, since they provide more precise information on the distribution of a species. However, it is important to remember that AOs by definition include also sink areas, that can be of limited conservation value (Tyre et al. 2001), and that in some cases represent important ecological traps.

Even though conceptually the distinction among EO and AO is simple and clear, practically it has many implications, of which the most important is the temporal and spatial scales of analysis. The EO should represent a large scale picture of the distribution of the species considered; a picture that theoretically summarizes distribution data collected over many years, e.g. museum databases (Boitani et al. 1999; Gaston 2003; Fortin et al. 2005).

On the contrary, the AO should ideally be measured at the finest scale possible. The best possible measure of the AO is constituted by the sum of the home ranges of all the individuals of the species considered. If obtained in this way, the AO can also be considered a measure of the abundance for a species or populations – if home ranges are exclusive and non-overlapping (Gaston 1991, 2003). Following this definition, the AO should be considered much more dynamic if compared to the EO, with continuous changes in its spatial distribution.

Any attempt to represent the distribution of a species will be positioned in the continuum between EO and AO. However, in most cases the data available are useful just to delineate the EO and in no case the location and boundaries of the home ranges of all the individuals of a species are available. The greatest problem to exactly measure the AO will always remain the lack of suitable data.

Many different solutions have been proposed to map how species occupy their ranges and they can be divided into two main groups: techniques based only on points of presence and techniques based on points of presence and environmental covariates (Fortin et al. 2005). The first uses kernel density methods and geo-statistics to generate density surfaces and relay heavily on the sampling scheme that has been adopted. The second tries to measure AO (or better to approximate AO) in terms of environmental covariates (Scott et al. 2002; Rondinini et al. 2005; Fortin et al. 2005; Maiorano et al. 2006) and have their origin in the ecological theory of habitat selection (Guisan and Thuiller 2005).

From EO to AO by means of habitat modeling

Ecological theory (Krebs 2001; Guisan and Thuiller 2005) and available observations suggest that there should be non-random associations between environmental variables and species presence and absence or abundance (Guisan and Zimmerman 2000; Fortin et al. 2005), and it is clear that we can use this association to predict species distribution (Nicholls 1989; Corsi et al. 2000; Guisan and Zimmerman

2000; Scott et al. 2002; Newbold and Eadie 2004; Fortin et al. 2005; Guisan and Thuiller 2005).

In particular, if we assume that a species will select and use areas that are able to completely satisfy its life requisites we can devise a tool that enables us to depict species distribution much more in detail than traditional EOs, practically providing a way of moving towards AOs along the EO-AO continuum. Habitat suitability modeling techniques provide such tools: they use information on species location records or expert-based knowledge and environmental factors to generate statistical functions that allow predictions of potentially suitable habitat distribution for species (Corsi et al. 2000). The key concept is that the use of environmental and biotic variables as surrogates to model the presence of a species can provide enhancement over traditional approaches of range mapping (Fortin et al. 2005).

Definition of models

A model can be defined as "an accurate or faithful representation of reality" (Starfield 1997) that should have three main properties: generality, reality and precision (Levins 1966). However, ecological processes are too complex to be predicted accurately in every aspect of time and space from a single, although complex, model (Guisan and Zimmerman 2000). So, limiting our consideration to species distribution models, a particular model is just one of the infinite representations of the species-environment spatial relationships. A model may be thought of as a hypothesis that we know is false for any given biological system, but we may choose to keep because it is useful (Van Horne 2002).

Recognizing this complexity, Levins (1966) proposed a general modeling framework that can be applied to habitat models. According to his framework only two of the three desirable properties of a model can be improved simultaneously (Fig. 4), allowing for distinction of three main groups: analytical, mechanistic, and empirical models.

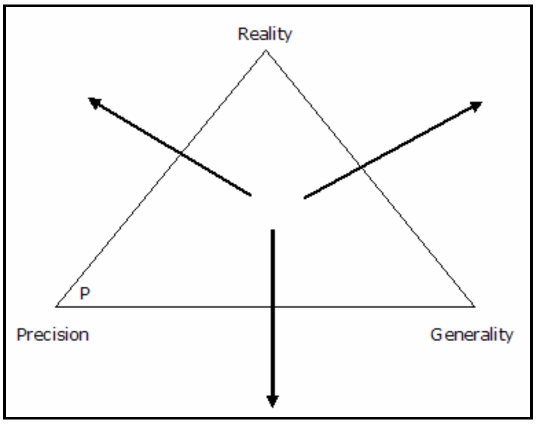


Figure 4. Classification of models based on their intrinsic properties. Modified from Guisan and Zimmerman 2000.

Analytical models focus on generality and precision and are specifically designed to predict accurate responses with limited and/or simplified reality (like the Lotka-Volterra, or the classical logistic equation). Mechanistic models (also called physiological, causal, or process models) base their prediction on real cause-effect relationships and are designed to be realistic and general. Empirical models (also called statistical, correlative, or phenomenological models) are not expected to describe realistic cause and effects among model parameters and predicted response, but only to describe empirical facts. These models sacrifice generality to attain higher precision and reality (Corsi et al. 2000; Guisan and Zimmerman 2000, Heglund 2002; Van Horne 2002; Barry and Elith 2006).

Correlative models

Levins' classification is obviously a simplification of a much more complex situation in which it can be extremely difficult to classify a specific model (Guisan and Zimmerman 2000). However, distribution models, in general, are used to describe the niche of an organism and to predict its pattern of occupancy. They are based on an analysis of the relationship between the presence of individuals of a species and the habitat variables that characterize the points of presence (Van Horne 2002). Thus, they are generally considered empirical models (Corsi et al. 2000; Guisan and Zimmerman 2000, Heglund 2002; Van Horne 2002; Guisan and Thuiller 2005; Barry and Elith 2006) and they have two main assumptions: animal distribution can be described in terms of correlated variables (i.e. there is a correlation between the basic needs of a species and the environmental variables used as surrogates); all the variables that are not included in the analysis have a neutral effect on the results of the model (that is the excluded variables do not add or subtract anything to the resulting model) (Corsi et al. 2000; Heglund 2002).

The relationship that is measured can be used to identify high quality or essential habitat for the species of interest, assuming that an individual is going to select only (or mainly) high quality habitats. The main strength of correlative models is that they can use a set of environmental variables whose spatial distribution can be easily mapped (e.g. vegetation types, land use/cover, mean annual temperature, elevation, etc.).

The correlation can be causal or descriptive. A causal correlation implies that the environmental variables considered are directly linked to the species' basic needs. This is the case, for example, of distribution models based on physiologically meaningful parameters (these models can also be described in terms of mechanistic models).

However, in many cases we do not have the quantity and quality of both location data and of environmental variables that are necessary to allow an assessment of cause-effect relationships in species' distribution. In fact, the pattern of presence and absence of a species that we are able to describe depends on the scale at which measurements are made (Walters 1992). Thus, in most cases, the correlation is intended only as a functional description and it is unknown why some ranges of values of the environmental variable are preferred by the species. For example a second variable, correlated to the one that we are able to measure, may be much more important in determining species presence/absence. Whichever is the mechanism behind, the available observations show that the species tends to occur more frequently within those ranges (Heglund 2002; Corsi 2004).

Whichever type of correlation is considered, the correlative approach can be used to "statistically" characterize the response of a species to environmental processes (based on the assumption that species distribution reflects these responses) even when the underlying mechanisms are not known (Barry and Elith 2006). Basically, species needs can be summarized in food, shelter, and adequate reproduction sites (Pausas et al. 1995) and correlative models just provide a way to condense these basic needs into a single map (Guisan and Zimmerman 2000).

These models try to mimic the ecological process of habitat selection producing what is commonly called habitat distribution models (or habitat suitability models, or simply distribution models), a theoretical representation of realized niche of a species obtained using some inferred or measured species-environment relationship (Corsi et al. 2000). The projection of the generated function to areas where environmental factors are known but species have not been sampled allows an optimal, cost effective, method to map species distributions in large regions (Guisan and Zimmerman 2000; Brotons et al. 2004; Corsi et al. 2000).

Habitat modeling framework

The history of species distribution models have seen three main phases (Guisan and Thuiller 2005): 1) non spatial statistical quantification of species environment relationships based on empirical data; 2) expert based (non statistical, non empirical) spatial modeling of species distribution; 3) spatially explicit statistical and empirical modeling of species distribution.

Guisan and Thuiller (2005) report on the earliest example of modeling strategies, that were a study of the correlation between species distribution and climate (Johnston 1924 quoted in Guisan and Thuiller 2005), the prediction of invasive spread of a cactus species in Australia, and the assessment of the climatic determinants of the distribution of several European species (Hittinka 1963 quoted in Guisan and Thuiller 2005).

An important step forward came with the development of computer based predictive modeling of species distribution in the mid-1970s, with Nix et al. (1977, quoted in Guisan and Thuiller 2005) being the first to publish a niche-based distribution model of crop species. These first examples were followed in the early 1980s by Habitat Evaluation Procedures (HEP) and Habitat Suitability Indexes (HSI) in the US (Anderson and Gutzwiller 1984) and by the pioneering distribution simulations by Ferrier in Australia (Guisan and Thuiller 2005). Soon after, Verner et al. (1986) and Margules and Austin (1991) published two important books that reviewed and promoted distribution models. These theoretical advances were supported also by the parallel development of powerful computers and by the availability of statistical theory.

As a result the number of related publications increased significantly after the early 1990s, and important reviews were published soon thereafter by Franklin (1995), Austin (1998), Guisan and Zimmerman (2000), and particularly Scott et al. (2002).

In recent years, predictive modeling of species distribution has become increasingly important and distribution models have been widely used (Table 1) as powerful tools for converting individual point-locality data into "hypothetical" distribution ranges for a large number of species (Butterfield et al. 1994; Corsi et al. 1999; Scott et al. 2002). In particular, habitat models have been developed to predict species' presence and/or absence, species' geographical distribution over large areas, population size of animal and plant species (Morrison et al. 1992; Scott et al. 2002), to estimate species probability of occurrence (Austin et al. 1996, Carroll et al. 1999) and to establish the importance of particular variables in determining the distributions of individual organisms (Hepinstall et al. 1996). Sometimes they have been used as tools for obtaining different scenarios, like for example in predicting shifts in distribution ranges following global climate change (Pearson and Dawson 2003; Townsend Peterson et al. 2003; McPherson et al. 2004; Araujo et al. 2005a; Guisan and Thuiller 2005; Williams et al. 2005; Thuiller et al. 2006a, 2006b).

Habitat models have been used also to predict species richness (Jorgensen and Demarais 1999), centers of endemism, the occurrence of particular species assemblages or individual species, and the breeding habitat of given species (McPherson et al. 2004). By delineating favorable habitats, distribution models can help defining the target for field surveys (Engler et al. 2004), can aid in the design of reserves (Loiselle et al. 2003; Rondinini et al. 2005), can inform wildlife management outside protected areas (Boitani et al. 1999), can guide mediatory actions in human–wildlife conflicts (Sitati et al. 2003; Treves et al. 2004). Distribution models can be used to monitor declining species (Osborne et al. 2001), to predict range expansions of a recovering species (Corsi et al. 1999), to estimate the likelihood of species' long-term persistence in areas considered for conservation (Cabeza et al. 2004), and to identify locations suitable for reintroductions (Schadt et al. 2002; Carrol et al. 2003). They allow biologists to identify sites vulnerable to local extinction or species invasion (Thuiller et al. 2005), and to explore broad-scale hypotheses in ecology and biogeography (Corsi et al. 1999; Cumming 2000; Scott et al. 2002; Phillips et al. 2006).

Field of application	**Use of species prediction**
Conservation Biology	Identify sites expected to hold important species Identify sites for species reintroductions Identify locations at risk of species extinction Identify gaps in distribution and diagnose their cause Identify areas of wildlife-human conflicts
Invasion ecology	Predict sites sensitive to alien invasion Model negative effects of non-indigenous species on native biota
Biogeography	Testing biogeographical, ecological and evolutionary hypotheses
Evolutionary ecology	Exploring speciation mechanisms Exploring competitive exclusion
Applied ecology	Predict distributional change in response to changing climate or land use

Table 1. Potential fields of application for habitat suitability models (modified from Manel et al. 2001; Guisan and Thuiller 2005).

Building a species distribution model

Guisan and Zimmerman (2000) defined distribution models as empirical models relating field observations to environmental predictor variables, based on statistically or theoretically derived response surfaces. Following this definition, the fundamental components of every distribution model are the environmental variables (independent variables), the resulting habitat suitability values (dependent variables), and the functional processes that link the two (Corsi et al. 2000).

Field observation of species can be simple presence, presence-absence or abundances, and are usually obtained through a random or stratified random sampling design, or from observations obtained opportunistically, like natural history museum collections (Graham et al. 2004). Environmental variables can have a direct or indirect effect on species distribution and can be classified into three main types: 1) limiting factors: factors controlling species' eco-physiology (e.g. temperature, soil, water); 2) disturbances: perturbations affecting the natural systems (can be natural or human related); 3) resources: compounds that can be assimilated by organisms to produce energy (Guisan and Zimmerman 2000).

The ideal model building process should follow a series of steps formalized by Guisan and Zimmerman (2000) and modified by Guisan and Thuiller (2005; Fig. 5): 1) conceptualization, 2) data preparation, 3) model fitting, 4) model evaluation, 5) spatial prediction and 6) assessment of model applicability.

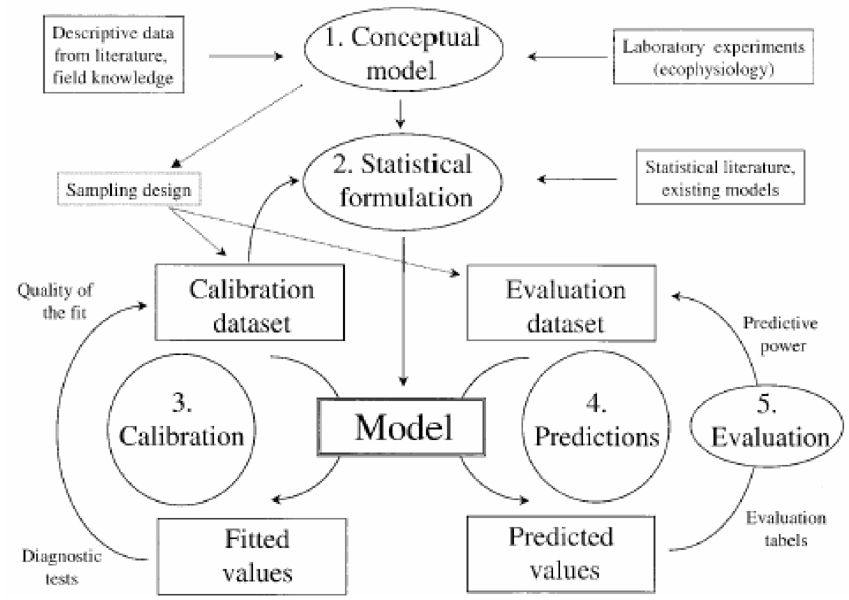


Figure 5. Sequence of steps necessary to build a model. Modified from Guisan and Zimmerman 2000.

Naturally, there are many different possible ways of performing each step, but there is no single best modeling approach. The variety of existing modeling algorithms can produce different model outputs, and hence different recommendations can be provided to conservation planners and wildlife managers, with potentially negative effects (Loiselle et al. 2003). Adopting an appropriate modeling strategy involves matching management objectives with model capabilities. The choice of the approach has to meet a balance between generality, the ability to describe an ecological phenomenon in many different conditions, and specificity, the ability to make precise predictions for the target population at a given time (Van Horne 2002).

Particularly important is the initial part of the procedure, the conceptualization phase. This can be split into two sub-phases (Guisan and Thuiller 2005): conceptualization of theory and data, and adoption of the proper modeling method. The first consists in: 1) definition of a conceptual model that properly describes the system at hand on the basis of sound ecological thinking and of clearly and explicitly defined objectives (Austin 2002; Huston 2002); 2) setup of multiple working hypotheses (Guisan and Theurillat 2000); 3) assessment of the available and missing data and of their relevance for the focal species and the given scale (Thuiller et al. 2004); 4) identification of the appropriate sampling strategy for acquisition of new data that complement existing data (Hirzel and Guisan 2002); 5) choice of the appropriate spatio-temporal resolution and geographic extent (Osborne and Suarez-Seoane 2002). The second consists in: 1) identification of the most appropriate method for modeling the response variable; 2) identification of the technique (resampling methods, statistical tests, etc.) necessary to evaluate the predictive accuracy of the model (Fielding 2002).

In most of the cases, however, there are few possibilities of deciding something at the beginning of a study, because of the lack of knowledge for the target species, or for the study area, or because of the lack of environmental and species data. For example the choice of the appropriate resolution might depend on the home range size and on the way the species uses the available resources; the choice of the study area might depend on knowledge of existing environmental gradients, etc (Austin 2002; Van Horn 2002). However, answers to these questions require a clear understanding of the system being simulated, with preliminary field observations, experimental studies, sensitivity analyses, all things that are extremely time consuming and, usually, beyond the scope of a modeling exercise.

Moreover, the conceptualization step, together with all the other modeling steps, is heavily influenced by many other factors and problems, such as overfitting (number of predictors is too large compared to the number of observations), overdispersion (dispersion is greater than expected from an assumed probability distribution), multicollinearity (high correlation between several predictors), etc. Guisan and Thuiller (2005) provide a detailed list of the problems in habitat modeling procedures, together with possible solutions.

Distribution models

The general framework proposed by Guisan and Zimmerman (2000) is usually summarized into two main steps: 1) identification of the relationship between species presence and the occurrence of certain values/classes of environmental variables, and 2) usage of this relationship as a rule on which species distribution is mapped based on the spatial distribution of the correlated variables. These two steps should be followed by model verification and/or validation.

The two steps can be implemented in many different ways and many classifications of spatially-explicit species distribution models have been based on one of the two steps. Stoms et al. (1992) built a classification system focused on the conceptual method used to define the species-environmental relationship, while Norton and Possingham (1993) based their classification on the result of the model and its applicability for conservation. Corsi et al. (2000) provided a review of these classification methods.

Following Stoms et al. (1992), many authors (Tobalske and Tobalske 1999; Corsi et al. 2000; Corsi 2004) have recognized two broad categories of distribution models: deductive models and inductive models. According to this classification, the identification of the relationship existing between species presence and the environmental variables is either 1) obtained through a deductive approach from published literature and/or specialists’ knowledge (Guisan and Zimmerman 2000; Corsi et al. 2000) or 2) obtained through induction comparing known species' locations with the environmental variables (Corsi et al. 2000). Both methods produce a classification rule that can be applied in step 2 to the definition of the species' distribution.

Both inductive and deductive models can be further classified according to the type of analysis performed to derive the species-environment relationship. In particular, it is possible to recognize two main categories: descriptive models and analytical models (Corsi et al. 2000).

Models pertaining to the first category use either the specialists’ *a priori* knowledge (and thus they are called deductive-descriptive) or the simple overlay of known locations of the species with the associated environmental variable layers (inductive-descriptive) to define the species-environment relationship. Descriptive models are generally based on very few environmental variable layers, most often one single layer. They tend to describe presence and absence in a deterministic way. No attempt is made to define confidence intervals for the individual estimate nor is any information provided on the relative importance of one variable compared with another. Moreover, no estimate of the degree of association or of its variability is provided with the relationship (Corsi et al. 2000).

Also analytical models can be deductive or inductive, but in any case they introduce in the modeling process the important concept of variability. For example, advice from different specialists is combined to define species-environment relationships, thus introducing variability in terms of different opinions of the experts (deductive-analytical).

Alternatively, species observation data are analyzed in a way that takes into account the range of acceptability of all the environmental variables measured, their confidence limits and their correlation (inductive-analytical). Both the deductive-analytical and the inductive-analytical approach tend to estimate the relative importance of the different environmental layers considered in the analysis, thus moving towards an objective combination of environmental variables layers (Corsi et al. 2000).

Models can be classified also on the basis of their output. In this case it is possible to distinguish categorical-discrete models and probabilistic-continuous models (Norton and Possingham 1993; Corsi et al. 2000; Corsi 2004). Most often models of the first type (categorical-discrete) can be represented as polygon maps in which each polygon is classified according to a presence/absence criterion or according to a nominal category (e.g. frequent, scarce, absent). Models of the second type (probabilistic-continuous) can be represented as continuous surfaces of an index that describes species presence in terms of the relative importance of any given location with respect to all the others. Indices that have been used are suitability indices (Akçakaya et al. 1995; Pereira and Itami 1991), probability of presence (Aspinall 1992; Clark et al. 1993), ecological distance from optimum conditions (Corsi et al. 1999), and species densities.

Categorical-discrete models do not account for species mobility and tend to give a static description of species distribution (Corsi 2000; Guisan and Zimmerman 2000). Probabilistic models can describe part of the stochasticity typical of locating an individual of a species and can be used to address problems of corridor design and meta-population modeling, thus introducing the geographical dimension into analysis of species viability (Corsi et al. 2000; Corsi 2004).

Ecological theory and distribution models

Surprisingly, ecological theory has been neglected in habitat modeling studies, generating many important limitations. Yet, insight from ecological theory should be used to inform any step of the modeling procedure, like the selection of the environmental variables (Pearson et al. 2004; Thuiller et al. 2004), the choice of realistic response curves for each variable (Austin and Gaywood 1994), or the assessment of the validity of the underlying assumptions (Araujo et al. 2005b). Moreover, many of the fundamental assumptions of distribution models derive directly or indirectly from the underlying ecological theory.

In particular, the concept of habitat selection, together with that of niche, is central to the problem of animal distributions. The use of these theories should allow to move from the concept of distribution range as described by EO toward that of AO, because both habitat selection and niche theories refer to the relationships between species and the impinging environment (that is, they both consider the effective environment that a given species experiences) (Mackey and Lindenmayer 2001).

Habitat selection

No species occurs everywhere and the distribution of its individuals across a landscape is neither random nor uniform but generally is aggregated (Gaston 1994; Krebs 2001; Smallwood 2002). Moreover, each species shows individualistic distribution patterns in relation to environmental and biological variables (Mackey and Lindenmayer 2001; Austin 2002; Holt et al. 2005). This is the result of habitat selection for a specific subset of environmental factors that a species requires for its survival and reproduction (Van Horne 2002).

Habitat selection is a natural process commonly present in both plants and animals. However, plants (and sessile animal) show habitat preferences in quite a different way than animals, because plants can not actively move from one habitat to another (Krebs 2001). So, habitat selection processes in plants are guided mainly by the habitat if we consider proximate causes, but are ultimately guided by plants through natural selection (Bazzaz 1991). In fact, for plants, habitat selection results from evolutionary adjustment of species to environmental factors, adjustments resulting in species occupying some habitats but not others. For example, plants can evolve different dispersal ability, or can modify their morphological and physiological characteristics. However, the characteristics of the habitat into which the seedlings disperse determine which species that disperse into the habitat becomes established. For this reason, habitat-selection concept has rarely been explicitly used for plants.

The process is different in terrestrial animals. In this case individuals actively choose to occupy or not to occupy a given habitat (any part of the biosphere where a species can live, either temporarily or permanently; Krebs 2001) and behavioral components can be extremely important.

Moreover, as a result of their mobility, there is an inherent degree of stochasticity in the distribution patterns of animals, and this is especially true in the case of terrestrial vertebrates. This means that some places which appear to support suitable conditions remain unoccupied (Van Horne 1983; Hanski 1994). The same pattern can be obtained considering historical factors that can influence the distribution of a species (Guisan and Zimmerman 2000). As an example, most of the Alpine range, which has potentially large areas suitable for the presence of large carnivores, is presently occupied only in part, by wolf, bear and lynx, because of the historical persecution that the species has seen in the area (Boitani 2003; Boitani et al. 2003; Molinari et al. 2001).

In general, habitat selection is defined as the disproportionate use of a habitat relative to its availability (White and Garrot 1990), and it can be viewed as the outcome of choices made at different levels by animals (Alldredge et al. 1998). In this framework each habitat is assumed to have a particular suitability (that is equivalent to fitness in evolutionary times) for the species being considered and different models (the ideal free distribution [Fretwell and Lucas 1970], the ideal despotic distribution [Fretwell 1972], etc.) have been proposed to explain the phenomenon.

Whichever model is adopted, habitat selection is inherently fractal, and it can be described following two main paths: the distribution of resources and the biological unit of analysis (Mackey and Lindenmayer 2001).

Habitat selection: resource distribution

Many different elements can influence the distribution of a species (Mackey and Lindenmayer 2001), going from the physical characteristics of the environment (like temperature, elevation, presence of a given type of vegetation cover and water), to physiological and behavioral factors (like sex, age, social structure, territoriality, season, and so on) to the presence of other species (predators, competitors, parasites), to inherent population pulses, to human activities (Krebs 1978; 2001; Mackey and Lindenmayer 2001; Guisan and Thuiller 2005).

All these factors operate at different temporal and spatial scales (Mackey and Lindenmayer 2001). Individual animals (or groups of animals) follow the spatial distribution of resources to seek food and shelter, to reproduce, to minimize competition and to avoid predation. Thus habitat selection can be described as a hierarchical process involving a series of innate and/or learned behavioral decisions about what habitat to use at different spatial scales (Krebs 2001). The criteria considered for the selection are usually different at each level or scale (Johnson 1980; Alldredge et al. 1998).

The first level of selection occurs for a species' geographic range, where biophysical factors (like temperature and moisture) play an extremely important role. Within the geographic range, a single individual (or a group of individuals depending on the social biology of the species considered) selects a home range on the basis of the presence of particular vegetation types and communities. Within the home range, general features, such as particular habitats, are selected; then further selection occurs for particular elements inside the habitat, such as food items or micro-habitat characteristics (Johnson 1980).

Habitat selection: biological unit

The second important dimension in the species-environment relationship framework is the biological unit of analysis. From this point of view, animal distribution can be described (at least) at four hierarchical levels: species, metapopulation, deme and individual organism.

Habitat selection operates at the level of individual animal (sometimes at the level of small groups of animals, e.g. a wolf pack) and follows the responses of animals to biophysical characteristics, involving behavioral and physiological adaptations of individuals to the ecological conditions. As a result of such adaptations, individual fitness may change, leading to changes in the distribution and abundance of the higher levels in the hierarchy (demes, metapopulations and species). In fact, the distribution and density of a group of animals (being it a deme, a metapopulation or a species) is ultimately determined by the collective responses of its individual organisms, and thus the description of species-habitat relationships at the higher levels is the summary (or better the central tendency) of the behavior of the individuals.

It should be noted anyway that for species and populations habitat selection cannot be limited to the simple statistical mean of the individuals' dynamics (Holt et al. 2005). In fact, the variation around the mean provides insights into interesting biological phenomena, but often it is the spread that tells the most about how populations and species occur in and select their environments.

Moreover, the spatial and temporal dimension of population and species are quite different from the individuals’ one, and new environmental factors can become the main actors in determining the population parameters and the distribution range. For example, passing through the different levels of the biological hierarchy new elements and interactions can arise, existing relationships can be strengthened or can become loser, like is the case for dispersal, social behavior, inter and intra-specific competition, density dependent processes and sink-source dynamics (Jones 2001).

Habitat selection: the interplay of resources and biological units

In summary, there are two fundamental hierarchies whose intersection must be explicitly considered when modeling the spatial distribution of an animal. These are: (1) the nested hierarchy of abiotic and biotic processes that determine the distribution and availability of the primary environmental resources (the environmental hierarchy), and (2) the often nested (but sometimes non-nested) hierarchy of patterns of distributional behavior associated with the set of biological units (the behavioral hierarchy) (Mackey and Lindenmayer 2001).

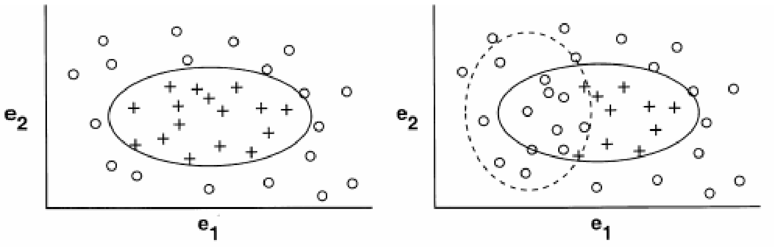
Both hierarchies are intrinsically scale dependent (Karl et al. 2000), and each level is dominated by a particular biophysical phenomenon and is specific for space, time and the biological unit. Each biological unit will be particularly sensitive to a corresponding level (or levels) in the environmental hierarchy. Patterns of distribution associated with the species in toto may reach equilibrium over the course of decades or centuries with global- and meso-scaled environmental processes associated with climate (Mackey and Lindenmayer 2001). At the meta-population level patterns of distributions usually show considerable year-to-year variation in conditions operating at extents and frequencies consistent with the topo-scale (Mackey and Lindenmayer 2001). A deme will be more responsive to processes operating at the micro-scale while individual organisms' patterns of movement can vary through the course of the day in response to nano-scaled affects (Mackey and Lindenmayer 2001).

Niche concept

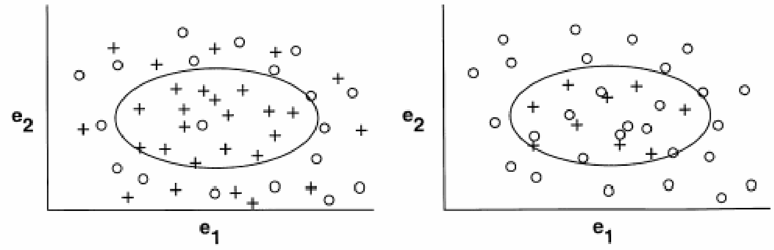
Distribution models are inherently multivariate (Clark et al. 1993; Browning et al 2005) and rely heavily on the concept of niche (Guisan and Zimmerman 2000; Guisan and Thuiller 2005). Niche, as reviewed by Leibold (1995), can be considered as driven either by the environmental requirement of species (as in the concepts of niche developed by Grinnell or Hutchinson) or by the impact that the species can have on their environments (as defined by Elton, Mac Arthur, and Levin).

The "environmental" niche is more related to an autoecological and physiological approach while the latter, usually named the "trophic" niche, is related more to trophic levels and food web theories. Given its nature, the environmental niche concept has been widely used in distribution modeling with many simplifications that have rarely been tested (Guisan and Thuiller 2005).

Whittaker et al. (1973) and Pulliam (2000) has provided a framework that can help clarify the relationships among niche and species distribution, and that distinguishes four different theoretical views of the niche concept (Fig. 6): *the Grinnellian niche* (or fundamental niche), where species occur wherever the environmental conditions are suitable (i.e. with a population growth rate ≥ 1); *the realized niche* (originally defined by Hutchinson), where a species is excluded from part of its fundamental niche by biotic interactions (e.g. competition, predation); *the source-sinks dynamics*, where a species commonly occurs in a sink habitat where its population growth rate is ≤ 1 and thus where it would disappear without constant immigration from source habitats; *the dispersal limitation situation*, where a species is frequently absent from suitable habitats because of recurring extinctions and limited dispersal.



A. Grinellian Niche B. Hutchinsonian Realized Niche



C. Source-Sink Dynamics D. Dispersal Limitation

Figure 6. Relationships among niche and species distribution. In each picture, the oval represents the fundamental niche of the species, i.e. the combination of environmental factors (in this case e1 and e2) for which the species has a finite rate of increase λ greater or equal to 1. In each diagram, the pluses indicate the presence of the species in a patch of habitat and the zeroes indicate the absence of the species. Diagram A (Grinnellian niche): a species is present only where the conditions are suitable and nowhere else. Diagram B (Hutchinson's realized niche): species are absent from those portions of the fundamental niche where a dominant competitor is present; species are present only in patches with suitable habitat conditions. Diagram C (source-sink theory): species can occur where $\lambda \leq 1$ and can be absent from patches where $\lambda \geq 1$. Diagram D (metapopulation dynamics): species are frequently absent from suitable habitat because of frequent local extinctions and because of the time required to recolonize suitable habitats. From Pulliam 2000.

All these theoretical scenarios should be considered when modeling species distribution, and it is important to underline that the niche of a species should be defined considering empirical observation of successfully reproducing individuals. On the contrary, distribution models are based most of the times on presence, or presence/absence, or sometimes on abundance values, but almost always there is no clue of the reproductive fate of the individuals being sampled. Moreover, in most cases, only habitat variables (like elevation, land cover, etc.) are used as predictors, since these are widely available. So, habitat models are usually based on the Grinnellian niche concept.

However, there is more to the occurrence of a species than habitat alone (Heglund 2002), and thus presence/absence or density of a species cannot be considered as proxies for reproductive success (Van Horne 1983). Behavioral responses, for example, can play an important role, as well as intra-specific competition and many other factors. Accordingly, loss of habitat may cause behavioral responses corresponding to increased density in remaining habitat, and social or source-sink population structures can cause increased densities in low quality habitat (Van Horne 1983).

All these phenomena can be extremely important for species-habitat relationships obtained from presence/absence or density data, because they can produce misleading results with important detrimental effects in conservation and management (Van Horne 1983). However, they have received only limited attention in distribution models.

A clear example is that of ecological traps. Recently the topic of ecological trap has received increasing interest in the conservation biology community (Battin 2004; Robertson and Hutto 2006). An ecological trap is a low quality habitat used for reproduction and survival that can not sustain by itself a viable population (or where the species does poorly relative to other available habitats), but that is preferred over other available habitats with higher quality. Thus, an ecological trap is simply a sink habitat that for some reason is preferred rather than avoided (Delibes et al. 2001). One possible explanation for the existence of ecological traps is that animals make errors in habitat assessment, possibly as a result of some mismatch between the environmental clues they use to select habitats and actual habitat quality (Battin 2004). In general, there are three main mechanisms that can create an ecological trap: 1) an increase in the attractiveness of a habitat in the absence of a change in its suitability; 2) a reduction in habitat suitability without a loss in attractiveness; 3) a simultaneous increase in the attractiveness and reduction in suitability of a habitat (Robertson and Hutto 2006).

Whichever is the mechanism it is important to underline that ecological traps can negatively influence the recommendation coming from distribution models for wildlife conservation and management (preserving an ecological trap can potentially damage a population much more than no protection at all). This is particularly important if we consider that human alteration of natural habitats can potentially create ecological traps for wildlife species.

General assumptions in habitat modeling procedures

Wildlife-habitat models rely on a number of assumptions and simplifications that constitute the necessary basis of every modeling effort (Corsi et al. 2000). However, most of the models that have been published do not even provide a clear statement of the null hypothesis that is behind the modeling procedure. Yet a clear understanding of the limitations and potential drawbacks of habitat models is extremely important for a correct application of the model.

The choice of the particular spatial scale (Wiens 1989), the environmental predictor variables that are used (Guisan and Zimmerman 2000), and the representation of habitat relationships within a particular statistical model, all reflect the assumptions and the inherent bias of the modeler (Ray and Burgman 2006). Some of these assumptions are relative to the particular data and methods used to build the model. Others are general assumptions that pertain to almost all distribution models. Usually these general assumptions are kept implicit and are not discussed, but in this essay I will focus on them, because they can have important consequences for the output of the models.

The equilibrium postulate

The most widely used null hypothesis in distribution models is that the species distribution is random with respect to a particular variable (or to a particular set of variables) over the entire environmental domain. This null hypothesis relies on a number of assumptions that commonly are not met. In fact, in a complex situation there is a high chance of detecting correlation that is spurious (Cumming 2000). As an example, Cumming (2000) proposed a model describing the distribution of *Amblyomma hebraeum* over the entire African continent and he obtained the species distribution is non random with respect to mean monthly temperature and mean monthly rainfall. However, the points of presence upon which the model was built where mainly distributed in South-East Africa that is clearly climatically distinct from the rest of the continent. In this situation it is easy to find a spurious correlation among species presence and climatic factors.

One of the main assumptions on which the null hypothesis outlined above is based is that the data available to build a model are of the correct ‘scope’ in both time and space. In an ideal world, the target species would be sedentary at a fixed point in space and its ecological requirements well known and measurable at the same spatio-temporal scale. In this situation we would be able to measure without great problems species requirements and environmental data. In reality, however, measurement of the known potential predictor variables may be difficult and species may have ecological requirements that are unknown or are immeasurable (Rushton et al. 2004).

Moreover, both species and environmental data are usually sampled during a limited period of time and/or space, and models fitted using these data can only reflect a snapshot view of the expected relationship. A working postulate (the so called equilibrium postulate) is to assume that the modeled species is in pseudo-equilibrium with its environment, at least within a short time frame and has suffered no major perturbation (Hirzel and Guisan 2002; Guisan and Thuiller 2005; Barry and Elith 2006). This assumption allows for one of the most appealing properties in habitat modeling procedures (at least for conservation biology): the possibility of building distribution maps also for areas where no data on species presence is available.

In fact, if the equilibrium postulate holds, observed patterns of occupancy should reflect the species' full biotic potential, implying that the species can potentially occur in all environmentally suitable locations, and its distribution has not been constrained locally by factors that cannot be modeled, such as historical accidents. The standard procedure is then to extrapolate the empirical evidence collected in a proportion of the range to a larger area or to the entire range of occurrence of the species (Pereira and Itami 1991; Aspinall and Matthews 1994; Corsi et al. 2000). To be acceptable, this implies that the species-environment relationship used to build the model is constant over space and time (Corsi et al. 2000; Guisan and Zimmerman 2000; Osborne and Suárez-Seoane 2002).

Whether this is plausible or not depends on the scale of the model, the dispersal ability of the organisms and the history and biology of the species (Tyre et al. 2001), but few studies have explored the validity of this fundamental assumption. Svenning and Skov (2004) suggested that many European tree species are still strongly controlled by dispersal constraints on their post-glacial expansion, and thus cannot be considered to be in equilibrium with their environment. Araujo and Pearson (2005) found similar results for European reptiles and amphibians.

In general, the equilibrium postulate will not be true in most of the cases, especially for generalist species, for species with limited dispersal ability or for species with a wide distribution range. In fact, these encounter large natural variation in habitat availability across their geographic range, variation that usually is coupled with varying habitat selection between individual animals belonging to different populations. As a consequence, the higher the variance of the species-environmental relationship, the higher the number of locations required to provide an adequate ecological profile for the species. In practice, errors resulting from the equilibrium assumption are most acute when trying to predict distributions of species recently introduced to new locations, or species that are expanding their range (Barry and Elith 2006; Rotenberry et al. 2002, 2006).

The alternative proposed by many authors, is that of building local models, encompassing areas where the habitat characteristics (and the biological characteristics of the local populations) are more homogeneous (Corsi et al. 2000; Osborne and Suárez-Seoane 2002).

Assumptions about species data

Usually, distribution models are developed starting from presence, presence/absence, or density data on the target species. However, the aim of distribution models is that of representing the niche of a species, i.e. the areas that support a positive growth rate for the population. An important assumption following this consideration is that it is possible to obtain information on habitat quality from data on species presence/absence. In practice, when locations with particular habitat characteristics are associated with the occurrence of a species, it is often assumed that the locations are good-quality habitats (i.e. habitat with high suitability). If density of individuals is known, it is often assumed that higher densities indicate habitat with higher suitability: the probability of occupancy is thus used as a surrogate for habitat quality.

However, in many cases, the habitat that is occupied may not be “good” habitat (Van Horne 1983; Pulliam 2000; Tyre et al. 2001). In landscapes where species exhibit source-sink population dynamics (Pulliam 1998), species occur both in “good” habitats (source areas, areas where birth rates exceed death rates) and in “bad” habitats (sink areas, areas where death rates exceed birth rates). Moreover, under certain habitat selection models (like the ideal despotic distribution model), there is the possibility of having higher densities in habitats that are worse from the animal’s perspective (for example because of lower food availability, or higher predation risks, etc.). The situation is made even more confusing by the existence of demographic stochasticity in fecundity or survival rates and of local dispersal: all these factors strongly limit the ability of habitat models to predict habitat quality as a function of occurrence (Pulliam 2000; Tyre et al. 2001).

If the modeling approach is based on presence-absence data (as is the case in most of the published literature) a further assumption is necessary. In fact, these models assume that absence indicates areas where species are not present due to a negative species-environmental relationship. However, failure to detect presence does not always mean absence of the species. Points at which the species was not detected are ambiguous in the sense that they could represent habitat that is suitable but currently unoccupied; habitat that is suitable and occupied, but the observer failed to detect the species; or habitat that is unsuitable (Hirzel et al. 2001;Tyre et al. 2001; Rotenberry et al. 2002;).

Temporal misclassification (not trapping long enough or during the proper season), population dynamics, rate of dispersal, historical factors (that can influence species presence independently from habitat quality), habitat fragmentation, all these factors may produce species absence from otherwise optimal habitat (Brotons et al. 2004).

Moreover, it is usually difficult to record real absences. Failure to detect species when they are present at a site is not uncommon in field surveys (MacKenzie et al. 2002; Gu and Swihart 2004). For example, using double-observer surveys for avian point counts, Nichols et al. (2000) showed that a single observer missed varying proportions of the birds actually present and similar results have been found by Kissling and Garton (2006).

Failure to detect presence results in false negatives, which when employed to discriminate between used and unused sites will change the mathematical functions describing occupied habitats (Browning et al. 2005).

Assumptions about environmental data

Probably the most important assumption in any habitat modeling exercise is that all the necessary data are available. In fact, as already mentioned in the paragraphs above, it is generally implicitly assumed that variables which are not included in the analysis have a neutral effect on the results of the model. Either it is assumed that the species' ecological response to these environmental variables is constant (and thus can be excluded from the analyses without important consequences) or that the response is highly correlated with the other variables that are included (Corsi et al. 2000). This assumption is generally used to account for all the biological factors (mainly all types of inter-specific interactions) that can influence the distribution of a species but that can seldom be mapped (and thus considered in the model).

Competition is an important factor that is usually absent from distribution models (Guisan and Thuiller 2005). The classical theory, which goes back to Darwin, says that along an environmental gradient species are limited in one direction by physical factors and in the other by biological factors (Brown et al. 1996). Even though this theory deserves further investigations (Guisan and Thuiller 2005), some analyses have shown that the inclusion of presence/absence of competitors can significantly increase the predictive ability of distribution models (Leathwick and Austin 2001; Anderson et al. 2002), even using relatively coarse resolution and regional extents.

The same is true for other biotic interactions, such as facilitation, pollination, herbivory, predation, parasitism, etc.

Another important point regarding environmental data is that usually land cover data are used in the modeling procedure as proxies for environmental classes that are related to the fitness of the individual animals. In practice, it is assumed that land types (or any other form of classification of the environment) represent natural spatial subdivisions with a biological meaning. However, it should be considered that discontinuities that are extremely clear for a classification algorithm or for a human being are not necessarily significant for species of other animals or plants.

Brooks et al. (2004) considered the case of 3 ecoregions, two located in North America (the North Central Rockies Forest ecorigion and the Northern Short Grassland ecoregion) and one in South America (the Northwestern Andean Montane Forest ecoregion). The two North American ecoregions are traditionally considered as very distinct, one being a forest and the other being grasslands. However, if we consider bird and amphibian species the two north American ecoregions are quite similar. On the contrary, it is possible to find great differences among the northern and the southern parts of the South American ecoregion, that is usually considered relatively homogeneous (and in any case is a single ecoregion).

Uncertainty and errors

The quality of the data used to construct a model obviously affects the predictive accuracy of the model itself. Ideally, data on species presence should result from a systematic, stratified, or random sampling design that adequately represents the study area and the range of habitat variables. At the same time data on the environmental parameters should be collected for the entire area considered with the necessary resolution and, possibly, representing the environmental characteristics that have a real, ecological meaning for the species considered.

However, observations on the species during sampling are not without error, and the same is true for environmental datasets. It is then important to understand the types of errors that commonly affect distribution models.

Different authors have distinguished among error and uncertainty. The first relates model prediction to truth (using error assessment), while the second represents the potential range of values around a predicted outcome (range that can be measured using uncertainty and sensitivity analyses; Johnson and Gillingham 2005). However, the two concepts are really interrelated and it is difficult to distinguish between them. Some authors use error and uncertainty interchangeably, and in that case errors include not only ‘mistakes’ and ‘faults’ but also uncertainty, through the statistical concept of ‘variation’ (Barry and Elith 2006).

Fielding and Bell (1997) provided a useful framework for the classification of errors, particularly referring to errors in the prediction of species’ occurrence. They proposed two categories: algorithmic errors, which are derived from model construction and data uncertainties, and biotic errors. Understanding and identifying the source for both biotic and model construction errors in habitat models is a necessary step towards identifying aspects of the model that can be improved.

Biotic errors are inevitable because the model is a simplification of reality and cannot include all of the habitat factors that influence the species distribution. For example, misclassification of locations by the model can be related to several aspects of the species’ ecology. Most inductive habitat models assume that the suitable area of the landscape is saturated by the species of interest (Capen et al. 1986); however, if this assumption is not met the model will result in a large percentage of commission errors, where the species is predicted to occur but is not found at the location.

In addition, intraspecific and interspecific interactions, the autocorrelation naturally existing in species occurrences, and the influence of historical events on the species' distribution can influence the performance of the model (Fielding and Bell 1997).

Regan et al. (2002) proposed a different framework for the classification of errors, concentrating their efforts on uncertainty. Broadly defined, uncertainty is the lack of sureness or confidence about something and it pervades all our attempts to ascertain the truth about the natural and physical environment. They developed a taxonomy of uncertainty types, identifying the main sources of uncertainty in biological systems and outlining appropriate methods for dealing with each type.

They propose that uncertainty falls broadly into two main groups: epistemic uncertainty (uncertainty about a determined fact) and linguistic uncertainty (uncertainty that arises because our natural language is vague, ambiguous, and context dependent). I will concentrate on the first.

Epistemic uncertainty can be further classified into five main types: measurement error, systematic error (e.g. bias in the measuring equipment), natural variation, subjective judgment and model uncertainty. All these types of uncertainty affect distribution models in conservation biology (Table 2) (Elith et al. 2002; Regan et al. 2002).

Uncertainty	**Causes**	**Possible solutions**
Measurement error	Imperfect measurements or techniques produce random variation in result, e.g. available equipment may not record location precisely	Provide bounds, confidence intervals (e.g. Stoms et al. 1992; Crosetto et al. 2000)
Systematic error	Methods produce biased data, e.g. sampling is close to roads	Recognise and remove bias (Kadmon et al. 2004)
Natural variation	Real systems change in ways that are difficult to predict and hard to characterise	Represent response with a probability distribution, or confidence intervals
Model uncertainty	Models are simplifications of real processes, and several models may fit the data	Validation; in explanatory variables: produce multiple realizations of the variable (e.g. Goovaerts 2001); different model structure (Ray and Burgman 2006)
Subjective judgement	Experts estimate facts or classifications	Assign degrees of belief or imprecise probabilities or reliability bounds (Burgman et al. 2001; Ray and Burgman 2006); multicriteria decision-making process (Clevenger et al. 2002)

Table 2. Classification of uncertainty types. Modified from Regan et al. 2002 and Elith et al. 2002.

Measurement error arises from imperfect measurements or techniques and produces random variation in results. This is true for presence-absence records, for counts, and for estimates of continuous and discrete variables (Elith et al. 2002). A whole population is rarely sampled, some individuals may be unintentionally sampled more than once, individual observers may provide different observations in identical circumstances, and locations may be recorded inaccurately or rounded inconsistently. Once more, particularly important are false negative errors. In fact, even if a species is present at a location, it may not be detected during the survey because, for example, the species is difficult to detect, or the population is small, or the survey methodology is insufficient or inappropriate (Hirzel et al. 2001; Tyre et al. 2001). Failing to detect a species when it does occur leads to false absences in the survey data and unreliable distribution information. Error in distribution data can also occur from mistakes in species identification and data recording.

Measurement errors also contribute to uncertainty in predictor variables. These are commonly produced by interpolation of field-based measurements, interpretation of aerial photos or satellite images, or modeling of physical processes. Uncertainty exists in the base data and is propagated as the data are summarized, classified, modeled and interpolated. Bounds and confidence intervals provide the possibility to deal with measurement errors (e.g. Stoms et al.1992; Crosetto et al. 2000).

Systematic errors result from biases in measuring equipment, sampling procedures or processing operations; it is not random, it is difficult to recognize except on theoretical grounds, and it can only be corrected by more careful consideration of the relevant theory and experimental methods, for example by double sampling or by post-hoc correction factors. However, systematic error is difficult to treat and solutions like post-hoc correction factors may indeed introduce further biases if the direction and magnitude of the error is unknown (Elith et al. 2002).

Uncertainty existing in species data can partly be considered as systematic error. This is particularly true when data are used beyond their original intention (i.e. for analysis that were not planned in advance), or when there are constraints on time or money. For instance, sampling is commonly performed close to rivers (Williams et al. 1996), roads (Williams et al. 2002; Kadmon et al. 2004), or other human related facilities (Freitag et al. 1996; Lawes and Piper 1998; van Jaarsveld et al. 1998; Maddock and du Plessis 1999; Reddy and Davalos 2003), or it may be focused in some vegetation types or landscapes only, or biased away from ecotones. In these cases efforts are sometimes made to supplement the existing data with records in poorly sampled strata or to adjust modeling methods to cope with incomplete coverage.

Predictor variables can be biased as well. In fact, as the grain at which data are recorded becomes coarser, units that exist at a finer grain are subsumed into more prevalent ones, leading to a bias against unusual classes (e.g. rare vegetation classes). Alternatively, mapping may be biased towards classes with unusual and noticeable properties, such as those with greater reflectivity in remote sensing imageries, e.g. a lake, road or grassland.

Fielding and Bell (1997), Guisan and Zimmerman (2000), Austin (2002), and Gu and Swihart (2004) discuss further cases of biological variation including intra- and inter-specific interaction, the spatial structure of historical events, the effect of individual variability on site selection for cryptic advantage, temporal and geographical variation in animal-landscape relationships, stochastic variation in environmental variables, and issues related to scale.

Subjective judgments are often confused with model uncertainty. However, subjective judgments are more related to decisions taken by the modeler while interpreting the data. These decisions can potentially generate errors and spurious results, especially when data are scarce and error prone (Elith et al. 2002; Ray and Burgman 2006), or when the modelers do not have a clear knowledge of the problem at hand (Ray and Burgman 2006). The modeler can introduce "uncertainty" in the model at different levels, starting from subjective judgments on how to model a habitat variable, and going on with selecting among many alternatives a single set of habitat variables and a single way of combining them. Another important point is that the modeler often has to decide a plausible way of computing habitat variables relevant for the presence of the species, a task that may be extremely difficult given that we know very little about how animals perceive their environment.

A further instance of uncertainty is that, independent of the model approach implemented, the scales used in most studies are decided arbitrarily, while the species-environment relationship that is used may only be relevant at a particular spatial scale (Burgman et al. 2001). Usually, the scale at which species-environment relationships are constructed is determined by the scale of the available information, without any explicit rationalization. Similarly, there is rarely any explicit treatment provided for the issue of extrapolating relationships developed from data collected within small sample quadrats to much larger landscape scales.

However, not all the uncertainty existing in habitat models is related to errors. Natural variation exists, and it can be extremely important in systems that change (for example, with respect to space or time) in ways that are difficult to predict. So we may be measuring for our modeling effort the value of a parameter that is going to change as a result of changes in other, independent variables (Regan et al. 2002). This is considered as a source of uncertainty because the true value of the quantity of interest is usually extraordinarily difficult to measure or predict across the full range of temporal and spatial values' (Elith et al. 2002). Also species data exhibit natural variation and it is unlikely that this variation would ever be fully characterized. This implies that distribution models based on species-environment relationship are usually incomplete because they do not incorporate all of the underlying mechanisms for variation (Elith et al. 2002).

Moreover, uncertainty occurs also as a result of our representation of physical and biological systems, and it is a fundamental part of a model, that, by definition, constitutes a simplification of the real processes (Ray and Burgman 2006). In this sense, uncertainty does not refer to the "errors" in parameter estimates, but rather addresses the simplifying assumptions and the abstraction of ecological processes required by any model (Crosetto et al. 2000; Elith et al. 2002; Gu and Swihart 2004). This imposes a limit on the confidence that we can have in the output of the models, a limit that should be considered explicitly.

A possible solution is that of representing the incomplete knowledge of natural variation in a dependent variable, building a probability distribution for the quantity in question, a distribution that encompasses the full range of possible values (Elith et al. 2002). This approach would favor the quantification of the confidence that we can have in the model, through the assessment of the uncertainties associated with the outcome of the model itself (Crosetto et al. 2000).

In particular, two main frameworks have been proposed and used to deal with the various types of uncertainty in habitat modeling: uncertainty analysis and sensitivity analysis. Uncertainty and sensitivity analysis are complementary approaches that allow us to explicitly quantify the range and distribution of predictions and to identify data, model structure or parameters that require improvements. Both provide support for model predictions and highlight areas where assumptions need to be addressed and source data improved or augmented (Crosetto et al. 2000; Crosetto and Tarantola 2001; Johnson and Gillingham 2005).

Typically, uncertainty analysis is conducted as a simulation (e.g. Monte Carlo simulation), where one runs a model multiple times and recalculates the predicted outcome for each systematic perturbation of the input variables. Following the simulation, the variation in outcomes indicates the level of uncertainty in model predictions. Uncertainty analysis allows us to consider all sources of uncertainty simultaneously and to determine if the model and input data reliably support the decision process (Bender et al. 1996; Burgman et al. 2001; Johnson and Gillingham 2005). Sensitivity analysis works in the opposite direction but uses a similar approach, to reveal model components or data with the greatest influence on the variation in the final prediction (Johnson and Gillingham 2005).

Evaluation procedures and classification accuracy

One of the most important steps in any modeling exercise is the evaluation of its applicability and of its predictive power (i.e. the number of cases in which species presence and/or absence is correctly assessed by the model [Stockwell and Peterson 2002]), a step that is usually called “model validation” (Guisan and Zimmerman 2000; Guisan and Thuiller 2005).

In the ecological literature, and especially in the context of simulation models, there is great discussion and confusion about the use of the term validation, because of semantic and philosophical considerations (Rykiel 1996). Oreskes et al. (1994) and Zimmermann and Guisan (2000) suggest using the term “evaluation” instead of “validation” to indicate the analysis of the predictive success; in fact validation is more related to a model’s veracity, that in evaluation is not called into question. Ryckiel (1996) defines validation as the demonstration that a model within its domain of applicability possesses a satisfactory range of accuracy consistent with the intended application of the model.

Leaving apart semantic questions, there is disagreement also on the importance of validation in a modeling exercise. Van Horne (2002) de-emphasizes model validation and accepts the position that habitat models are a means of quantitatively assembling the best knowledge of animal-habitat relationships to make the most informed decisions possible and to identify research needs, rather than expecting the models to be predicted with $P < 0.05$ (or whatever other value). For Conroy and Moore (2002), validation demonstrates neither the truth nor the usefulness of a model, only the model’s internal consistency; thus a validated model may nonetheless be inadequate for management if it is based upon faulty assumptions or logic. On the contrary Rykiel (1996), Elith and Burgman (2002) and Rushton et al. (2004) consider testing as a vital stage in the development of predictive distribution models.

Most scientific papers consider the assessment of the accuracy of a prediction as extremely important and refer to it as validation; here I will use both validation and evaluation in the same sense and I will suggest that validation is a fundamental part of a modeling exercise.

Importance of validation procedures

Models cannot be tested as being true or false, but for providing good testable hypothesis relevant to important problems and for the accurate prediction of biological patterns (Guisan and Zimmermann 2000). Complete confirmation is logically precluded by incomplete access to natural phenomena and thus models can only be evaluated in relative terms, and their predictive value is always open to questions (Oreskes et al. 1994).

However, model validation is important because predictions from models will always contain a level of error resulting from a wide range of factors, including insufficient sample size, measurement error in the biological data, measurement error and insufficient spatial resolution in the mapped environmental variables, failure to incorporate critical habitat and/or other factors (e.g., predation, competition, dispersal), etc. (Pearce et al. 2002). Evaluation of the nature and magnitude of prediction error assists in determining the suitability of models for particular applications and in identifying specific weaknesses requiring correction.

Model performance may be contingent on the goals, assumptions and data used for aparticular analysis (Segurado and Araújo 2004). For example, if the goal of a model is to predict occurrences of species outside their known range, interest could be focused on methods that optimize the overall fit, i.e. the balance between false positives (absent, but predicted to be present) and false negatives (present, but predicted to be absent) (Fielding and Bell 1997). However, if the goal is to minimize unexplained variation by models (i.e. minimize false negatives), then a measure of performance would be required that accounts for the proportion of false negatives alone (e.g. Araújo and Williams 2000).

Species distribution models can be sensitive to the spatial patterns that are considered (Manel et al. 2001; Brotons et al. 2004; McPherson et al. 2004; Segurado and Araújo 2004). In other words, model performance is not independent from the geographical and/or environmental distributions of the species (Segurado and Araújo

2004; Luoto et al. 2005) and therefore, distribution models are not equally reliable for all species (Luoto et al. 2005).

To maximize their utility, it is necessary to understand whether the variation in performance reveals inherent ecological differences or whether it reflects statistical artifacts (McPherson et al. 2004). Boone and Krohn (1999) postulated that the incidence of species in surveys is closely related to the likelihood of their species-occurrence models being judged correct. Species unlikely to occur in surveys, such as rare or elusive species, are less likely than common species to be judged correctly, independently from the quality of their occurrence data.

Furthermore, there are indications that the performance of distribution models is simultaneously affected by several geographical attributes of species (Luoto et al. 2005), e.g. latitudinal range/marginality (Araujo and Williams 2000; Segurado and Araujo 2004); prevalence (calculated as the ratio of presence sites to the total sample of sites [Manel et al. 2001; Brotons et al. 2004; McPherson et al. 2004]); spatial autocorrelation (measured using Moran’s I [Boone and Krohn 1999]) and rarity (Karl et al. 2002).

Modeling performance was related negatively to prevalence (Manel et al. 2001; Luoto et al. 2005) and latitudinal range, and positively to the spatial autocorrelation of the species distribution (Luoto et al. 2005): species at the margin of their range or with low prevalence were better predicted than widespread species, and species with clumped distributions were better predicted than scattered/dispersed species. These variables accounted for more than 75% of the variation in the modeling accuracy (Luoto et al. 2005).

This pattern corresponds with observations made by Segurado and Araujo (2004), who reported that species with large areas of occupancy and great areas of occurrence (i.e. truly widespread) had greater overall errors (i.e. Kappa statistic), although the amount of unexplained variation (i.e. sensitivity) was not larger for species of this group than for species with other distribution profiles. Similarly, Araújo and Williams (2000) explored the relationship between model performance (sensitivity and specificity) and the total number of records per species (i.e. area of occupancy). They found that sensitivity (proportion of false negatives) was higher for widespread and lower for restricted-range species, while specificity (proportion of false positives) was lower for widespread species and higher for restricted-range species.

Moreover, Karl et al. (2002) related avian species commonness and model accuracy using field and simulated data and concluded that habitat relationships for rare species were likely to be as accurate as for common species, despite increasing error estimates with decreasing sample sizes. Also Elith and Burgman (2002) did not find clear associations between modeling success and species characteristics such as rarity.

Range size is another ecological characteristic, likely to differ from species to species, that might influence the success of distribution models (Manel et al. 2001; Stockwell and Peterson 2002). Such influence could have ecological roots. Species with large ranges or disjunctive distributions, for example, may exhibit subspecific variation in habitat associations because of local adaptation (Osborne and Suarez-Seoane 2002; Stockwell and Peterson 2002). To an automated model-fitting algorithm, such disjoint habitat preferences could appear statistically incoherent and therefore less predictable. Poor performance of models for narrow-ranging species may instead have methodological roots. Their habitat associations may be perfectly coherent at fine spatial scales, but may not manifest themselves at the spatial grain of analysis (Cumming 2000; McPherson et al. 2006).

Validation procedures

Many accuracy statistics of varying utility have been applied to species distribution models and much has been published about their desirable properties (Fielding and Bell 1997; Fielding 2002). Two properties in particular are worth highlighting. The first is the ability to describe model accuracy in terms of the observed predictive performance, (i.e. a measure of the probability of making the correct prediction at a site). The second, and perhaps most important, property for accuracy measures is the ability to compare accuracy meaningfully between the same model in different applications or between models developed for different species or with different training and test data (Vaughan and Ormerod 2005). Such comparisons require accuracy statistics either largely independent of, or possibly corrected for, potentially confounding properties of the particular data used to test a model (Manel et al. 2001; Fielding 2002).

Model testing can be conducted on many levels and in a variety of ways; commonly what is tested is the final output comparing a sample of a model’s predictions against the observed species’ distributions (Rushton et al. 2004; Vaughan and Ormerod 2005);

however testing the assumptions, variables, and components of the model are valuable levels of validation as well (Schamberger and O'Neil 1986).

Ideally, testing should have three aims (Vaughan and Ormerod 2005), to: (i) provide an overall assessment of a model's predictive performance; (ii) provide clear guidance for the use of a model and/or its predictions to the planners and practitioners dependent on its outputs; (iii) perform a diagnostic function, identifying weaknesses in predictive performance, possible causes and identifying priorities for future model development.

Several methods and data sources for model validation are frequently used. To obtain an unbiased estimate of a model's predictive performance, an independent data set should be used, because the accuracy achieved with the original data is often much grater than that achieved with new data (Fielding 2002).

When two data sets originated from distinct sampling strategies are available, the first (the calibration or training dataset) is used to adjust the model, whereas the second (the evaluation or testing dataset) is used to evaluate the quality of model predictions. If independent data are not available, then partitioned and statistical resampling techniques (e.g. cross-validation, bootstrap, and jackknife) may be used to reduce bias in the measurement of predictive performance (Verbyla and Litvaitis 1989; Pearce and Ferrier 2000; Guisan and Zimmermann 2000; Boyce et al. 2002), but always keeping in mind that resampling techniques provide a biased assessment of model performances, because models tend to overfit their training data (Fielding 2002).

In cross-validation, the single data set is divided into K groups of roughly equal size (in the special case of jackknife or leave-one-out each group consists of just one site, that is sequentially held out with the remaining observations forming the training set [Capen et al. 1986]). For each group of sites a model is fitted to the data from the other K - 1 groups. The model is, then, used to predict a probability of occurrence for each of the sites in the group excluded from the fitting of the model. This procedure is repeated for all groups until predicted values have been calculated for all sites. These predicted values are then used to assess the accuracy of the predictive model (Pearce and Ferrier 2000; Boyce et al. 2002).

Cross-validation is a less rigorous approach to model evaluation than using a truly independent dataset (Chatfield 1995; Manel et al. 1999), particularly in situations where the model development sites are not distributed representatively across the region under consideration (Verbyla and Litvaitis 1989; Pearce and Ferrier 2000). In addition, the inevitable reduction in size of the training set will usually produce a corresponding decrease in the model accuracy. There is, therefore, a tradeoff between having a larger test set that gives a good assessment of the model and a small training set that is likely to result in a poor model (Fielding 2002).

Validation statistics: presence-absence datasets

Several options exist to quantify the association between predicted and observed values (Rushton et al. 2004). However, if the predictions of a statistical model are probabilistic, they need to be transformed back to the scale of the real observation. For binary presence/absence data, this can be done by truncating probabilities at a given threshold (Guisan and Zimmermann 2000; Boyce et al. 2002; Rushton et al. 2004). In the context of habitat modeling, the choice of a threshold is usually based partly on knowledge of the prior probability of occurrence of the species of interest or is set to an arbitrary value (Pearce and Ferrier 2000).

For model based on presence/absence data the most common approaches are:

1. Confusion matrix or contingency table: the predicted presence and absence are compared with the test data in a 2 x 2 table. From this table different threshold dependent measures can be obtained, and include matching coefficient, sensitivity (i.e. agreement between the predicted probability of occurrence and observed presence), specificity (i.e. the ability of the model to distinguish absence locations percent correctly classified), false positive and false negative fraction; and kappa (Cohen 1960; Fielding and Bell 1997; Pearce and Ferrier 2000; Moisen et al. 2006). Kappa uses all of the information in the confusion matrix and assesses the improvement in classification over chance agreement between observed and predicted values (Fielding and Bell 1997; Karl et al. 2000; McPherson et al. 2004). Kappa measures the actual agreement minus the agreement expected by chance. Kappa approaches 1 as coding is perfectly reliable and goes to 0 when there is no agreement other than what would be expected by chance. Kappa is computed as:

$$K = \frac{P_A - P_C}{1 - P_C}$$

where: P_A is the proportion of units on which there is agreement and P_C = the proportion of units for which agreement is expected by chance (Cohen 1960). k values above 0.7 describe 'very good' discrimination ability (Pearson et al. 2006). Confusion matrices have some limitations. In fact, most of the statistics based on confusion matrices are influenced by the choice of the threshold probability to transform the predictions to presence/absence (Vaughan and Ormerod 2005). Moreover, the frequency of occurrence or prevalence of the species can influence the resulting statistics (Fielding and Bell 1997; Manel et al. 1999, 2001; Fielding 2002; McPherson et al. 2004; Rushton et al. 2004), even though kappa is more resistant to prevalence than sensitivity and specificity (Manel et al. 2001). A possible solution has been proposed by Pearson et al. (2006) and Moisen et al. (2006), who used k by maximizing the statistic over a range of thresholds above which model outputs are considered to represent species presence. However, Kappa and, more in general, confusion matrices are not appropriate for comparisons of model accuracy between species or regions unless certain precautions are taken (McPherson et al. 2004).

2. <u>Receiver Operating Characteristic (ROC) plot</u> is a methodology that was developed to provide a threshold independent measure of accuracy (Pearce and Ferrier 2000; Guisan and Zimmermann 2000; Rushton et al. 2004). This technique evaluates the proportion of correctly and incorrectly classified predictions over a continuous range of threshold levels. ROC cannot, however, be calculated from those techniques that predict presence/absence, because the calculation of ROC requires model output to be a suitability, or probability, value scaled from 0 to 1 (Pearson et al. 2006). To obtain a ROC curve, sensitivity (true positive fraction) and specificity (true negative fraction) are evaluated at different cut-offs within the data and plotted (sensitivity as a function of 1 – specificity). The area under the curve (AUC) gives an assessment of model performance (Cumming 2000), that is independent of any particular threshold (Fielding 2002; Rushton et al. 2004). The AUC has a value between 0.0 and 1.0. A model with no predictive power would have an AUC of 0.5, while a perfect

model would correspond to an AUC of 1.0 (Pearce and Ferrier 2000; Boyce et al. 2002). Generally, model accuracy is considered good if 0.9 < AUC <= 1.0, reasonable if 0.7 < AUC <= 0.9, and poor if 0.5 < AUC <= 0.7 (McPherson et al. 2006), but other classifications can be adopted (Araújo et al. 2005a; Randin et al. 2006; Pearson et al. 2006). The ROC curve can also be used to identify the optimal threshold value by balancing the cost that would arise from an incorrect decision against the benefit to be gained by a correct decision, i.e. the point on the curve at which the sum of sensitivity and specificity is maximized (Pearce and Ferrier 2000; Manel et al. 2001). The area under the ROC plot can then be compared among competing models (Cumming 2000). The ROC method is becoming more widespread (Rushton et al. 2004; McPherson et al. 2006), but Manel et al. (2001) found the method to be highly correlated with Cohen's kappa statistic, which is simpler to compute. ROC plots are thought to be independent of prevalence, because the true positive and false positive fractions determining their curve are each expressed as a proportion of all sites with a given observed state (McPherson et al. 2004; Person et al. 2006).

3. <u>Correlation coefficient and slope:</u> R between observed and estimated values (Lek et al. 1996), or the slope of the regression between values estimated by models and values observed (Lek et al. 1996).

A limitation of confusion matrices, which also applies to other measures of fit, is that they are only marginally relevant to the model and ignore the geographical pattern of the predictions (Barry and Elith 2006). In particular, measures of fit do not identify where and how the errors occur, either spatially or environmentally. Others have recognized this problem and suggested evaluations that take into account the spatial context of the errors (Fielding and Bell 1997). In particular, Pontius (2000) and Pontius and Cheuk (2006) have proposed modifications of k to account for the spatial component of the errors.

Validation statistics: presence-only datasets

When the validation dataset consists only of presence data, model evaluation is more difficult because of the absence of a truly binary statistic. Boyce et al. (2002) have proposed an approach based on use-availability data to explore model performance (the so-called Boyce index) that has been further developed by Pearce and Boyce (2006) and by Hirzel et al. (2006). In this method k-fold cross-validation is used to correlate prediction ranks with area-adjusted frequencies of predicted values. Prediction ranks are obtained by breaking the range of predicted values into 10 (or some other arbitrary number) evenly spaced bins. Area-adjusted frequencies of predicted values are then obtained by counting the number of occupied sites within the predicted value bins, and dividing these values by the area of the study area assigned the predicted values associated with than bin. This graphical approach holds great promise as a method to visualize predictive performance and to assign thresholds of prediction. However, as yet there is no suitable single measure of performance (or statistic) available to compare and contrast models.

An important feature of this approach is being able to examine how well model predictions are related to the probability of occurrence. A good model is one in which model predictions are proportional to the probability of occurrence (Manly et al. 2002). In the k-fold cross-validation graph, this would imply linear correspondence between the test-case area-adjusted frequencies and model predictions. There is no guarantee that any of the models described above will capture the true shape of the selection function, and thus might not be proportional to the probability of occurrence. Standard transformations of model predictions, e.g. logarithmic, square root, etc., might be necessary to scale the resource selection function appropriately. Proportionality is important because it allows model predictions to be used explicitly, such as when linking habitats to populations (Boyce and McDonald 1999).

The main shortcoming of the Boyce index, as described above, is its sensitivity to the number of bins and to their boundaries. To fix this problem, Hirzel et al. (2006) derived a new evaluator based on a “moving window” of width W instead of fixed classes. Computation starts with a first class covering the suitability range [0, W[and the predicted/expected ratio is plotted against the average suitability value of the class, W/2. Then, the moving window is shifted a small amount upwards and the predicted/expected ratio is plotted again. This operation is repeated until the moving window reaches the last possible range, [100-W, 100]. This provides a smooth predicted/expected curve, on which a “continuous Boyce index” can be computed by a Spearman rank correlation coefficient.

Practically, one often gets a sigmoid curve, the F increasing exponentially and then stabilizing and oscillating around a maximum value (Hirzel et al. 2006). Looking at the shape of this curve allows one to define where is the threshold between suitable and unsuitable habitat, from which point the model doesn’t add significant information, etc.

References

Akçakaya H.R., M.A. McCarthy and J. Pearce. 1995. Linking landscape data with population viability analysis: management options for the Helmeted Honeyeater. Biological Conservation 73:169–176.

Alldredge J.R., D.L. Thomas and L.L. McDonald. 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural, Biological, and Environmental Statistics 3:237-253.

Anderson S.H. and K.J. Gutzwiller. 1994. Habitat evaluation methods. Pp. 592-606 in: Bookhout T. A. (Ed). Research and management techniques for wildlife and habitats. 5th ed. Bethesda, MD, The Wildlife Society.

Anderson R.P., A. Townsend Peterson and M. Gòmez-Laverde. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos 98:3-16.

Araujo M.B., R.J. Whittaker, R.J. Ladle and M. Erhard. 2005a. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14:529-695.

Araujo M.B., R.G. Pearson, W. Thuiller and M. Erhard. 2005b. Validation of species climate impact models under climate change. Global Change Biology 11:1504-1513.

Araujo M.B. and R.G. Pearson. 2005. Equilibrium of species' distributions with climate. Ecography 28:693-695.

Araujo M.B and P.H. Williams. 2000. Selecting areas for species persistence using occurrence data. Biological Conservation 96:331-345.

Aspinall R.J. 1992. An inductive modelling procedure based on Bayes theorem for analysis of pattern in spatial data. International Journal of Graphical Information Systems 6:105-121.

Aspinall R.J. and K. Matthews. 1994. Climate change impacts on distribution and abundance of wildlife species: an analytical approach using GIS. Environmental Pollution 86:217-223.

Austin M.P. 1998. An ecological perspective on biodiversity investigations: example from Australian eucalypt forests. Annals of the Missouri Botanical Garden 85:2-17.

Austin M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecological Modelling 157:101-118.

Austin M.P. and M.J. Gaywood. 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. Journal of Vegetation Science 5:473-482.

Austin M.P., J.G. Pausas and A.O. Nicholls. 1996. Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia. Australian Journal of Ecology 21:154164.

Baillie J.E.M., C. Hilton-Taylor and S.N. Stuart. 2004. IUCN red list of threatened species. A global species assessment. IUCN SSC, Gland, Switzerland.

Barry S.C. and J. Elith. 2006. When things go wrong: error and uncertainty in habitat models. Journal of Applied Ecology 43:413–423.

Battin J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482-1491.

Bazzaz F.A. 1991. Habitat selection in plants. American Naturalist 137:S116-S130.

Bender L.C., G.J. Roloff and J.B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24:347-352.

Boitani L. 2003. Wolf conservation and recovery. Pp. 317-340 in Mech D.L. and L. Boitani (Eds). Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, USA.

Boitani L., F. Corsi, A. De Biase, I. D’Inzillo Carranza, M. Ravagli, G. Reggiani, I. Sinibaldi and P. Trapanese. 1999. A databank for the conservation and management of African mammals. Istituto di Ecologia Applicata, Rome, Italy.

Boitani L., S. Lovari and A. Vigna Taglianti (Eds). 2003. Fauna d’Italia: Mammalia III, Carnivora – Artiodactyla. Calderoni, Bologna, Italy.

Boone R.B. and W.B. Krohn. 1999. Modeling the occurrence of bird species: Are the errors predictable? Ecological Applications 9:835–848.

Boyce M.S. and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268-272.

Boyce M.S., P.R. Veriner, S.E. Nielsen and F.K.A. Schmiegelow. 2002. Evaluating resources selection function. Ecological Modeling 157:281-300.

Brooks T.M., G.A.B. da Fonseca and A.S.L. Rodrigues. 2004. Species, data and conservation planning. Conservation Biology 18:1682-1688.

Brotons L., W. Thuiller, M.B. Araujo and A.H. Hirzel. 2004. Presence-absence versus presence-only modeling methods for predicting bird habitat suitability. Ecography 27:437-448.

Brown J.H. and M.V. Lomolino. 1998. Biogeography. Sinauer Associates.

Brown J.H., G.C. Stevens and D.M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Reviews of Ecology and Systematic 27:597-623.

Browning D.M., S.J. Beaupré and L. Duncan. 2005. Using partitioned Mahalanobis $D^2(K)$ to formulate a GIS-based model of timber rattlesnake hibernacula. Journal of Wildlife Management 69:33–44.

Burgman M.A., D.R. Breininger, B.W. Duncan and S. Ferson. 2001. Setting reliability bounds on habitat suitability indices. Ecological Applications 11:70–78.

Burgman M.A. and J.C. Fox. 2003. Bias in species range estimates from minimum convex polygons: implication for conservation and options for improved planning. Animal Conservation 6:19-28.

Butterfield B.R., B. Csuti and J.M. Scott. 1994. Modeling vertebrate distributions for Gap Analysis. Pp. 53-68 in Miller R.I. (Ed). Mapping the diversity of nature. Chapman and Hall, London.

Cabeza M., M.B. Araujo, R.J. Wilson, C.D. Thomas, M.J.R. Cowley and A. Moilanen. 2004. Combining probabilities of occurrence with spatial reserve design. Journal of Applied Ecology 41:252-262.

Capen D.E., J.W. Fenwick, D.B. Inkley and A.C. Boynton. 1986. Multivariate models of songbird habitat in New England forests. Pp. 171-175 in Verner J.A., M.L. Morrison and C.J. Ralph (Eds). Wildlife 2000: Modelling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, USA.

Cardillo M., D.W. Macdonald and S.P. Rushton. 1999. Predicting mammal species richness and distributions: testing the effectiveness of satellite-derived land cover data. Landscape Ecology 14:423-435.

Carroll C., R.F. Noss, P.C. Paquet and N. Schumaker. 2003. Use of population viability analysis and reserve selection algorithms in regional conservation plans. Ecological Applications 13:1773-1789.

Carroll C., W.J. Zielinski and R.F. Noss. 1999. Using survey data to build and test spatial habitat models for the fisher (*Martes pennanti*) in the Klamath region, U.S.A. Conservation Biology 13:1344-1359.

Chatfield C. 1995. Model uncertainty, data mining and statistical inference. Journal Royal Statistical Society 158:419–466.

Clark J.D., J.E. Dunn and K.G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519-526.

Clevenger A.P., J. Wierzchowski, B. Chruszcz and K. Gunson. 2002. GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conservation Biology 16:503-514.

Cohen J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement 20:37-46.

Conroy M.J. and C.T. Moore. 2002. Wildlife habitat modeling in an adaptative framework: the role of alternative models. Pp. 205-218 in Scott J.M., Heglund P.J., Morrison M.L., Haufler J.B., Raphael M.G., Wall W.A. and F.B. Samson (Eds). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, CA.

Corsi F. 2004. Applications of existing biodiversity information: capacity to support decision -making. Unpublished PhD, ITC and Wageningen.

Corsi F., I. De Leeuw and A.K. Skidmore. 2000. Modeling species distribution with GIS. Pp. 389-434 in Boitani L. and T.K. Fuller (Eds). Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York.

Corsi F., E. Duprè and L. Boitani, 1999. A large scale model of wolf distribution in Italy for conservation planning. Conservation Biology 13:150-159.

Crosetto M., S. Tarantola and A. Saltelli. 2000. Sensitivity and uncertainty analysis in spatial modeling based on GIS. Agriculture, Ecosystems and Environment 81:71-79.

Crosetto M. and S. Tarantola. 2001. Uncertainty and sensitivity analysis: tools for GIS-based model implementation. International Journal of Geographical Information Science 15:415-437.

Cumming G.S. 2000. Using between-model comparisons to fine-tune linear models of species ranges. Journal of Biogeography 27:441-455.

Delibes M., P. Gaona and P. Ferreras. 2001. Effects of an attractive sink leading into maladaptive habitat selection. The American Naturalist 158:277-285.

Elith E. and M. Burgman. 2002. Predictions and their validation: rare plants in the Central Highlands, Victoria, Australia. Pp. 303-313 in Scott J.M., Heglund P.J., Morrison M.L., Haufler J.B., Raphael M.G., Wall W.A. and F.B. Samson (Eds). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, CA.

Elith J., M.A. Burgman and H.M. Regan. 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distribution. Ecological Modeling 157:313–329.

Engler R., A. Guisan and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology 41:263-274.

Ferrier S., G.V.N. Powell, K.S. Richardson, G. Manion, J.M. Overton, T.F. Allnutt, S.E. Cameron, K. Mantle, N.D. Burgess, D.P. Faith, J.F. Lamoreux, G. Kier, R.J. Hijmans, V.A. Funk, G.A. Cassis, B.L. Fisher, P. Flemons, D. Lees, J.C. Lovett and R.S.A.R. van Rompaey. 2004. Mapping more of terrestrial biodiversity for global conservation assessment. BioScience 54:1101-1109.

Fortin M.J., T.H. Keitt, B.A. Maurer, M.L. Taper, D.M. Kaufman and T.M. Blackburn. 2005. Species' geographic ranges and distributional limits: pattern analysis and statistical issues. Oikos 108:7-17.

Franklin J. 1995. Predictive vegetation mapping: geographic modeling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19:474-499.

Fielding A.H. 2002. What are the appropriate characteristics of an accuracy measure? Pp. 271-280 in Scott J.M., Heglund P.J., Morrison M.L., Haufler J.B., Raphael M.G., Wall W.A. and F.B. Samson (Eds). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, CA.

Fielding A.H. and J.F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38-49.

Franklin J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19:474–499.

Freitag S., A.O. Nicholls and A.S. van Jaarsveld. 1996. Nature reserve selection in the Transvaal, South Africa: what data should we be using? Biodiversity and Conservation 5:685-698.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. 1. Theoretical development. Acta Biotheoretica 19:16-36.

Fretwell, S.D. 1972. Populations in Seasonal Environments. Princeton University Press, Princeton, NJ

Gaston K.J. 1991. How large is a species' geographic range? Oikos 61: 434-438.

Gaston K.J. 1994. Rarity. Chapman and Hall, London.

Gaston K.J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, New York.

Goovaerts P. 2001. Geostatistical modeling of uncertainty in soil science. Geoderma 103:3-26.

Graham C.H., S. Ferrier, F. Huettman, C. Moritz and A.T. Peterson. 2004. New developments in museum based informatics and applications in biodiversity analysis. Trends in Ecology and Evolution 19:497-503.

Gu W. and R.K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biological Conservation 116:195-203.

Guisan A. and J.P. Theurillat. 2000. Equilibrium modeling of alpine plant distribution: how far can we go? Phytocoenologia 30:353-384.

Guisan A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 9:993-1009.

Guisan A. and N.E. Zimmerman. 2000. Predictive habitat distribution models in ecology. Ecological Modeling 135:147-186.

Guo Q., M. Taper, M. Schoenberger and J. Brandle. 2005. Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108:47-57.

Hanski I. 1994. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology and Evolution 9:131-135.

Heglund P.J. 2002. Foundations of species-environment relations. Pp. 35-42 in Scott J.M., P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F.

Samson (Eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Henebry G. and J.W. Merchant. 2002. Geospatial data in time: limits and prospects for predicting species occurrences. Pp. 291-302 in Scott J.M., P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson (Eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Hepinstall J.A., L.P. Quenn and P.A. Jordan. 1996. Applications of a modified habitat suitability index model for moose. Photogrammetric Engineering and Remote Sensing 62:1281-1286.

Higgins J.V., T.H. Ricketts, J.D. Parrish, E. Dinerstein, G. Powell, S. Palminteri, J.M. Hoekstra, J. Morrison, A. Tomasek and J. Adams. 2004. Beyond Noah: saving species is not enough. Conservation Biology 18: 1672-1673.

Hirzel A.H. and A. Guisan. 2002. Which is the optimal sampling strategy for habitat suitability modeling? Ecological Modeling 157:331-341.

Hirzel A.H., G. Le Lay, V. Helfer, C. Randin and A. Guisan. 2006. Evaluating habitat suitability models with presence-only data. Ecological Modeling 199:142-152.

Hirzel, A.H., V., Helfer and F. Métral. 2001. Assessing habitat-suitability models with a virtual species. Ecological Modelling 145:111–121.

Holt R.D., T.H. Keitt, M.A. Lewis, B.A. Maurer and M.L. Taper. 2005. Theoretical models of species' borders: single species approaches. Oikos 108:18-27.

Huston M.A. 2002. Introductory essay: critical issues for improving predictions. Pp. 7-21 in Scott J.M., Heglund P.J., Morrison M.L., Haufler J.B., Raphael M.G., Wall W.A. and F.B. Samson (Eds). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, CA.

IUCN (World Conservation Union), Conservation International and NatureServe. 2004. Global Amphibian Assessment. http://www.globalamphibians.org

IUCN (World Conservation Union) 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK. ii + 30 pp.

Johnson D.H. 1980. The comparison of usage and availability measurements for evaluating resource preferences. Ecology 61:65-71.

Johnson C.J. and M.P. Gillingham. 2005. An evaluation of mapped species distribution models used for conservation planning. Environmental Conservation 32:117–128.

Jones, J. 2001. Habitat selection studies in avian ecologie: a critical review. The Auk 118:556-562.

Jorgensen E.E. and S. Demarais. 1999. Spatial scale dependence of rodent habitat use. Journal of Mammalogy 80:421–429.

Kadmon R., O. Farber and A. Danin. 2004. Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. Ecological Applications 14:401–413.

Karl J.W., P.J. Heglund, E.O. Garton, J.M. Scott, N.M. Wright and R.L. Hutto. 2000. Sensitivity of species habita-relationships model performance to factors of scale. Ecological Applications 10:1690-1705.

Karl J., L. Svancara, P. Heglund, N.M. Wright and J.M. Scott. 2002. Species commonness and the accuracy of habitat relationships models. Pp. 573-580 in Scott J.M., P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson (Eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Kissling M.L. and E.O. Garton. 2006. Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. The Auk 123:735-752.

Krebs C.J. 1978. A review of Chitty's hypothesis of population regulation. Canadian Journal of Zoology 56:2463-2480.

Krebs C.J. 2001. Ecology: the experimental analysis of distribution and abundance. 5th ed. Benjamin Cummings, San Francisco, CA.

Lawes M.J. and S.E. Piper. 1998. There is less to binary maps than meets the eye: the use of species distribution data in the southern African sub-region. South African Journal of Science 94:207–210.

Lawton J.H. 1993. Range, population abundance, and conservation. Trends in Ecology and Evolution 8:409-413.

Leathwick J.R. and M.P. Austin. 2001. Competitive interactions between tree species in New Zealand’s old growth indigenous forests. Ecology 82:2560-2573.

Leibold M.A. 1995. The niche concept revisited: mechanistic models and community context. Ecology 76:1371-1382.

Lek S., M. Delacoste, P. Baran, I. Dimopoulos, J. Lauga and S. Aulagnier. 1996. Application of neural networks to modeling nonlinear relationships in ecology. Ecological Modeling 90:39–52.

Levins R. 1966. The strategy of model building in population ecology. American Scientist 54:421-431.

Loiselle B.A., C.A. Howell, C.H. Graham, J.M. Goerck, T. Brooks, K.G. Smith and P.H. Williams. 2003. Avoiding pitfalls of using species distribution models in conservation planning. Conservation Biology 17:1591-1600.

Luoto M., J. Pöyry, R.K. Heikkinen and K. Saarinen. 2005. Uncertainty of bioclimate envelope models based on the geographical distribution of species. Global Ecology and Biogeography 14:575–584.

Mack E.L., L.G. Firbank P.E. Bellamy S.A. Hinsley and N. Veitch. 1997. The comparison of remotely sensed and ground-based habitat area data using species-area models. Journal of Applied Ecology 34:1222-1228.

MacKenzie D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Mackey B.G. and D.B. Lindenmayer. 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. Journal of Biogeography 28:1147-1166.

Maddock A.H. and M.A. du Plessis. 1999. Can species data only be appropriately used to conserve biodiversity? Biodiversity and Conservation 8:603-615.

Maiorano L., A. Falcucci and L. Boitani. 2006. Gap analysis of terrestrial vertebrates in Italy: priorities for conservation planning in a human dominated landscape. Biological Conservation 133:455-473.

Manel S., J.M. Dias, S.T. Buchton and S.J. Ormerod. 1999. Alternative methods for predicting species distribution: an illustration with Himalayan river birds. Journal of Applied Ecology 36:734-747.

Manel S., H.C. Williams and S.J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38:921-931.

Manly B.F.J., L.L. McDonald, D.L. Thomas, T.L.McDonald and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluver Academic Press.

Margules C.R. and M.P. Austin. 1991. Nature conservation: cost effective biological survey and data analysis. CSIRO, Canberra, Australia.

Margules C.R. and M.P. Austin, 1994. Biological models for monitoring species decline: the construction and use of data bases. Philosophical Transactions of the Royal Society of London 344: 69-75.

McPherson J.M., W. Jetz and D.J. Rogers. 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? Journal of Applied Ecology 41:811–823.

McPherson J.M., W. Jetz and D.J. Rogers. 2006. Using coarse-grained occurrence data to predict species distributions at finer spatial resolutions – possibilities and limitations. Ecological Modeling 192:499-522.

Mitchell-Jones A.J., G. Amori,W. Bogdanowicz, B. Kryštufek, P.J.H. Reijnders, F. Spitzenberger, M. Stubbe, J.B.M. Thissen, V. Vohralìk and J. Zima. 2002. The atlas of European mammals. Poyser Natural History, London.

Moisen G.G., E.A. Freeman, J.A. Blackard, T.S. Frescino, N.E. Zimmermann and T.C. Edwards Jr. 2006. Predicting tree species presence and basal area in Utah: a comparison of stochastic gradient boosting, generalized additive models, and tree-based methods. Ecological Modelling 199:176-187.

Molinari P., L. Rotelli and M. Catello. 2001. Present status and distribution of the Eurasian lynx (*Lynx lynx*) in the Italian Alps. Hystrix – Italian Journal of Mammalogy 12:3-9.

Morrison M.L., B.G. Marcot and R.W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. The University of Wisconsin Press, Madison.

Newbold S. and J.M. Eadie. 2004. Using species-habitat models to target conservation: a case study with breeding mallards. Ecological Applications 14:1384-1393.

Nicholls A.O. 1989. How to make biological surveys go further with generalised linear models. Biological Conservation 50:51–75.

Nichols J.D., J.E. Hines, J.R. Sauer, F.W. Fallon, J.W. Fallon and P.J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. The Auk 117:393-408.

Norton T.W. and H.P. Possingham. 1993. Wildlife modelling for biodiversity conservation: a review and future directions. Pp. 243-266 in Jakeman A.J., B. Beck and M. McAleer (Eds). Modeling Change in Environmental Systems. John Wiley and Sons Ltd.

Oreskes N., K. Shrader-Frechette and K. Belitz. 1994. Verification, validation, and confirmation of numerical models in the Earth Sciences. Science 263:641-646.

Osborne P.W., J.C. Alonso and R.G. Bryant. 2001. Modeling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. Journal of Applied Ecology 38:458-471.

Osborne P.E. and S. Suarez-Seoane. 2002. Should data be partitioned spatially before building large-scale distribution models? Ecological Modeling 157:249-259.

Pausas J.G., L.W. Braithwaite and M.P. Austin. 1995. Modeling habitat quality for arboreal marsupials in the South Coastal forests of New South Wales. Forest Ecology and Management 78:39-49.

Pearce J.L. and M.S. Boyce. 2006. Modeling distribution and abundance with presence-only data. Journal of Applied Ecology 43:405–412.

Pearce J.L. and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modeling 133:225-245.

Pearce J.L., L.A. Venier, S. Ferrier and D.W. McKenney. 2002. Measuring prediction uncertainty of species distribution. Pp. 383-390 in Scott J.M., P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson (Eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Pearson R.G. and T.P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361-371

Pearson R.G., Dawson T.E. and C. Liu. 2004. Modeling species distribution in Britain: a hierarchical integration of climate and land cover data. Ecography 27:285-298.

Pearson R.G., W. Thuiller, M.B. Araújo, E. Martinez-Meyer, L. Brotons, C. McClean, L. Miles, P. Segurado, T.P. Dawson and D.C. Lees. 2006. Model-based uncertainty in species range prediction. Journal of Biogeography 33:1704-1711.

Pereira J.M. and R.M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. Photogrammetric Engineering and Remote Sensing 57:1475-1486.

Phillips S.J., R.P. Anderson and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modeling 190:231-259.

Pontius Jr. R.G. 2000. Quantification error versus location error in comparison of categorical maps. Photogrammetric Engineering and Remote Sensing 66:1011-1016.

Pontius Jr. R.G. and M.L. Cheuk. 2006. A generalized cross-tabulation matrix to compare soft-classified maps at multiple resolutions, International Journal of Geographical Information Science 20:1-30.

Pulliam H.R. 1988. Sources, sinks and population regulation. American Naturalist 132:652-661.

Pulliam H.R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349-361.

Randin C.F., T. Dirnböck, S. Dullinger, N.E. Zimmermann, M. Zappa and A. Guisan. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33:1689-1703.

Rapoport E.H. 1982. Aerography: Geographical Strategies of Species. Pergamon Press, New York.

Ray N. and M.A. Burgman. 2006. Subjective uncertainties in habitat suitability maps. Ecological Modeling 195:172-186

Reddy S and L.M. Davalos. 2003. Geographical sampling bias and its implications for conservation priorities in Africa. Journal of Biogeography 30:1719-1727.

Regan H.M., M. Colyvan and M.A. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecological Applications 12:618-628.

Robertson M.P., N. Caithness and M.H. Villet. 2001. A PCA-based modeling technique for predicting environmental suitability for organisms from presence records. Diversity and Distribution 7:15–27.

Robertson B.A. and R.L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075-1085.

Rodrigues A.S.L., S.J. Andelman, M.I. Bakarr, L. Boitani, T.M. Brooks, R.M. Cowling, L.D.C. Fishpool, G.A.B. da Fonseca, K.J. Gaston, M. Hoffmann, J.S. Long, P.A. Marquet, J.D. Pilgrim, R.L. Pressey, J. Schipper, W. Sechrest, S.N. Stuart, L.G. Underhill, R.W. Waller, M.E.J. Watts and X. Yan. 2003. Global gap analysis: towards a representative network of protected areas. Advances in Applied Biodiversity Science 5. Conservation International, Washington D.C., USA.

Rodrigues A.S.L., S.J. Andelman, M.I. Bakarr, L. Boitani, T.M. Brooks, R.M. Cowling, L.D.C. Fishpool, G.A.B. da Fonseca, K.J. Gaston, M. Hoffmann, J.S. Long, P.A. Marquet, J.D. Pilgrim, R.L. Pressey, J. Schipper, W. Sechrest, S.N. Stuart, L.G. Underhill, R.W. Waller, M.E.J. Watts and X. Yan. 2004. Effectiveness of the global protected area network in representing species diversity. Nature 428:640-643.

Rondinini C., S. Stuart and L. Boitani. 2005. Habitat suitability models and the shortfall in conservation planning for African vertebrates. Conservation Biology 19:1488-1497.

Rotenberry J.T., S.T. Knick and J.E. Dunn. 2002. A minimalist approach to mapping species habitat: Pearson’s planes of closest fit. Pp. 281–289 in Scott J.M., P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson (Eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Rykiel E.J. 1996. Testing ecological models: the meaning of validation. Ecological Modeling 90:229-244.

Rushton S.P., S.J. Ormerod and G. Kerby. 2004. New paradigms for modeling species distributions? Journal of Applied Ecology 41:193-200.

Schadt S., E. Revilla, T. Wiegand, F. Knauer, P. Kaczensky, U. Breitenmoser, L. Bufka, J. Cerveny, P. Koubek, T. Huber, C. Stanisa and L. Trepl. 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. Journal of Applied Ecoloy 39:189-203.

Schamberger M.L. and L.J. O'Neil. 1986. Concepts and constraints of habitat-model testing. Pp 5-10 in Verner J., M.L. Morrison and C.J. Ralph (Eds). Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Scott J.M., P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson (Eds.). 2002. Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Segurado P. and M.B. Araújo. 2004. Evaluation of methods for modeling species probabilities of occurrence. Journal of Biogeography 31:1555-1568.

Sindaco R. Doria G., Razzetti E. and F. Bernini (Eds). 2006. Atlas of Italian amphibians and reptiles. Societas Herpetologica Italica, Edizioni Polistampa, Firenze.

Sitati N.W., M.J. Walpole, R.J. Smith and N. Leader-Williams. 2003. Predicting spatial aspects of human–elephant conflict. Journal of Applied Ecology 40:667-677.

Smallwood K.S. 2002. Habitat models based on numerical comparisons. Pp. 83-95 in Scott J.M., P.J. Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson (Eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

Starfield AM. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61:261–270.

Stockwell D.R.B. and A.T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. Ecological Modeling 148:1-13.

Stoms D.M., F.W. Davis and C. Cogan. 1992 Sensitivity of wildlife habitat models to uncertainties in GIS data. Photogrammetric Engineering and Remote Sensing 58:843-850.

Svenning J.C. and F. Skov. 2004. Limited filling of the potential range in European tree species. Ecology Letters 7:565-573.

Thuiller W., M.B. Araújo and S. Lavorel. 2004. Do we need land cover data to model species distribution in Europe? Journal of Biogeography 31:353-361.

Thuiller W., O. Broennimann, G. Gughes, R. Alkemade, G.F. Midgley and F. Corsi. 2006a. Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. Global Change Biology 12:424-440.

Thuiller W., S. Lavorel, M.T. Sykes and M.B. Araújo. 2006b. Using niche-based modeling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distributions 12: 49-60.

Thuiller W., D.M. Richardson, P. Pyšek, G.F. Midgley, G.O. Hughes and M. Rouget. 2005. Niche-based modeling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11:2234-2250.

Tobalske C. and B.W. Tobalske. 1999. Using atlas data to model the distribution of woodpecker species in the Jura, France. The Condor 101:472-483.

Townsed Peterson A., Ortega-Huerta M.A., Bartley J., Sanchez-Cordero V., Sobéronk J., Buddemeier R.H. and D.R.B. Stockwell. 2003. Future projections for Mexican faunas under global climate change scenarios. Nature 416:626-629.

Treves A., L. Naughton-Treves, E.K. Harper, D.J. Mladenoff, R.A. Rose, T.A. Sickley and A.P. Wydeven. 2004. Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. Conservation Biology 18:114-125.

Tyre A.J., H.P. Possingham and D.B. Lindenmayer. 2001. Inferring process from pattern: can territory occupancy provide information about life history parameters? Ecological Applications 11:1722-1737.

van Horne B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

van Horne B. 2002. Approaches to habitat modeling: the tensions between pattern and process and between generality and specificity. Pp. 63-72 in Scott J.M., P.J.

Heglund, J.B. Haufler, M. Morrison, M.G. Raphael, W.B. Wall and F. Samson (Eds.). Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California.

van Jaarsveld A.S., K.J. Gaston, S.L. Chown and S. Freitag. 1998. Throwing biodiversity out with the binary data? South African Journal of Science 94:210–214.

Vaughan I.P. and S.J. Ormerod. 2003. Modeling the distribution of organisms for conservation: optimizing the collection of field data for model development. Conservation Biology 17:1601-1611.

Vaughan I.P. and S.J. Ormerod. 2005. The continuing challenges of testing species distribution models. Journal of Applied Ecology 42:720-730.

Verbyla D.L. and J.A. Litvaitis. 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. Environmental Management 13:783-787.

Verner J., Morrison M.L. and C.J. Ralph. 1986. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

Walters C. 1992. Trends in applied ecological modeling. Pp. 117-122 in McCullough D.R. and R.H. Barrett (Eds). Wildlife 2001: populations. Elsevier Science, London, UK.

White G.C. and R.A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.

Whittaker, R. H., S. A. Levin and R. B. Root. 1973. Niche, Habitat, and Ecotope. The American Naturalist 107:321-338.

Wiens J.A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Williams P., L. Hannah, S. Andelman, G. Midgley, M.A. Araújo, G. Hughes, L. Manne, E. Martinez-Meyer and R. Pearson. 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conservation Biology 19:1063-1074.

Williams P.H., C.R. Margules and D.W. Hilbert. 2002. Data requirements and data sources for biodiversity priority area selection. Journal of Bioscience 27 (suppl. 2):327-338.

Williams P.H., G.T. Prance, C.J. Humphries and K.S. Edwards. 1996. Promise and problems in applying quantitative complementary areas for representing the diversity of some neotropical plants (families Dichaperalaceae, Lecythidaceae, Caryocaraceae, Chrysobalanaceae and Proteaceae). Biological Journal of the Linnean Society 58:125-157.

Wilson K.A., M.I. Westphal, H.P. Possingham and J. Elith. 2005. Sensitivity of conservation planning to different approaches to using predicted species distribution data. Biological Conservation 122:99-112.

Zunino M. and A. Zullini. 2004. Biogeografia: la dimensione spaziale dell’evoluzione. Casa Editrice Ambrosiana, Milano.

CHANGES IN LAND-USE/LAND-COVER PATTERNS IN ITALY AND THEIR IMPLICATIONS FOR BIODIVERSITY CONSERVATION[1]

Introduction

Habitat loss is usually regarded as one of the most important factors causing the global biodiversity crisis (Sala et al. 2000) and, in general, it has been proved to be a remarkably good predictor of the number of threatened or extinct endemic species in biodiversity hotspots (Brooks et al. 2002). Land-use/land-cover changes and the associated habitat loss are a consequence of natural and human driven processes (Houghton 1994; Ojima et al. 1994; Pimm et al. 1995; Vitousek et al. 1997; Pimm and Lawton 1998; Sanderson et al. 2002), and many studies indicate high rates of change since the 1970s associated to high human population growth rates, land-use intensification, and loss of natural habitat (Houghton 1994; Dobson et al. 1997; Matson et al. 1997; Lambin et al. 2003; Sodhi et al. 2004; Brown et al. 2005; Lepers et al. 2005).

The Mediterranean basin, one of the four most significantly altered hotspots on Earth (Myers et al. 2000), has been intensively affected by human populations for thousands of years especially along the coasts, significantly longer than any other hotspot (Covas and Blondel 1998; Lavorel et al. 1998; Blondel and Aronson 1999; Vallejo et al. 2005). As a result, only 4.7% of its primary vegetation remains; the agricultural lands, evergreen woodlands and maquis habitats that dominate the hotspot today are the result of anthropogenic disturbances over several millennia. However, the integration of natural ecosystems and traditional human activities is one of the reasons for the high environmental diversity that characterizes the region (Balletto and Casale 1991; Cowling et al. 1996; Preiss et al. 1997; Blondel and Aronson 1999; Heywood 1999; Lobo et al. 2001).

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In the last 40 years, a particular pattern of land-use/land-cover change has taken place in the Mediterranean basin, especially in Mediterranean Europe: plains are being increasingly utilized, hilly and mountain areas are being abandoned by humans and naturally reforested, human settlements are quickly increasing along the coastline, with resident population doubling every 30 years and tourist presence doubling every 15 years (UNEP 1989; Ales et al. 1992; Garcia-Ruiz et al. 1996; Debussche et al. 1999; MacDonald et al. 2000; Santos 2000; Lambin et al. 2003).

These new patterns are largely independent from planned conservation strategies and appear to have a substantial impact on landscape and biodiversity (Ales et al. 1992; Covas and Blondel 1998; Tellini-Florenzano 2004), especially because they affect large areas. However, most of the studies on land-use/land-cover change in the Mediterranean have concerned limited areas (Garcia-Ruiz et al. 1996; Preiss et al. 1997; Debussche et al. 1999), and have not analyzed the large scale effects of these patterns. Moreover, most of the studies used very different datasets, going from land-use/land-cover data obtained from postcards (Debussche et al. 1999) to the United Nations FAO's Production Yearbooks (Lambin et al. 2003), that lacks any spatially explicit detail inside the country level. The high heterogeneity of the datasets, together with the relatively small study areas that are usually considered, can generate spurious results and incompatibilities in the resulting rates of change (William and Turner 1992), making it particularly difficult to extrapolate the results outside the study areas and to obtain clear and consistent conservation indications for the Mediterranean basin.

In this paper, we have measured the land-use/land-cover changes that have occurred in the last 40 years in the entire Italian peninsula and we have explored their conservation implications. We have related the trends in land-use/land-cover change to human population changes during the same period and we have provided measures of uncertainty associated to these rates of changes.

Methods

We used three land-use/land-cover maps covering Italy and spanning the time frame 1960–2000. The Map of Land Cover (MLC1960) was produced from 1956 to 1968 by the National Research Council using cadastral datasets at a geographic scale of

1:200,000, with a legend of 22 classes. The CORINE Land Cover maps were produced in 1990 (CLC1990) and in 2000 (CLC2000). The two maps are part of the program started in 1985 by the European Community to generate digital land-use/land-cover maps covering the European continent (EC 1993). The maps have a legend of 44 classes and a spatial detail comparable to that of a paper map on a scale of 1:100,000. The maps were produced using satellite images (Landsat5 TM for CLC1990 and Landsat7 ETM+ for CLC2000) and other ancillary data (Digital Elevation Model, hydrology, and aerial photos).

The Italian Institute of Statistics provided data on the human population for the period 1960–2000. The data were obtained from national censuses and geo-referenced using the same administrative boundaries used as basic units for the censuses. We used maps of human population for 1960, 1990 and 2000.

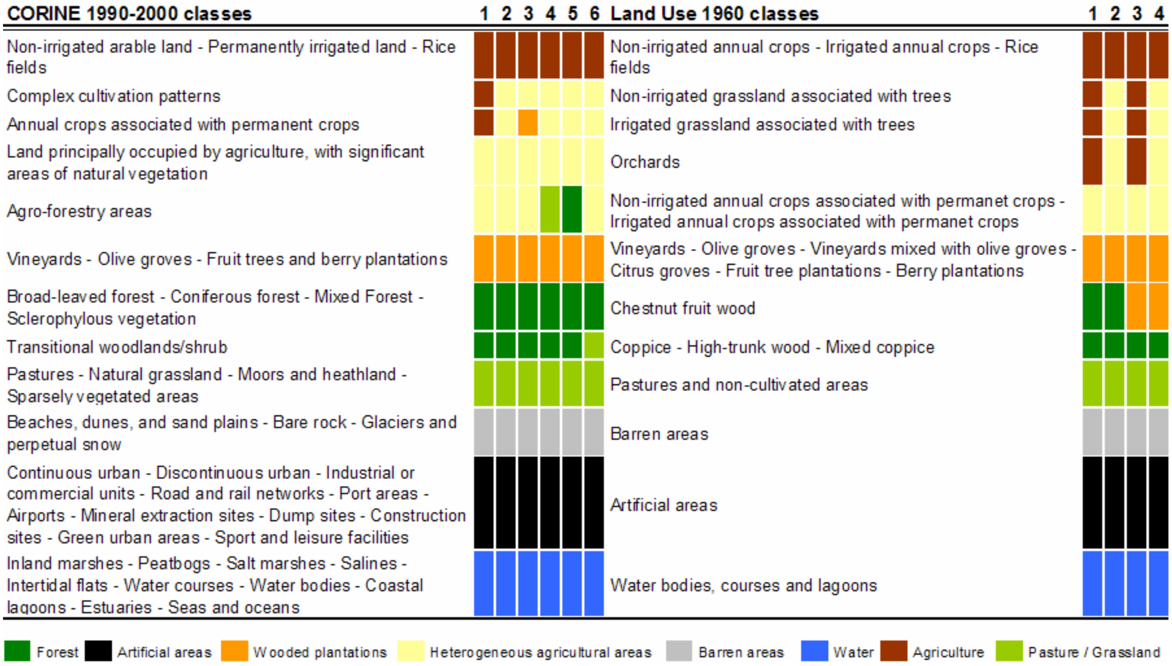
Analysis of changes

Combining heterogeneous data for land-use/land-cover change analysis requires a prior equalization of their thematic and spatial characteristics (Petit and Lambin 2002). In our case, the legend and spatial scale of MLC1960 are different from those of the two CLC maps, and the datasets had to be integrated.

However, both spatial and thematic aggregation of land-use/land-cover maps generate spurious results and errors, usually classified as: (1) spatial aggregation errors, associated with different levels (coarser or finer) of aggregation and with a change in data models (change from coverage to raster), (2) classification errors and (3) thematic aggregation errors (Moody and Woodcock 1994). We used different combinations of spatial and thematic aggregation in order to evaluate these errors and to estimate the reliability of the change detection analysis.

We reclassified each map in order to obtain eight land-use/land-cover categories (thematic generalization sensu Petit and Lambin 2002): ‘‘agricultural areas’’ (AGRICULTURE), ‘‘heterogeneous agricultural areas’’ (HETEROGENEOUS), ‘‘wooded cultivations’’ (WOODED), ‘‘forests’’ (FOREST), ‘‘pastures and grasslands’’ (PASTURE), ‘‘barren areas’’ (BARREN), ‘‘artificial areas’’ (ARTIFICIAL), and ‘‘water’’ (WATER). The matching of the 44 classes of the CLC and the final land-use/land-cover classes was carried out according to the definitions given in Bossard et al. (2000). The matching of the 22 classes of the MLC1960 and the final land-use/land-cover classes was carried out following the Memorie Illustrative, Maps of Soil Utilization, National Research Council.

Different classification options were available on the basis of the definitions of the land-use/land-cover classes in the original legends (e.g. the class "Chestnut woods" in the MLC1960 could be reclassified in the final legend as FOREST or as WOODED; on the contrary, the class "Artificial areas" in the MLC1960 can only be reclassified as ARTIFICIAL; Fig. 1). We performed six alternative thematic aggregations for the CLC legend and four for the MLC1960, giving a total of 24 combinations for the time frame 1960–1990 (4 in 1960 by 6 in 1990), and a total of six combinations for the time frame 1990–2000 (each trial in 1990 compared with the corresponding trial from 2000).



CORINE 1990-2000 classes	1	2	3	4	5	6
Non-irrigated arable land - Permanently irrigated land - Rice fields	🟫	🟫	🟫	🟫	🟫	🟫
Complex cultivation patterns	🟫	🟨	🟨	🟨	🟨	🟨
Annual crops associated with permanent crops	🟫	🟨	🟧	🟨	🟨	🟨
Land principally occupied by agriculture, with significant areas of natural vegetation	🟨	🟨	🟨	🟨	🟨	🟨
Agro-forestry areas	🟨	🟨	🟨	🟢	🟩	🟨
Vineyards - Olive groves - Fruit trees and berry plantations	🟧	🟧	🟧	🟧	🟧	🟧
Broad-leaved forest - Coniferous forest - Mixed Forest - Sclerophylous vegetation	🟩	🟩	🟩	🟩	🟩	🟩
Transitional woodlands/shrub	🟩	🟩	🟩	🟩	🟩	🟢
Pastures - Natural grassland - Moors and heathland - Sparsely vegetated areas	🟢	🟢	🟢	🟢	🟢	🟢
Beaches, dunes, and sand plains - Bare rock - Glaciers and perpetual snow	⬜	⬜	⬜	⬜	⬜	⬜
Continuous urban - Discontinuous urban - Industrial or commercial units - Road and rail networks - Port areas - Airports - Mineral extraction sites - Dump sites - Construction sites - Green urban areas - Sport and leisure facilities	⬛	⬛	⬛	⬛	⬛	⬛
Inland marshes - Peatbogs - Salt marshes - Salines - Intertidal flats - Water courses - Water bodies - Coastal lagoons - Estuaries - Seas and oceans	🟦	🟦	🟦	🟦	🟦	🟦

Land Use 1960 classes	1	2	3	4
Non-irrigated annual crops - Irrigated annual crops - Rice fields	🟫	🟫	🟫	🟫
Non-irrigated grassland associated with trees	🟫	🟨	🟫	🟨
Irrigated grassland associated with trees	🟫	🟨	🟫	🟨
Orchards	🟫	🟨	🟫	🟨
Non-irrigated annual crops associated with permanet crops - Irrigated annual crops associated with permanet crops	🟨	🟨	🟨	🟨
Vineyards - Olive groves - Vineyards mixed with olive groves - Citrus groves - Fruit tree plantations - Berry plantations	🟧	🟧	🟧	🟧
Chestnut fruit wood	🟩	🟩	🟧	🟧
Coppice - High-trunk wood - Mixed coppice	🟩	🟩	🟩	🟩
Pastures and non-cultivated areas	🟢	🟢	🟢	🟢
Barren areas	⬜	⬜	⬜	⬜
Artificial areas	⬛	⬛	⬛	⬛
Water bodies, courses and lagoons	🟦	🟦	🟦	🟦

🟩 Forest ⬛ Artificial areas 🟧 Wooded plantations 🟨 Heterogeneous agricultural areas ⬜ Barren areas 🟦 Water 🟫 Agriculture 🟢 Pasture / Grassland

Figure 1. "Rosetta stone" for possible land-use/land-cover classifications. The final reclassification schemes (six possibilities for the Corine Land Cover maps and four possibilities for the map of land use) are provided together with the original legends.

In order to obtain three spatially homogeneous layers, we transformed the three maps from the original vector data format to the raster data format, assigning the same origin, extent and cell size to each raster. To account for the inherently scale dependency of landscape patterns (Turner et al. 1989; Wu 2004) we performed the analyses using five different cell sizes: 100, 200, 300, 400, and 500 m.

Thus, we obtained 120 possible combinations for 1960 vs. 1990 (24 thematic combinations times 5 pixel sizes) and 30 possible combinations for 1990 vs. 2000 (6 thematic combinations times 5 pixel sizes).

We then performed a land-use/land-cover change detection for pairs of successive maps, using post-classification comparisons (Petit and Lambin 2002). This method, despite its limitations (Coppin and Bauer 1996), was the only available option, primarily because no collateral spectral information was available for 1960. We used the function CROSSTAB in Idrisi Andes over all the possible combinations, and we obtained the mean change and the standard deviation for 1960 vs. 1990 and for 1990 vs. 2000.

The land-use/land-cover change detection was performed on a national scale as well as for six relatively distinct ecological macro-regions (Fig. 2): the Alps, the Apennines, the Po river plain, the coastal areas, the island of Sardinia and the island of Sicily. The macro-regions were identified using geographic, geomorphologic and bioclimatic factors (Tomaselli et al. 1973) together with national and international agreements (Alpine Convention 96/191/CE; http://www.convenzionedellealpi.org/index; APE—Apennines Park of Europe G.U. 29/03/2001).

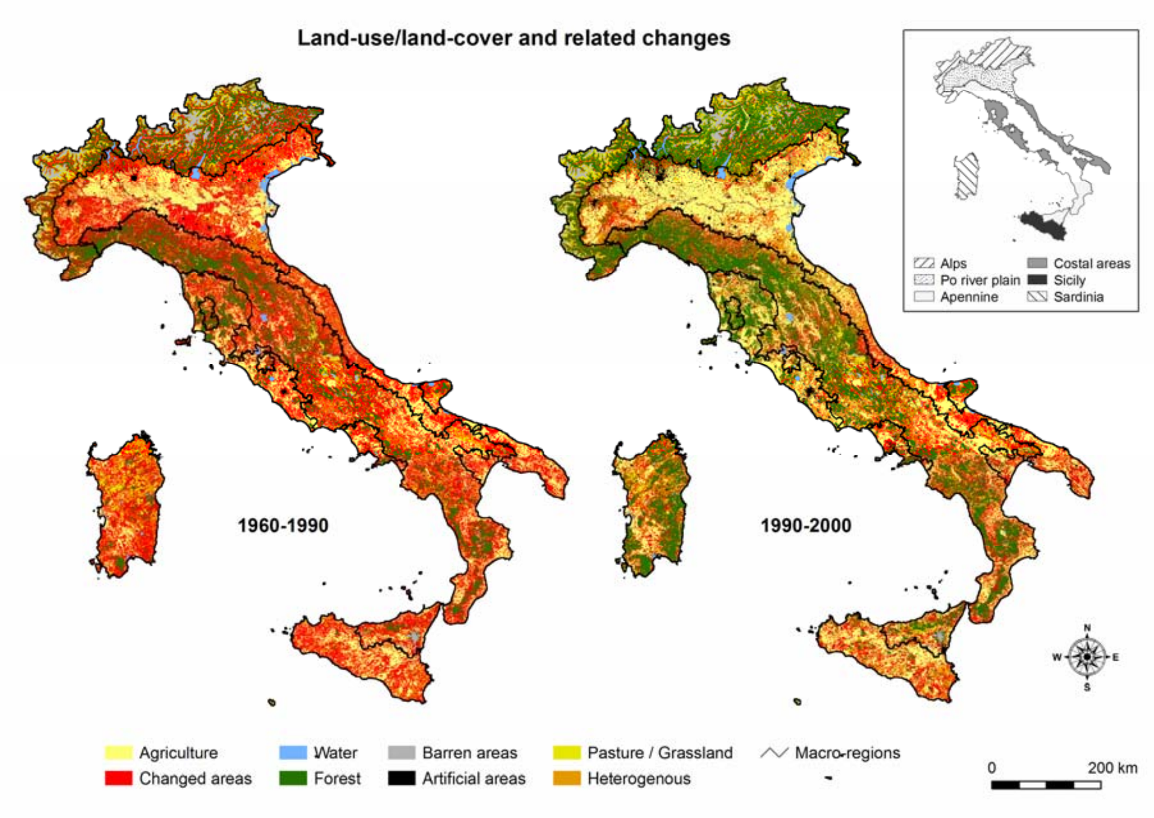


Figure 2. Land-use/land-cover change for 1960-1990 and for 1990-2000 with macro-regions distribution. The areas where no change was detected are represented following the legend given in Table 1.

Land-use/land-cover change and human population change

We investigated the relationship between land-use/land-cover changes and human population changes calculating, for each of the 8,100 administrative units (called comuni), the rate of change of human population considering 1960 as a baseline. We calculated the rates of change for FOREST, PASTURE and total agriculture (the sum of AGRICULTURE, HETEROGENEOUS and WOODED), taking 1960 as the baseline. Then, for each land-use/land-cover types considered, we classified the administrative units into two groups: those where the land-use/land-cover class increased and those where the land-use/land-cover class decreased from 1960 to 1990. The same was done for the 1990–2000 period.

We used the above classification to test the significance of the differences in the rate of change of human population using a median test (normal approximation in SAS8.2; PROC UNIVARIATE) for the time frame 1960–1990. We chose the median test due to large changes in human population through the 30-years period. For the time frame 1990–2000, we tested the significance of the differences using a Wilcoxon test (normal approximation in SAS8.2; PROC UNIVARIATE) as there were no extreme observations.

Error checking

We explicitly included in the analyses the variability linked to thematic aggregation errors and to one of the components of spatial aggregation errors. However, we have not included spatial aggregation errors associated with changes in data models (changes from coverage to raster) and classification errors.

No measure of classification errors was possible for the MLC1960 map, as no collateral information was readily available at the necessary scale and resolution. For both CLC maps Büttner et al. (2004) measured a thematic accuracy greater than 85% across the European continent.

We measured the spatial aggregation error associated with the transformation from vector to raster comparing the composition of MLC1960 in the vector format with the mean composition in the raster format with five different cell sizes: 100, 200, 300, 400, and 500 m. For each land-use/land-cover class we calculated the percentage of area lost or gained with the transformation. We made the same measurements for CLC1990 and CLC2000.

Results

Change in land-use/land-cover

In the time frame 1960–1990, 51.63% (±2.31%) of the Italian peninsula changed from one land-use/land-cover class to another. In the time frame 1990–2000, changes in land-use/land-cover occurred for 23.34% (±1.51%) of the Italian peninsula (Fig. 2).

In the 1960s, the agricultural land-use classes dominated the Italian landscape (58.12%), in particular with AGRICULTURE (37.89%) and HETEROGENEOUS (10.44%). ARTIFICIAL covered a small percentage of the national territory (1.34%), while FOREST and PASTURE occupied, respectively, 18.70 and 18.72% (Fig. 3).

In 1990, agriculture was still the dominant feature in Italy (51.86%), AGRICULTURE (28.44%) and HETEROGENEOUS (16.09%) being the two most important components. We found a marked increase for the ARTIFICIAL (from 1.34% in the 1960s to 3.98% in the 1990s) and FOREST (from 18.70 to 30.58%), and a marked decrease for PASTURE (from 18.72 to 10.09%) (Fig. 3).

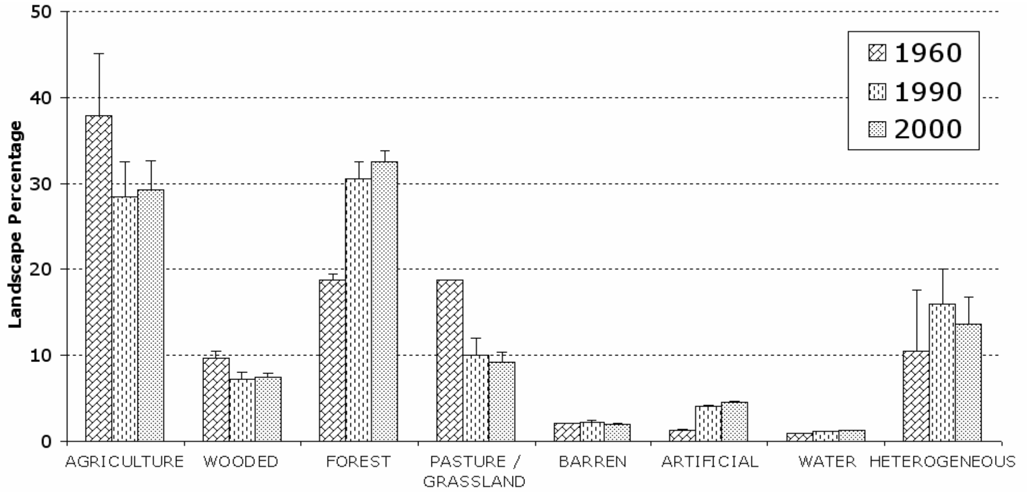


Figure 3. Percentage of the Italian peninsula occupied by the different land-use/land-cover classes.

In 2000, agriculture was still the dominant land-use class (50.46%), and AGRICULTURE and HETEROGENEOUS were the prominent components (respectively, 29.31 and 13.65% of Italy). ARTIFICIAL increased from 3.98% in the 1990s to 4.55% in 2000, FOREST increased from 30.58 to 32.54%, and PASTURE decreased from 10.09 to 9.23% (Fig. 3).

The geographical distribution of the different land-use/land-cover classes was about the same in the three maps. AGRICULTURE was found mainly on plains, coasts and islands, as well as ARTIFICIAL. The more ''natural'' land-use/land-cover classes (e.g., FOREST and PASTURE) were found mostly in the mountain areas, where most of the changes occurred.

Comparing MLC1960 and CLC1990, AGRICULTURE, FOREST, BARREN, ARTIFICIAL, and WATER were the classes that showed the greater stability (all of them remained unchanged for more than 50% of their extent; Table 1); all other classes were stable for less than 35%. Notable are the changes occurred to PASTURE, with high percentage of change towards AGRICULTURE, HETEROGENEOUS and FOREST in particular, and to HETEROGENEOUS, with high percentage of changes towards AGRICULTURE and FOREST.

Comparing CLC1990 and CLC2000, all land-use/land-cover classes remained stable for more than 56% of their extent (Table 2). The most important changes occurred to PASTURE (mainly with changes to FOREST), to HETEROGENEOUS (mainly towards other agricultural land classes and towards FOREST), and to WOODED (mainly to HETEROGENEOUS and to FOREST).

		MLC1960							
		BARREN	**PASTURE**	**FOREST**	**WATER**	**AGRIC**	**HETER**	**ARTIFICIAL**	**WOODED**
CLC1990	**BARREN**	1.25 (0.00)	0.75 (0.02)	0.11 (0.01)	0.01 (0.00)	0.12 (0.02)	0.03 (0.02)	0.00 (0.00)	0.04 (0.00)
	PASTURE	0.50 (0.05)	5.19 (0.77)	1.33 (0.48)	0.01 (0.00)	2.03 (0.39)	0.70 (0.19)	0.02 (0.01)	0.29 (0.09)
	FOREST	0.27 (0.05)	7.92 (0.84)	14.58 (0.81)	0.06 (0.00)	4.24 (0.78)	1.89 (0.68)	0.06 (0.01)	1.55 (0.61)
	WATER	0.01 (0.00)	0.15 (0.00)	0.04 (0.00)	0.76 (0.00)	0.13 (0.02)	0.03 (0.02)	0.03 (0.00)	0.01 (0.00)
	AGRIC	0.04 (0.01)	2.04 (0.21)	0.86 (0.15)	0.06 (0.01)	19.89 (3.87)	3.93 (3.36)	0.17 (0.04)	1.43 (0.93)
	HETER	0.04 (0.01)	2.02 (0.24)	1.22 (0.17)	0.03 (0.00)	7.50 (2.77)	2.52 (2.08)	0.15 (0.04)	2.62 (0.91)
	ARTIFICIAL	0.03 (0.00)	0.23 (0.01)	0.15 (0.01)	0.01 (0.00)	1.48 (0.49)	0.69 (0.48)	0.86 (0.01)	0.52 (0.02)
	WOODED	0.02 (0.00)	0.43 (0.07)	0.39 (0.05)	0.01 (0.00)	2.49 (0.69)	0.64 (0.60)	0.05 (0.00)	3.31 (0.27)

Table 1. Land-use/land-cover change (measured as a percentage of the total study area) for the time span 1960 – 1990. The table shows the mean value and, in parentheses, the standard deviation obtained with the 120 possible combinations for 1960 versus 1990. (AGRIC = Agriculture; HETER = Heterogeneous).

		CLC1990							
		BARREN	**PASTURE**	**FOREST**	**WATER**	**AGRIC**	**HETER**	**ARTIFICIAL**	**WOODED**
CLC2000	**BARREN**	1.67 (0.02)	0.16 (0.02)	0.08 (0.02)	0.01 (0.00)	0.02 (0.00)	0.03 (0.01)	0.01 (0.00)	0.01 (0.00)
	PASTURE	0.42 (0.02)	6.12 (0.97)	1.37 (0.07)	0.01 (0.00)	0.53 (0.08)	0.61 (0.15)	0.04 (0.01)	0.13 (0.03)
	FOREST	0.14 (0.02)	2.36 (0.64)	26.85 (1.78)	0.03 (0.00)	0.77 (0.22)	1.74 (0.20)	0.09 (0.01)	0.56 (0.07)
	WATER	0.02 (0.00)	0.02 (0.00)	0.04 (0.00)	1.07 (0.01)	0.05 (0.01)	0.03 (0.01)	0.02 (0.00)	0.01 (0.00)
	AGRIC	0.03 (0.00)	0.70 (0.08)	0.64 (0.15)	0.04 (0.01)	24.06 (3.41)	2.76 (0.65)	0.27 (0.08)	0.81 (0.32)
	HETER	0.02 (0.00)	0.55 (0.19)	1.21 (0.19)	0.02 (0.00)	1.66 (0.28)	8.97 (2.29)	0.21 (0.07)	1.01 (0.36)
	ARTIFICIAL	0.01 (0.00)	0.07 (0.01)	0.11 (0.01)	0.01 (0.00)	0.51 (0.12)	0.41 (0.12)	3.27 (0.08)	0.15 (0.02)
	WOODED	0.01 (0.01)	0.11 (0.02)	0.27 (0.05)	0.00 (0.00)	0.84 (0.60)	1.54 (0.60)	0.07 (0.01)	4.65 (0.38)

Table 2. Land-use/land-cover change (measured as a percentage of the total study area) for the time span 1990 – 2000. The table shows the mean value and, in parentheses, the standard deviation obtained with the 30 possible combinations for 1990 versus 2000. (AGRIC = Agriculture; HETER = Heterogeneous).

Land-use/land-cover changes occurred with different intensities in the various part of the peninsula (Fig. 4). PASTURE decreased markedly in all Italy, but particularly in the Apennines, in the coastal areas and in Sardinia. On the contrary, FOREST increased in all Italy, almost doubling its extension in the Alps and the Apennines and increasing even more in Sardinia. AGRICULTURE decreased in the Alps, in the Apennines, in the coastal areas and in Sicily, but it increased in the rest of Italy. HETEROGENEOUS and WOODED followed a more complex trend, with important changes especially in Sardinia, where we measured a marked increase in HETEROGENEOUS. ARTIFICIAL increased throughout the peninsula: coastal areas, Sardinia, Sicily and the Po river plain showed a marked increase, while only a limited increase was measured in the Apennines and, especially, in the Alps.

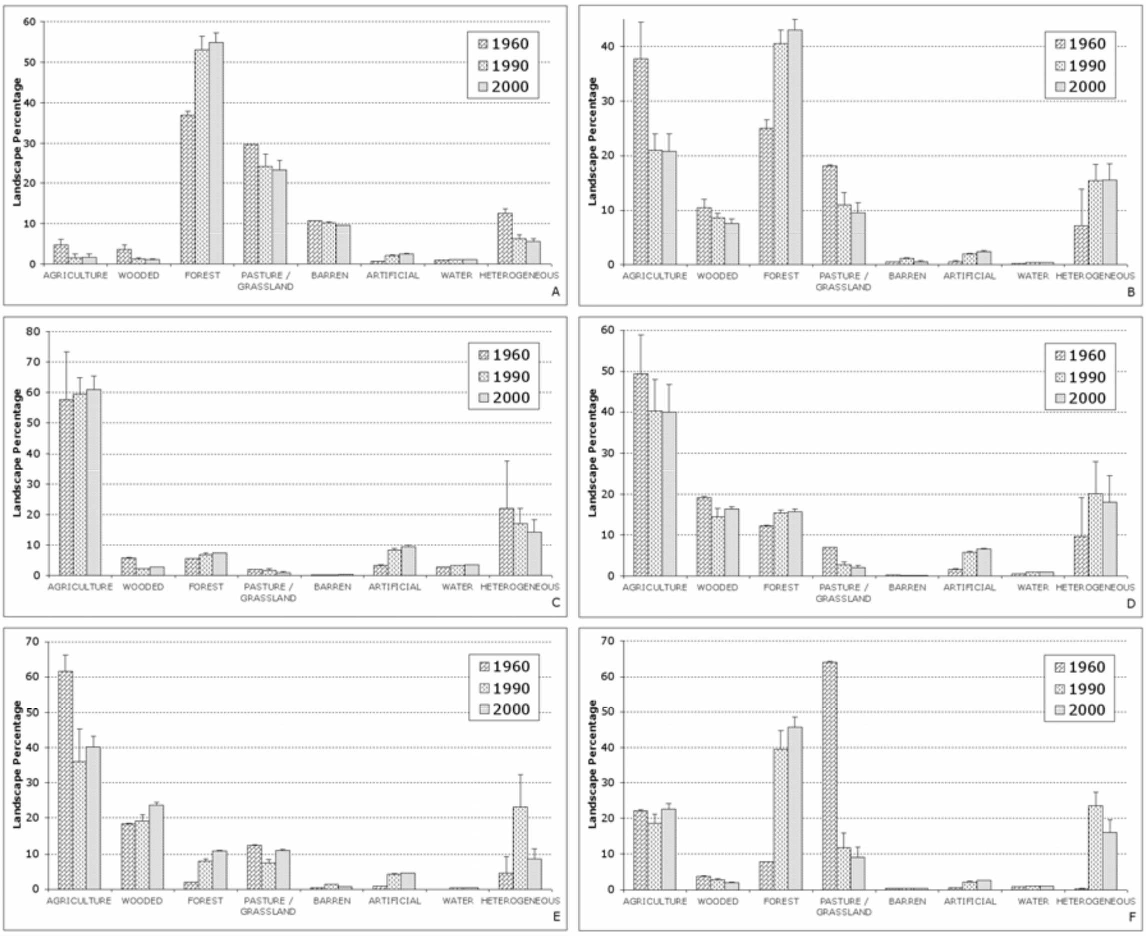


Figure 4. Percentage of the Italian macro-regions occupied by the different land-use/land-cover classes. A = Alps; B = Apennines; C = Po river plain; D = coastal areas; E = Sicily; F = Sardinia.

Land-use/land-cover change and human population change

From 1960 to 1990, human population – measured in each administrative unit – increased on average by 3.25% (SD = 53.40%; n = 8,100); the median change was – 5.66% (interquartile-range = 46.35%).Most of the administrative units where a decrease in population has been measured are located in the Apennines, in the Alps and in the central and mountainous part of Sicily and Sardinia. An increase in population was measured along the coastline and in the main river valleys (in the Alps and in the Apennines) and in the plains (Fig. 5).

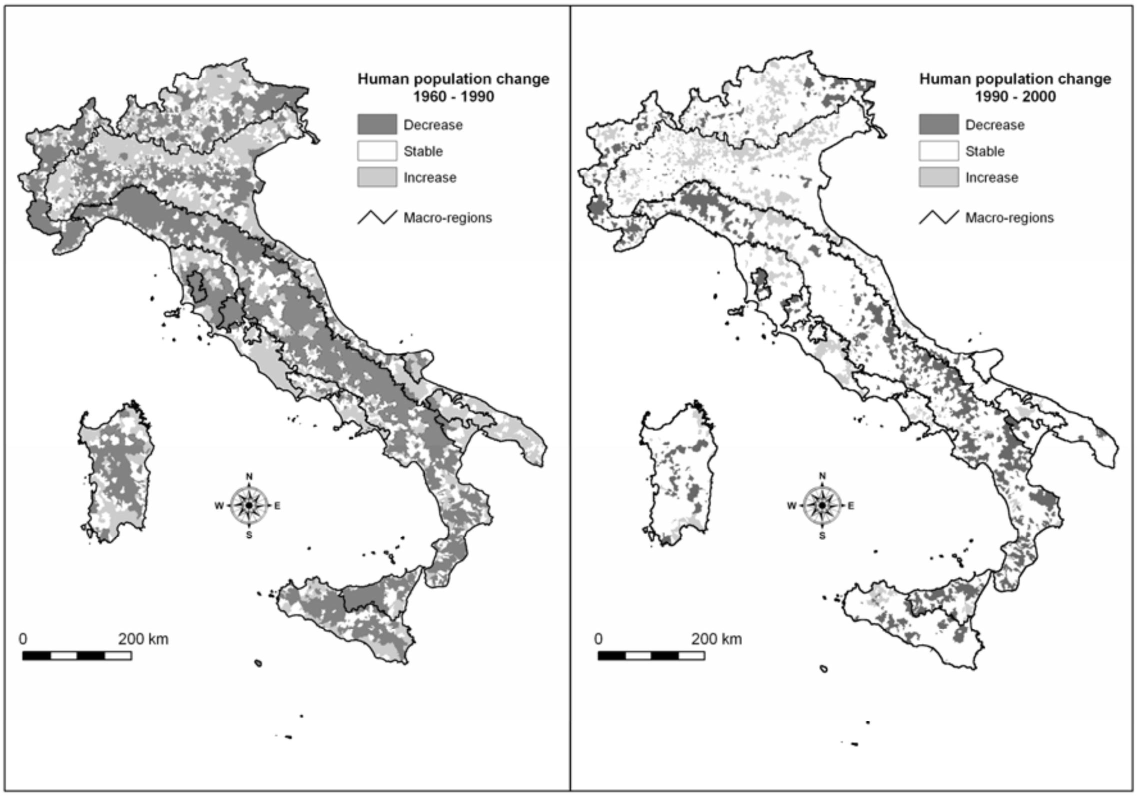


Figure 5. Human population changes from 1960 to 1990 and from 1990 to 2000.

The administrative units where we found an increase in FOREST showed a negative rate of population change significantly lower ($P < 0.0001$) than the rate of population change measured in the administrative units where we found a decrease in FOREST. No statistically significant difference was found for human population changes between administrative units with an increase and a decrease in PASTURE: both showed a negative rate of population change. The administrative units where agriculture decreased had a human population rate of change which was negative but significantly higher ($P < 0.001$) than the human population rate of change of the administrative units where agriculture increased (Fig. 6).

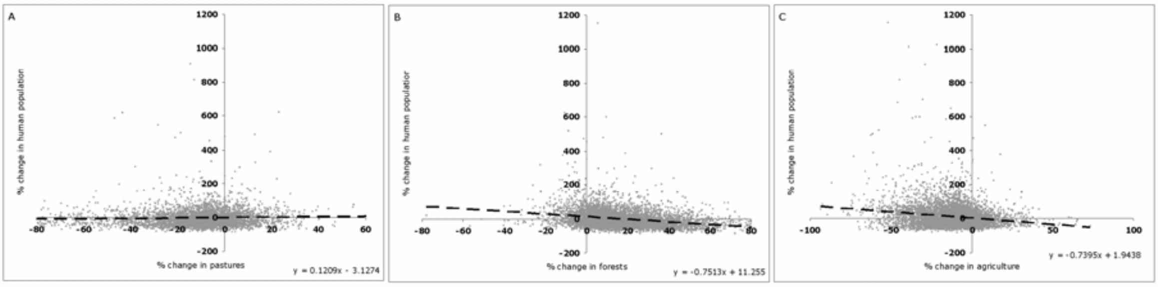


Figure 6. Relationships among land cover changes (A = Pastures, B = Forests, C = Agriculture) and human population change.

From 1990 to 2000, human population increased on average by 1.34% (SD = 11.35%; n = 8,100) per administrative unit; the median change of human population was 0.73% (interquartile range = 12.37%). Most of the administrative units showed a predominantly constant population size. We measured a decrease in population size for some administrative units in the Apennines, in the Alps, and in central Sardinia, while administrative units where we measured an increase in population were located almost exclusively in the Po rive plain and around big cities/towns (Figs. 5, 6). The administrative units where FOREST increased had a rate of change of human population that was slightly negative and significantly lower ($P < 0.001$) than the rate of change of human population measured for administrative units that showed a decrease in FOREST. The same results were obtained for PASTURE and agriculture.

The results of the significance tests presented above should be considered with caution due to the spatial autocorrelations in the data (Legendre 1993). The tests however give a useful indication of the general trend of change that is occurring in the study area.

Error checking

Spatial aggregation errors related to the transformation from vector to raster format were negligible. The differences between percentages of land-use/land-cover classes calculated using rasters and coverages were much smaller than 1%, with the exception of: ARTIFICIAL in MLC1960 (error = 1.22%), ARTIFICIAL (error = 1.3%) and WATER (error = 1%) in CLC1990.

Discussion

Any analysis of land-use/land-cover change based on datasets from different sources is subject to technical problems (Coppin and Bauer 1996; Petit and Lambin 2001, 2002; Lepers et al. 2005) and the same process of data integration may cause different types of errors. For this reason, we performed a check for errors associated with changes in data format, obtaining extremely low error estimates. Moreover, our results are provided together with an explicit measure of the uncertainty associated with each land-use/land-cover change, a measure that in most cases is extremely low (Table 1, 2), confirming that our land-use/land-cover change analysis was reliable.

We have no direct measure of the classification error associated with our analysis. However, we considered in the analyses different possible classification schemes, allowing for uncertainty in the results. Moreover, the final legend that we used for the analysis further reduces the potential occurrence of misclassification errors, because the number of classes is limited (only 8; Fig. 1) and they represent markedly distinct land-use/land-cover types. The only exception that we found is for the class HETEROGENEOUS, that apparently can be confounded with AGRICULTURE, and for which we obtained the higher level of uncertainty (Table 1, 2; Fig. 3).

Our analysis is supported in its results by other studies that have indirectly considered the Italian peninsula. FAO (2005), using completely different datasets and techniques (and with no spatial detail inside the country level), reports that in 2005 34% of the Italian territory was covered by forests (compared to the 32.54% that we measured for 2000) and that the annual rate of change in forest cover for the time period 1990–2000 was 0.3% (compared to the 0.2% that we measured for the same time frame). Comparable results have been obtained from EEA (2005) that measured the same trends that we described for pastures and forests using the same datasets but different techniques. These studies give a further confirmation of the reliability of the change rates that we obtained.

Our results demonstrate that from the 1960s, Italy’s mountainous and hilly areas (particularly the Alps and the Apennines) have changed towards more ‘‘pristine’’ conditions and the coastal areas towards a more human dominated landscape (Figs. 5, 6). The land-use/land-cover changes seem to be associated to changes in human population density (but see Lambin et al. 2001), which appear to be inversely related to the increase in forest cover (Alps and Apennines) and decrease in pastures and other traditional agricultural uses (as is the case in Sardinia). These results are generally similar to those obtained for other study areas in Europe (MacDonald et al. 2000), but should be interpreted with caution. First, in fact, the results of the standard significance tests that we used should be considered only as a general indication. This is because in the presence of spatial dependence, that is likely to occur in spatially explicit data, single observations (comuni in our case) are not independent from other observations. As a consequence, the P-values that we obtained are too small compared to P-values obtained from uncorrelated data (Legendre 1993). Second, the relationships between population change and land-use/land-cover dynamics can potentially be complex and non- linear (MacDonald et al. 2000; Gellrich and Zimmerman 2006). Population change is often used as a proxy for unobserved economic factors but the relationship with land-use/land-cover changes is usually complicated by complex spatially explicit economic factors (Irwin and Geoghegan 2001). Thus our results should be considered only as a general indication of a much more complex phenomenon.

FOREST increased from the 1960s to 2000, replacing mainly agricultural areas and PASTURE (refers to Tables 1, 2). During the same period, PASTURE drastically decreased and agriculture (including AGRICULTURE, HETEROGENEOUS and WOODED) remained mostly unchanged. However, the land-use classes representing more traditional and less intensive cultivations decreased (WOODED and, in the Alps, HETEROGENEOUS) or remained stable (HETEROGENEOUS), while AGRICULTURE, the land use type that includes the more intensive cultivation types, increased in plain areas (despite an overall decrease), indicating an increase in modern-industry-based agriculture and a decrease in traditional types of agriculture.

A major caveat on these results is given by their purely quantitative aspects. The type of data used does not permit any insight into the ‘‘quality’’ of the land-use/land-cover classes and we could not obtain any indication regarding the ecological functionality of what we found. However, Tellini-Florenzano (2004) measured, for the Apennines, a significant aging for different types of woods (*Fagus sylvatica, Quercus cerris* and other broadleaves, *Abies alba* and other conifers). In particular, an important part of the Foreste Casentinesi National Park woods became of mature age classes (> 80 years); this trend, combined with the retention of dead and dying trees, indicates that the ecological functionality of these forests and woods is potentially fully retained. Obviously, we cannot extrapolate these results to the entire study area, since the Foreste Casentinesi National Park is just a small area in the Apennines (36,000 ha) but there is, at least, an indication of the ecological trends in the land-use/land-cover change that we measured. Similar studies should be carried out locally along the entire Italian peninsula in order to evaluate the significance of the changes that we measured.

Similar patterns of land-use/land-cover change have already been found in other parts of the world, but usually for areas much smaller than the Italian peninsula (Farina 1991; Ales et al. 1992; Garcia-Ruiz et al. 1996; Preiss et al. 1997; Debussche et al. 1999; Olsson et al. 2000; Robinson and Sutherland 2002; Brown et al. 2005). The consequences for biodiversity have been discussed (Alkorta et al. 2003; Dale et al. 2005; Hansen et al. 2005; Huston 2005), and several studies have suggested that a reduction of human population density in agricultural regions can produce indirect environmental benefits (Huston 2005), with abandonment of marginal agricultural lands (both for cultivation and for pasture) and substantial forest regeneration. Moreover, it has been suggested that an increase in intensive agriculture can potentially reduce the ecological footprint related to food production allowing for the preservation of less productive lands (Huston 2005). We argue that these considerations cannot be considered to hold for Italy and for the Mediterranean basin in general, where the integration among biodiversity and traditional human activities is much tighter than in the North American context (Farina et al. 2003; Foster et al. 2003).

In the Mediterranean, agricultural intensification has led to a widespread decline of farmland biodiversity for many taxa (Matson et al. 1997; Preiss et al. 1997; Lavorel et al. 1998; Donald et al. 2001; Benton et al. 2003), cessation of pasture grazing and increased reforestation have reduced the availability of habitats for many species, and an increase in the size of cities has led to large ecological footprints (Rees 1997).

We did not directly measured any relationship among land-use/land-cover changes and biodiversity patterns over the entire Italy but considering their geographical distribution, the pattern of changes in land-use/land-cover that we measured show interesting relations to concurrent and important changes of biodiversity patterns. From 1960 to 2000, the Alps and the Apennines showed a substantial increase in FOREST, while agriculture and human population dropped. As a result of land abandonment, the floristic species richness is decreasing in higher successional stages and, depending on the altitude, the structural diversity of the landscape is changing (Höchtl et al. 2005). In the same time period and in the same area, Italy has experienced a real "renaissance" of large vertebrates: wolves increased from about 100 individuals in the 1970s—localized in the central Apennines—to more than 500 individuals in 2000, spreading from the southern Apennines to the central Alps (Boitani and Ciucci 2000); wild ungulate populations increased both in numbers and distribution (Boitani et al. 2003); brown bears (*Ursus arctos*) were successfully reintroduced in the eastern Alps while the central Italy subspecies (*U. arctos marsicanus*) has seemingly increased its range (Boitani et al. 2003); temperate forest birds are following the same pattern, increasing their ranges throughout the mountain areas of the Mediterranean region (Preiss et al. 1997; Laiolo et al. 2004; Tellini-Florenzano 2004).

Almost the opposite situation can be found in Sardinia, Sicily and in the coastal areas, among the most important portions of the Mediterranean hotspot for biodiversity conservation (Blondel and Aronson 1999; Médail and Quézel 1999). Here total agriculture increased (Sardinia) or remained stable (Sicily and coastal areas), while FOREST remained stable (coastal areas) or increased (Sicily and particularly Sardinia). ARTIFICIAL sharply increased indicating a substantial increase of human presence, mainly linked to an increase in tourist activities. In Sardinia and the coastal areas, the drastic decrease of PASTURE followed the decrease in traditional sheep grazing, and represents an important conservation problem: the little bustard (*Tetrax tetrax*), a species of open spaces, is disappearing from continental Italy and its numbers are critically low in Sardinia (de Juana and Martinez 2001; Wolff et al. 2001); the griffon vulture (*Gyps fulvus*), dependent on traditional pasture, has completely disappeared from continental Italy (Dentesani et al. 1996), and has drastically dropped in number in Sardinia; the Egyptian vulture (*Neophron percnopterus*) dropped drastically in number and distribution from 1970 to 1990 following the reduction of traditional cattle husbandry techniques (Liberatori and Penteriani 2001), typical Mediterranean bird and plant species, usually restricted to the earlier stages of ecological successions (Blondel and Farré 1988), are decreasing in range and population sizes, following the decrease of Mediterranean forests and open areas and the intensification of agriculture (Farina 1991, 1997; Preiss et al. 1997; Brotons et al. 2004).

Even though the Italian landscape is not representative of the entire Mediterranean hotspot (Vallejo et al. 2005), we suggest that our results may provide an important insight into conservation planning in the entire region. In fact, many of the ecological and socio-political processes that have occurred in Italy during the past few decades are already occurring or expected to occur over most of the Mediterranean region. The transition from traditional to mechanized agriculture and the intensive development of tourism along the coastal areas are likely to lead towards situations which are broadly similar to Italy today.

Protected areas cannot be easily adapted to follow these patterns: Italian protected areas already cover 11% of the territory (Maiorano et al. 2006); most of them are located in mountain regions (where land-use/land-cover changes favor reforestation and the increase of large vertebrate populations) while only few (mostly small ones) can be found in coastal areas, where the Mediterranean forest, woodlands and scrubs are concentrated and where human pressure is high. Much more can be done for the Mediterranean hotspot where protected areas cover less than 5% and the extent of habitat conversion exceeds that of habitat protection by a factor which is greater than 8 (Hoekstra et al. 2005). In comparison, the extent of habitat conversion exceeds that of habitat protection by a factor of 4 in temperate broadleaf and mixed forests, tropical dry forests, and tropical conifer forests, usually considered among the most endangered ecosystems in the world (Myers et al. 2000).

However, despite their importance, protected areas cannot be the only conservation tool used in regions of high human densities (Tilman et al. 1994; Carroll et al. 2003). Our results suggest that a comprehensive management plan to take into account biodiversity conservation in the little remaining natural matrix of the Mediterranean coastal areas is urgently needed to complement the function of the protected areas. Moreover, much more emphasis should be placed on preserving and reintroducing traditional land use management activities, because the Mediterranean landscape and its biotic assemblages have developed as a consequence of past (and now disappearing) human activities.

Future conservation efforts should address the broad socio-political and ecological processes that are most likely to occur across the whole hotspot, especially along coastal areas, and the network of protected areas should be functionally integrated in a conservation strategy that explicitly includes the human dominated matrix and the traditional land-use practices. In this context, analysis of land-use/land-cover changes within the various macro-regions provide significant support to conservation planning by producing accurate information regarding local threats and costs of action.

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References

Ales R.F., A. Martin, F. Ortega and E.E. Ales. 1992. Recent changes in landscape structure and function in a Mediterranean region of SW Spain (1950–1984). Landscape Ecology 7:3–18.

Alkorta I., I. Albizu and C. Garbisu. 2003. Biodiversity and agroecosystems. Biodiversity Conservation 12:2521–2522.

Balletto E. and A. Casale. 1991. Mediterranean insects conservation. Pp. 122-142 in: Collins N.M. and J.A. Thomas (Eds). The conservation of insects and their habitat. Academic Press, London, UK.

Benton T.G., J.A. Vickery and J.D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18:182–188.

Blondel J. and H. Farré. 1988. The convergent trajectories of bird communities along ecological successions in European forests. Oecologia 75:83–93.

Blondel J. and J. Aronson. 1999. Biology and wildlife of the Mediterranean region. Oxford University Press, Oxford, UK.

Boitani L. and P. Ciucci. 2000. Action plan for the conservation and management of the wolf in the Alps. WWF, Rome, Italy.

Boitani L., S. Lovari and A. Vigna-Taglianti. 2003. Fauna d’Italia. Mammalia III – Carnivora and Artiodactyla. Calderini, Bologna, Italy.

Bossard M., J. Feranec and J. Otahel. 2000. The revised and supplemented Corine land cover nomenclature. EEA, Copenhagen, Denmark.

Brooks T.M., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, A.B. Rylands, W.R. Konstant, P. Flick, J. Pilgrim, S. Oldifeld, G. Magin and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16:909–923.

Brotons L., S. Manõsa and J. Estrada. 2004. Modeling the effects of irrigation schemes on the distribution of steppe birds in Mediterranean farmland. Biodiversity and Conservation 13:1039–1058.

Brown D.G., K.M. Johnson, T.R. Loveland and D.M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. Ecological Applications 15:1851–1863.

Büttner G., J. Feranec, G. Jaffrain, L. Mari, G. Maucha and T. Soukup. 2004. The European CORINE land cover 2000 project. Paper presented at the XXth Congress of ISPRS, 12–13 July 2004, Istanbul, Turkey.

Carroll C., R.F. Noss, P.C. Paquet and N. Schumaker. 2003. Extinction debt of protected areas in developing landscapes. Conservation Biology 18:1110–1120.

Coppin P.R. and M.E. Bauer. 1996. Digital change detection in forests ecosystems with remote sensing imagery. Remote Sensing Reviews 13:207–234.

Covas R. and J. Blondel. 1998. Biogeography and history of the Mediterranean bird fauna. Ibis 140:395–407.

Cowling R.M., P.W. Rundel, B.B. Lamont, M.K. Arroyo and M. Arianoutsou. 1996. Plant diversity in Mediterranean-climate regions. Trends in Ecology and Evolution 11:362–366.

Dale V., S. Archer, M. Chang and D. Ojima. 2005. Ecological impacts and mitigation strategies for rural land management. Ecological Application 15:1879–1892.

Debussche M., J. Lepart and A. Dervieux. 1999. Mediterranean landscape changes: evidence from old postcards. Global Ecology and Biogeography 8:3–15.

de Juana E. and C. Martinez. 2001. Action plan for the conservation of little bustard (Tetrax tetrax). BirdLife International.

Dentesani B., F. Genero and F. Perco. 1996. Il grifone in Italia e nel mondo: biologia e strategie di conservazione. Muzzio Editore, Italia.

Dobson A.P., A.D. Bradshaw and A.J.M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. Science 277:515–522.

Donald P.F., R.E. Green and M.F. Heath. 2001. Agricultural intensification and the collapse of Europe’s farmland bird population. Proceedings of the Royal Society of London Series B 268:25–29.

EC (European Community). 1993. CORINE land cover technical guide. Report EUR 12585EN. Office for Publications of the EC, Luxembourg.

EEA (European Environmental Agency). 2005. The European environment: state and outlook (2005). Copenhagen.

FAO (Food and Agriculture Organization of the United Nations). 2005. State of the World’s forests. FAO, Rome.

Farina A. 1991. Recent changes of the mosaic patterns in a montane landscape (north Italy) and consequences on vertebrate fauna. Options Mediterranees 15:121–134.

Farina A. 1997. Landscape structure and breeding bird distribution in a sub-Mediterranean agro-ecosystem. Landscape Ecology 12:365–378.

Farina A., A.R. Johnson, S.J. Turner and A. Belgrano. 2003. ‘Full’ world versus ‘empty’ world paradigm at the time of globalization. Ecological Economics 45:11–18.

Foster D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. BioScience 53:77–88.

Garcia-Ruiz J.M., T. Lasanta, P. Ruiz-Flano, L. Ortigosa, S. White, C. Gonzàles and C. Martì. 1996. Land-use changes and sustainable development in mountain areas: a case study in the Spanish Pyrenees. Landscape Ecology 11:267–277.

Gellrich M. and N.E. Zimmermann. 2006 Investigating the regional-scale pattern of agricultural land abandonment in the Swiss mountains: a spatial statistical modeling approach. Landscape and Urban Planning DOI: 10.1016/j.landurb-862 plan.2006.03.004.

Hansen A.J., R.L. Knight, J.M. Marzluff, S. Powell, K. Brown, P.H. Gude and K. Jones. 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecological Applications 15:1893–1905.

Heywood V.H. 1999. The Mediterranean region: a major centre of plant diversity. Options Mediterranees 38:1–15.

Höchtl F., S. Lehringer and W. Konold. 2005. ‘‘Wilderness’’: what it means when it becomes a reality – a case study from the southern Alps. Landscape and Urban Planning 70:85–95.

Houghton R.A. 1994. The worldwide extent of land-use change. Bioscience 44:305–309.

Huston M.A. 2005. The three phases of land-use change: implications for biodiversity. Ecological Applications 15:1864–1878.

Irwin E.G. and J. Geoghegan. 2001. Theory, data, methods: developing spatially explicit economic models of land use change. Agricultural Ecosystems and Environment 85:7–23.

Laiolo P., F. Dondero, E. Ciliento and A. Rolando. 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. Journal of Applied Ecology 41:294–304.

Lambin E.F., B.L. Turner, H.J. Geist, S.B. Agbola, A. Angelsen, J.W. Bruce, O.T. Coomes, R. Dirzo, G. Fischer, C. Folke, P.S. George, K. Homewood, J. Imbernon, R. Leemans, X. Li, E.F. Moran, M. Mortimore, P.S. Ramakrishnan, J.F. Richards, H. Skanes, W. Steffen, G.D. Stone, U. Svedin, T.A. Veldkamp, C. Vogel and J. Xu. 2001. The causes of land-use and land-cover change: moving beyond the myths. Global Environmental Change 11:261–269.

Lambin E.F., H.J. Geist and E. Lepers. 2003. Dynamics of land-use and land-cover change in tropical regions. Annual Review of Environmental Research 28:205–241.

Lavorel S., J. Canadell, S. Rambal and J. Terradas. 1998. Mediterranean terrestrial ecosystems: research priorities on global change effects. Global Ecology and Biogeography Letters 7:157–166.

Legendre P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

Lepers E., E.F. Lambin, A.C. Janetos, R. DeFries, F. Achard, N. Ramankutty and R.J. Scholes. 2005. A synthesis of information on rapid land-cover change for the period 1981–2000. BioScience 55:115–124.

Liberatori F. and V. Penteriani. 2001. A long-term analysis of the declining population of the Egyptian vulture in the Italian peninsula: distribution, habitat preferences, productivity and conservation implications. Biological Conservation 101:381–389.

Lobo J.M., J.P. Lumaret and P. Jay-Robert. 2001. Diversity, distinctiveness and conservation status of the Mediterranean coastal dung beetle assemblage in the Regional Natural Park of the Camargue (France). Diversity and Distribution 7:257–270.

MacDonald D., J.R. Crabtree, G. Wiesinger, T. Dax, N. Stamou, P. Fleury, J. Gutierrex Lazpita and A. Gibon. 2000. Agriculture abandonment in mountain areas of Europe: environmental consequences and policy response. Journal of Environmental Management 59:47–69.

Maiorano L., A. Falcucci and L. Boitani. 2006. Gap analysis of terrestrial vertebrates in Italy: priorities for conservation planning in a human dominated landscape. Biological Conservation 133:455-473.

Matson P.A., W.J. Parton, A.G. Power and M.J. Swift. 1997. Agricultural intensification and ecosystem properties. Science 277:504–509.

Médail F. and P. Quézel. 1999. Biodiversity hotspots in the Mediterranean basin: setting global conservation priorities. Conservation Biology 13:1510–1513.

Moody A. and C.E. Woodcock. 1994. Scale-dependent errors in the estimation of land-cover datasets. Photogrammetric Engineering and Remote Sensing 60:585–594.

Myers N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Ojima D.S., K.A. Galvin and B.L. Turner II. 1994. The global impact of land-use change. Bioscience 44:300–305.

Olsson E.G.A., G. Austrheim and S.N. Grenne. 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. Landscape Ecology 15:155–170.

Ott L., R.F. Larson and W. Mendenhall. 1983. Statistics: a tool for the social sciences. Duxbury Press, Boston, USA.

Petit C.C. and E.F. Lambin. 2001. Integration of multi-source remote sensing data for land cover change detection. International Journal of Geographic Information Science 15:785–803.

Petit C.C. and E.F. Lambin. 2002. Impact of data integration technique on historical land-use/land-cover change: comparing historical maps with remote sensing data in the Belgian Ardennes. Landscape Ecology 17:117–132.

Pimm S.L. and J.H. Lawton. 1998. Planning for biodiversity. Science 279:2068–2069.

Pimm S.L., G.J. Russell, J.L. Gittleman and T.M. Brooks. 1995. The future of biodiversity. Science 269:347–350.

Preiss E., J.L. Martin and M. Debussche. 1997. Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. Landscape Ecology 12:51–61.

Rees W.E. 1997. Urban ecosystems: the human dimension. Urban Ecosystems 1:63–75.

Robinson R.A. and W.J. Sutherland. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39:157–176.

Sala O.E., F.S. Chapin III, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker and D.H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Sanderson E.W., M. Jaiteh, M.A. Levy, K.H. Redford, A.V. Wannebo and G. Woolmer. 2002. The human foot- print and the last of the wild. BioScience 52:891–904.

Santos C.P. 2000. Succession of breeding bird communities after the abandonment of agricultural fields in south-east Portugal. Ardeola 47:171–181.

Sodhi N.S., L.P. Koh, B.W. Brook and P.K.L. Ng. 2004. Southeast Asian biodiversity: an impending disaster. Trends in Ecology and Evolution 19:654–660.

Tellini-Florenzano G. 2004. Birds as indicators of recent environmental changes in the Apennines (Foreste Casentinesi National Park, central Italy). Italian Journal of Zoology 71:317–324.

Tilman D., R.M. May, C.L. Lehman and M.A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Tomaselli R., A. Balduzzi and S. Filipello. 1973. Carta bioclimatica d'Italia. Ministero Politiche Agricole e Forestali, Roma, Italia.

Turner M.G., R.V. O'Neill, R.H. Gardner and B.T. Milne. 1989. Effects of changing spatial scale on the analysis of landscape pattern. Landscape Ecology 3:153–162.

UNEP. 1989. State of the Mediterranean marine environment. MAP Technical Report Series 28, Athens, Greece.

Vallejo R., J. Aronson, J.C. Pausas and J. Cortina. 2005. Restoration of Mediterranean woodlands. Pp. 193-207 in: van Andel J. and J. Aronson (Eds). Restoration ecology: a European perspective. Blackwell Science, Oxford, UK.

Vitousek P.M., H.A. Mooney, J. Lubchenco and J.M. Melillo. 1997. Human domination of earth’s ecosystems. Science 277:494–499.

William B.M. and B.L. Turner II. 1992. Human population growth and global land-use/cover change. Annual Review of Ecology and Systematics 23:39–61.

Wolff A., J.P. Paul, J.L. Martin and V. Bretagnolle. 2001. The benefits of extensive agriculture to birds: the case of the little bustard. Journal of Applied Ecology 38:963–975.

Wu J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology 19:125–138.

LAND-COVER CHANGE AND THE FUTURE OF THE ABRUZZO BROWN BEAR: A PERSPECTIVE FROM THE PAST[1]

Introduction

The brown bear (*Ursus arctos*) is a species facing high extinction risks throughout most of Europe. The species was widespread in the holarctic region (Swenson et al. 2000) till the beginning of 1800s when, facing direct persecution and habitat destruction, it declined markedly. Today, it is present with important numbers in Eastern and Northern Europe (Zedrosser et al. 2001). In Western Europe, the species is restricted to small, isolated and endangered populations, with exception of the populations in the eastern Alps - Dinaric mountains (Taberlet et al. 1995; Swenson et al. 2000).

In Italy, the species has seen a progressive reduction in its range since the 1600s, due essentially to legal hunting before 1938, poaching and habitat destruction (Fabbri et al. 1983; Febbo and Pellegrini 1990). Today it is restricted to two populations in the Alps and one in the Apennines (Boitani et al. 2003).

The central-Apennine population, a subspecies (*U.a. marsicanus*, hereafter the Abruzzo brown bear) endemic to Italy (Vigna-Taglianti 2003) is restricted to roughly 1,500 km^2 of mountainous areas in the Abruzzo-Lazio-Molise National Park (PNALM) (Bologna and Vigna-Taglianti 1992; Boscagli 1999; Posillico et al. 2004). Dispersing individuals from this population can be found in other parts of the central Apennines (Fabbri et al. 1983; P. Ciucci pers. comm.).

The subspecies is protected by law and the PNALM itself, along with other adjacent protected areas, have been instituted to secure its conservation. The Abruzzo brown bear is considered endangered by the Italian WWF red list (Bulgarini et al. 1998), and critically endangered by the IUCN Red List (L. Boitani pers. com.). Moreover, Swenson et al. (2000) consider the subspecies as highly threatened; CITES includes the Abruzzo brown bear in its Appendix II; the European Community lists the bear in the Bern

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convention (1979) as strictly protected, and in the Habitat Directive (1992), as endangered.

Notwithstanding its legal status, the Abruzzo brown bear is still facing serious problems, and significant efforts are needed for successful conservation of the subspecies. The population has been completely isolated from other bear populations for the last 400 years (Randi et al. 1994). Current population size is unknown, but the number of bears probably does not exceed 40-60 individuals (Boitani et al. 2003), well below what is required for a viable population (Wiegand et al. 1998; Wieglus, 2002; but see Sæther et al. 1998). Moreover, the Abruzzo brown bear lives in a human-dominated landscape, suffers consistent human-caused mortality (Posillico et al. 2002; L. Gentile, com. pers.), and lacks a coordinated interagency and inter-institutional conservation strategy to overcome political and administrative fragmentation. Such a strategy is difficult to achieve in the absence of reliable knowledge on the status, ecology and threats of the population upon which to prioritize conservation interventions.

Habitat loss and degradation have often been considered two of the main reasons for the Abruzzo brown bear’s decline (Fabbri et al. 1983; Febbo and Pellegrini 1990; Bologna and Vigna-Taglianti 1992), and are considered major long-term threats for its future (Swenson et al. 2000). However, no formal evaluation of bear habitat status and trends has been undertaken over the bear’s current and historical range. Simply assuming that habitat loss is (and has been) the main cause of bear population decline might diminish the potential role of other threats (e.g., human-induced mortality, low recruitment rates, limited mobility). In this context, conducting a large-scale habitat evaluation is important for several reasons. First, any hypothesis of demographic recovery must consider space and habitat availability, possibly with explicit reference to habitat changes in time. Second, a large-scale approach seems most appropriate for a species with as large area requirements as the bear, as it could also identify large-scale connections among existing protected areas. This would facilitate conservation strategies based on metapopulation dynamics, providing spatially-explicit references for intensive management actions (law enhancement, conflict resolutions, population augmentation, etc.), and/or habitat restoration.

Our primary goal is to assess historic (1960s and 1990) to current (2000) changes in critical habitat for Abruzzo brown bears and use them to project likely changes in future (2020) habitat for this important species. We also evaluate changes in human population density for the same time frames as a surrogate for human encroachment into bear's habitat. In addition, we investigate distribution and location of suitable areas in central Italy which are still unoccupied by bears and where individuals from the core population might eventually expand in the near future. This further allows us to measure the potential contribution of existing and proposed protected areas to the goal of large-scale and long-term conservation for the Abruzzo brown bear.

Materials and Methods

Our study area (2.2 million hectares) corresponds to the approximate distribution range of the Abruzzo brown bear at the beginning of 1800 (Boitani et al. 2003; Fig. 1).

We characterized habitat using a digital elevation model (DEM; cell size=75m), and three land-cover maps: the Land-Cover 1960 (LC1960), the CORINE Land-Cover 1990 (CLC1990) and the CORINE Land-Cover 2000 (CLC2000).

The LC1960 (scale 1:200,000; 22-classes legend) was produced from 1956 to 1968 by the National Research Council. The CLC maps (scale 1:100,000; 44-class legend) were produced in 1990 and in 2000 by the Ministry for the Environment.

Since legends and spatial scales of the land-cover maps were different we reclassified the CLC and the LC1960 according to the legend in Table 1. To match the original and the final legend we used the definitions given in Bossard et al. (2000) and in Memorie Illustrative, Maps of Soil Utilization, National Research Council.

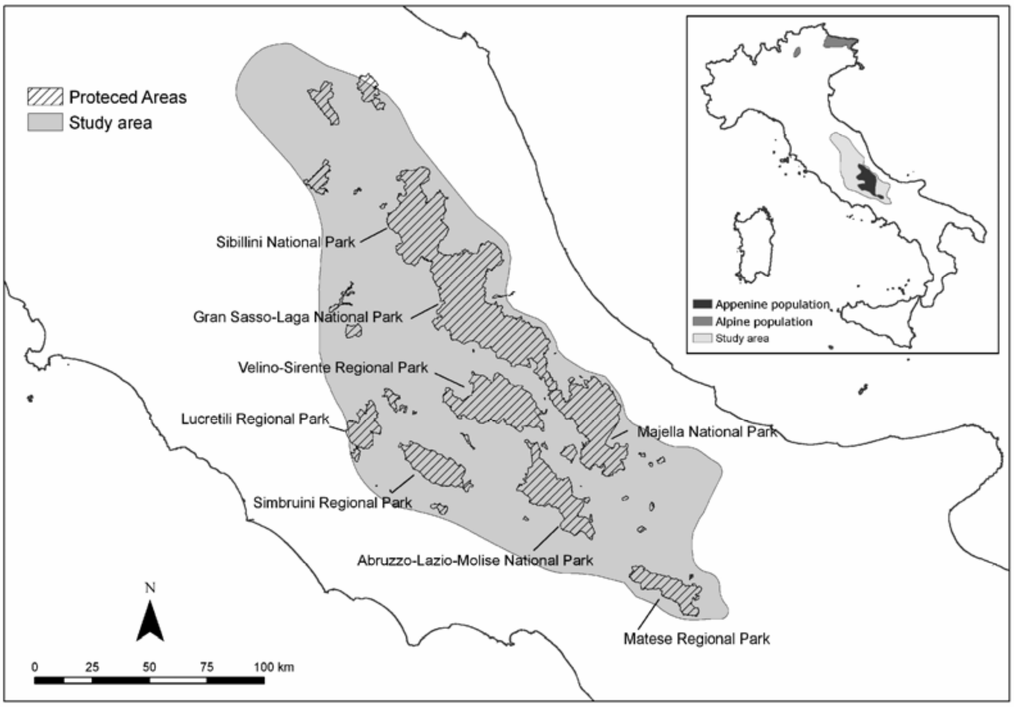

Figure 1. Study area and existing protected areas.

To obtain three spatially homogeneous layers, we transformed the land-cover maps from vector to raster, assigning the same origin, extent and cell size (200m). Cell size was chosen considering the coarser resolution of the LC1960. The DEM was re-sampled to match the resolution and the extent of the land-cover layers.

For the period 1960-2000, we used spatially explicit data on human population based on national censuses (Italian Institute of Statistics).

We used 1847 point observations on bear presence (sightings, tracks and signs) collected from 1999 to 2003 by PNALM and Forestry Service field personnel, including 304 locations where bear were hair-snag sampled following standard protocols (Wood et al. 1999). Existing protected areas (PA) and the NATURA2000 network were obtained from Maiorano et al. (2006).

Land cover class	Land cover score	Alternative score
Artificial	0	/
Non irrigated arable lands	1	0
Irrigated arable lands	0	/
Vineyards	0	/
Wooden cultivations	2	1
Olive groves	0	/
Pastures	1	/
Complex agricultural areas	1	0
Agricultural areas with natural vegetation	2	/
Broadleaf forests	3	/
Coniferous forests	2	1
Mixed forests	3	2
Natural prairies	1	/
Moors	2	/
Sclerophyllous vegetation	2	1
Forest-shrubs transitional areas	3	2
Beach and dunes	0	/
Scarcely vegetated areas	1	/
Marshes	0	/
Bare rocks	1	/
Rivers	0	/
Lakes	0	/

Table 1. Scores assigned to land-cover classes for the final model and for the alternative models (0, 1, 2, and 3 correspond to the definitions in Table 2). A backslash indicates that no alternative score has been considered.

Land-cover in 2020

To project land-cover in 2020, we used the two CLC maps in a combined Cellular-Automata Markov-Chain Multi-Criteria/Multi-Objective Land Allocation land-cover prediction procedure (CA_MARKOV procedure, IDRISI3.2).

The CA_MARKOV algorithm is based on the assumption that future land-cover changes can be predicted using past land-cover changes (Eastman 2001). We used CLC1990 and CLC2000 to obtain a transition-area file, quantifying changes from each land-cover category in 1990 to each other category in 2000. The suitability of each pixel for each land-cover type (lc-suitability) is determined on the basis of a set of lc-suitability maps, one for each land-cover type. We built the lc-suitability maps using Mahalanobis distance statistics (Corsi et al. 1999) based on topographic and anthropogenic layers (aspect, elevation, slope, main and secondary road densities, distance to main and secondary roads). We used a contiguity filter to down-weight the lc-suitability of pixels far from existing areas of each land-cover class, thus giving preference to contiguous suitable areas (Eastman 2001).

CLC2000 was the starting point for land-cover change projection in 2020. We ran the entire procedure 100 times and we assigned the value that occurred most often for each pixel to the final 2020 land-cover. Further details on the CA_MARKOV algorithms can be found in Eastman (2001).

Distribution models

To model the distribution of the Abruzzo brown bear, we built four deductive models (DMs, sensu Corsi et al. 2000) for 1960, 1990, 2000 and 2020. We chose a deductive approach because it allows for the generalization of species-habitat relationships over large areas providing a synthesis of the available knowledge (Johnson and Gillingham 2005), and because points of presence are available only for 2000.

Although little is known on the ecology of the Abruzzo brown bear, information on the basic biology of the population is available (Boitani et al. 2003), as well as extensive knowledge on the ecology of the species from other parts of its range (Swenson et al. 2000). Based on these data, land-cover and elevation classes were used as surrogates of bear habitat qualifiers and, for each of the four time frames, they were combined according to suitability scores. We assigned a suitability score to the different land-cover classes according to the expected relationship between the bear and vegetation-types, their productivity and cover value. Scores for land-cover classes ranged from 0 (unsuitable) to 3 (high suitability). We classified elevation in terms of absolute range (500-2800m, maximum and minimum elevation where the species can be found), and optimal range (800-1800m, the range where the bear presence is expected to be stable). Therefore, suitability scores for elevation ranged from 0 (unsuitable) to 2 (optimal).

Scores for land-cover classes and elevation were integrated to produce the final DM (Table 2).

		Elevation		
		0	1	2
Land Cover	0	Non-suitable	Non-suitable	Non-suitable
	1	Non-suitable	Low Suitability	Low Suitability
	2	Non-suitable	Low Suitability	Medium Suitability
	3	Non-suitable	Medium Suitability	High Suitability

Table 2. Combinations of elevation and land-cover scores to obtain the final suitability scores for deterministic models. Elevation scores: 0 = out of the absolute elevation range; 1 = inside the absolute elevation range; 2 = inside the optimum elevation range. Land-cover scores: 0 = land-cover class that does not support the presence of the bear; 1 = land-cover class that fulfils partial resource requirements (food, cover, water); 2 = land-cover class that fulfils resources requirements at a sub-optimal level; 3 = land-cover class that fulfils optimal resources requirements.

Habitat availability and human population density

We investigated the relationship between bear habitat availability and human population changes. For each administrative unit (n=592) we calculated changes in human population from 1960 to 2000. Administrative units were classified into two groups: those where human population increased and those where human population decreased. For each unit we calculated the percentage of area occupied by each suitability class and tested the significance of the differences using a median test.

Habitat availability and PAs

We measured habitat availability inside PAs and inside NATURA2000 and tested the difference in suitability between PAs and the rest of the study area using a median test. In particular, we drew 1,000 random points in PAs and 3,500 outside (0.2 points per km^2). For each point, we built a circular buffer with a 500m radius and measured the area occupied by the different suitability classes. The same procedure was used considering PAs plus the NATURA2000 network.

Habitat connectivity and landscape indices

To measure large-scale habitat connectivity between PNALM (the source population) and the other PAs, we ran a least-cost-path analysis (Walker and Craighead 1997) using suitability scores as proxies for movement costs (lower suitability implying higher costs).

To monitor the changes occurring in the landscape structure and to numerically quantify the least-cost-path analysis, we measured the following metrics for each DM (over the entire study area, over the PAs, and over the non-PAs): Percentage of the Landscape (PLAND), Number of Patches (NP), Largest Patch Index (LPI), Euclidean Nearest Neighbor Median (ENNMD), Normalized Landscape Shape Index (NLSI) (McGarigal and Marks 1995; Turner et al. 2001).

Validation and sensitivity analyses

Obviously, no validation is possible for the 2020 projected land-cover. However, to have an idea of the stability of the land-cover projection we measured the percentage of the study area classified in the same land-cover class in all the 100 runs of the CA_MARKOV procedure.

To evaluate the DM developed for 2000 we calculated the Boyce index (Boyce et al. 2002; Hirzel et al. 2006) using the 1847 points of presence. The index goes from -1 to 1, with negative values indicating a model that predicts poor quality areas where presences are more frequent, with positive values indicating a model whose predictions are consistent with the presences distribution in the evaluation dataset, and with values close to zero indicating that the model is not different from a chance model. The index is built calculating the predicted vs the expected ratio for each suitability class, where the former is computed as the proportion of validation points that fall in the suitability class, and the latter as the proportion of the map’s total area occupied by the suitability class (see below).

To calculate the predicted suitability we built for each validation point a 500m circular buffer and we assigned to each point the suitability class with the highest share inside the buffer. Alternatively, if two or more suitability classes had the same share, the highest suitability was chosen. To calculate the expected suitability we used 20,000 random locations, and we assigned a suitability class to each location following the same procedure outlined for the points of presence.

No validation was possible for the DMs of other time frames, because no presence datasets were available.

However, we performed a sensitivity analysis (Ray and Burgman 2006) to evaluate the extent of the deviations in the results by using different suitability scores (Table 1) and changing the elevation ranges (original ranges ±100m). We ran a total of 639 different sensitivity models and measured the correlation existing among them and the final DM model using Cramer’s V (significance tested with a chi-square statistic; Ott *et al.* 1983).

Results

Most of the high and medium suitability areas for the Abruzzo brown bear are in the internal, mountainous parts of the study area (Fig. 2), while most of the low suitability and unsuitable areas are in lowlands, with higher human population densities.

From 1960 to 1990 habitat availability increased (Fig. 2, 3). Unsuitable areas covered 24% of the study area both in 1960 and in 1990. However, low suitability areas occupied almost 50% of the study area in 1960 and 29% in 1990. The opposite was true for higher suitability classes that increased in 1990. The pattern of suitability did not change significantly for 1990, 2000, and 2020.

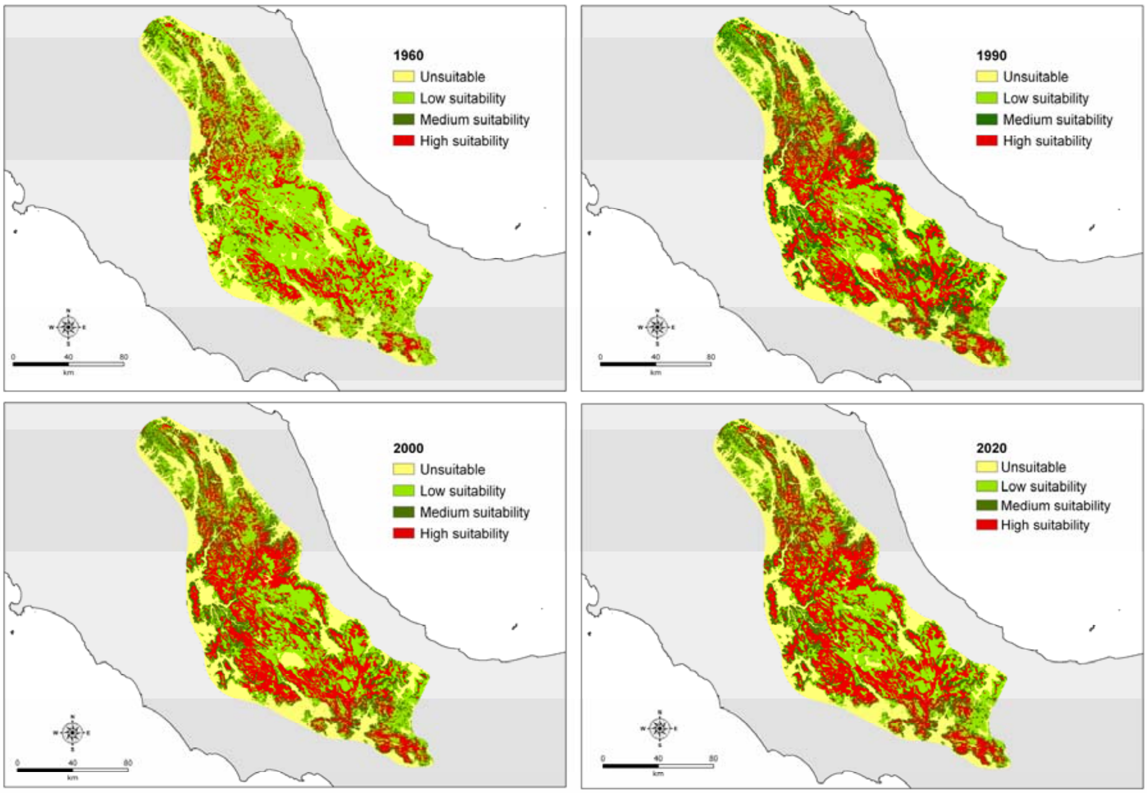

Figure 2. Deterministic habitat suitability models (DMs) for the Abruzzo brown bear in 1960, 1990, 2000 and 2020. Only the 2000 DM was validated through an independent dataset of 1847 bear presence points, while for other DMs validation was not possible, because no presence datasets were available.

Habitat availability and human population density

Median human population density decreased from 1960 to 2000 (Fig. 4). In particular, human population decreased for 487 (82.3%) administrative units from 1960 (median = 0.65n/ha) to 1990 (0.45n/ha) and for 398 (67.2%) from 1990 to 2000 (0.44n/ha).

Administrative units where human population decreased from 1960 to 1990 hosted a higher percentage of medium and high suitability areas if compared with administrative units where human population increased ($p<0.0001$). The same was true for 1990–2000.

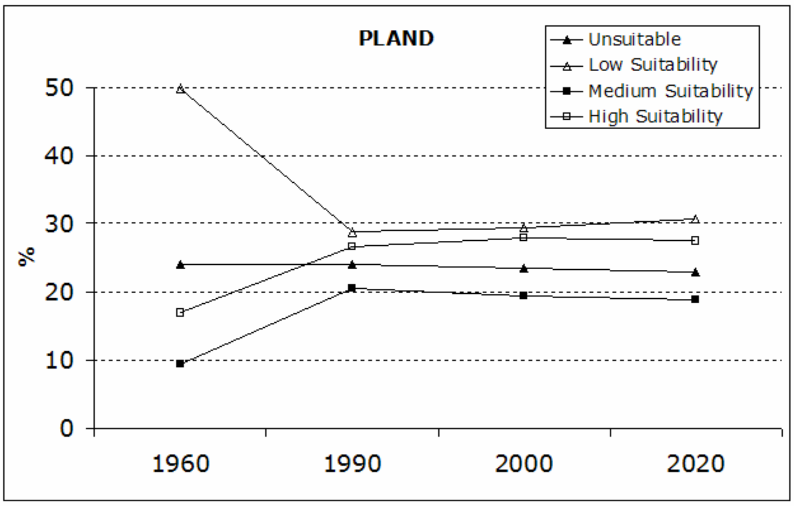

Figure 3. Percentage of the landscape (PLAND) in the four suitability classes from 1960 to 2020.

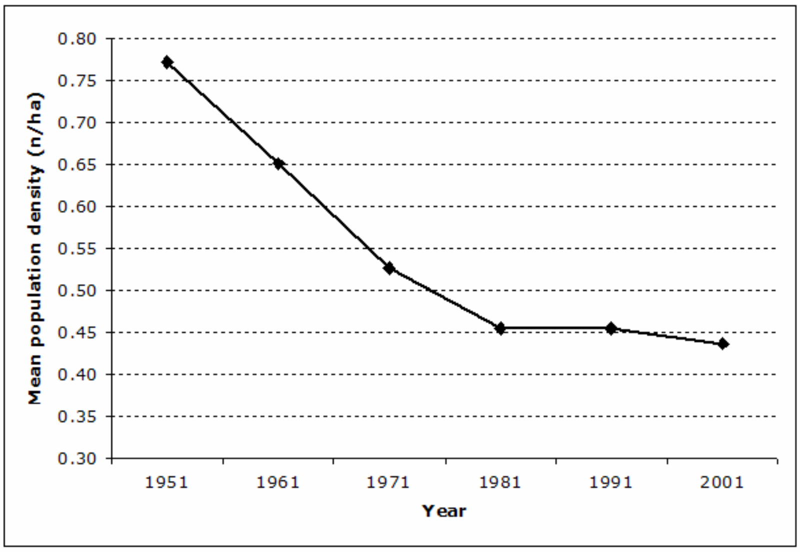

Figure 4. Median of human population density per administrative unit from 1951 to 2001 (data source: ISTAT).

Habitat availability and PAs

PAs cover more than 23% of the study area (523,000ha). Including also the NATURA2000 network, the percentage of PAs exceeds 38% of the study area (851,500ha).

If compared to the rest of the study area, PAs host a higher percentage of high and low suitability areas, and a lower percentage of unsuitable and medium suitability areas ($p<0.0001$) (Fig. 5), and the same results were obtained combining PAs and the NATURA2000 network.

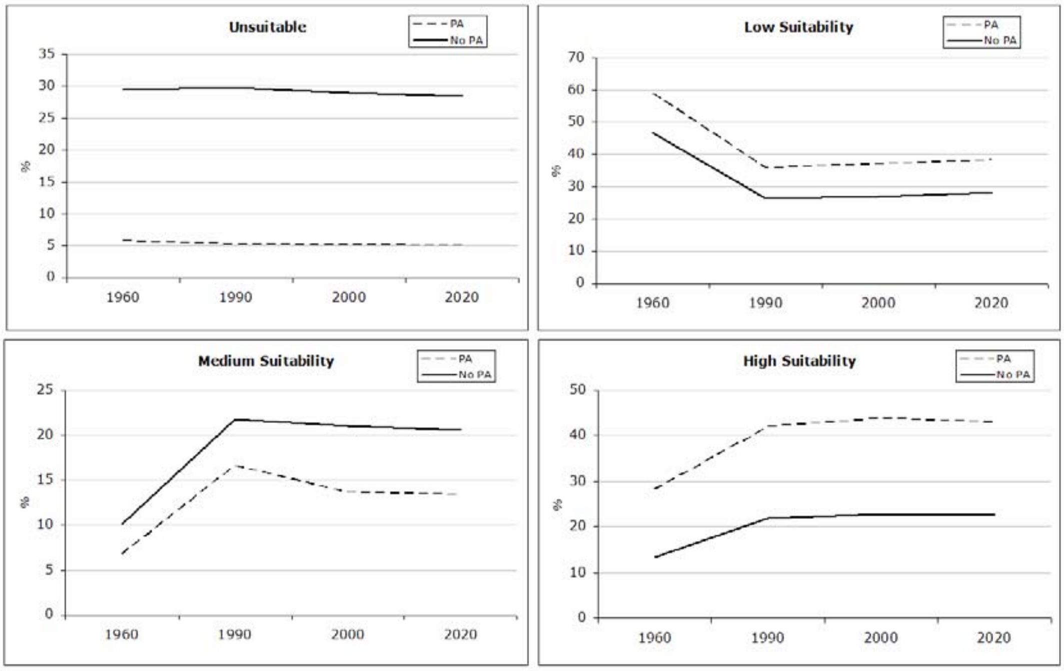

Figure 5. Percentage of protected areas (PA) and non protected areas (No PA) occupied by the different land-cover classes in the four time frames.

Habitat connectivity and landscape indexes

According to our least-cost-path analysis, in 1960 bear habitat in the PNALM appeared to be fairly well connected to the other PAs in the southern portion of the study area, although northward connections were limited. In 1990, the entire landscape was much more homogeneous, and the large-scale connectivity increased widely, with barriers to movement of the animals existing only in correspondence to intensively cultivated areas. In 2000 and in 2020, the connectivity within the landscape was similar to that estimated in 1990 (Fig. 6).

The landscape indices give indications comparable to those obtained with the least-cost-path analysis, suggesting a decreasing trend in the fragmentation of brown bear habitat.

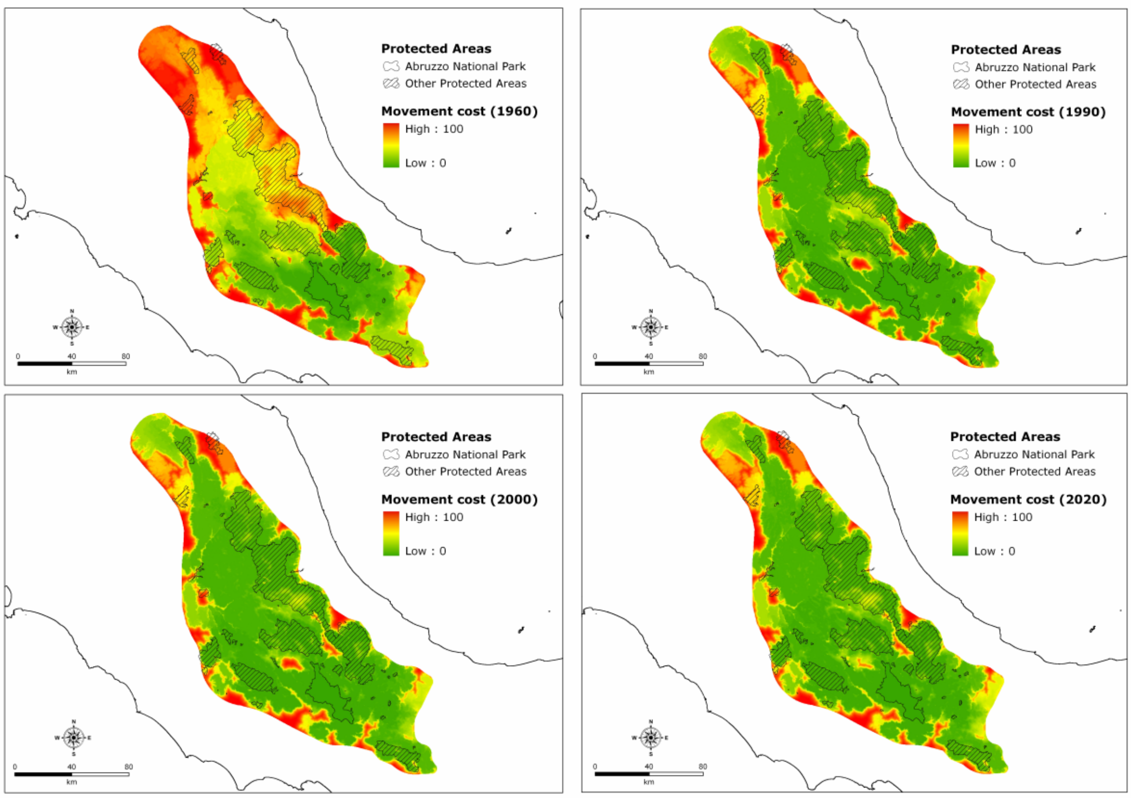

Figure 6. Brown bear movement cost from the Abruzzo National park to the other protected areas from 1960 to 2020, as estimated by the least-cost-path analysis, using suitability scores (cf. Table 2) as proxies for movement costs.

Most landscape indices calculated for the four time frames consistently show a different trend for the unsuitable and the low suitability versus the medium and high suitability areas (Fig. 7). In 1960, unsuitable areas were highly contiguous (low PN, high PLAND, and low NLSI), but in 1990, the NP for unsuitable areas increased and the LPI decreased, indicating an increasing fragmentation. Projections from 2000 to 2020 suggest a tendency toward increasing fragmentation of unsuitable areas, with NLSI, PLAND and LPI that should remain almost unchanged, while NP should decrease and ENNMD increase (Fig. 7).

We revealed a similar pattern for low suitability areas, which in 1960 represented the prevalent class (LPI=36%), but appeared increasingly fragmented in 1990 (PLAND<30%, LPI<5%, and both NP and NLSI increased with respect to 1960). Projections from 2000 to 2020 suggest that patterns of low suitable areas should stabilize or show a tendency towards higher fragmentation (Fig. 7).

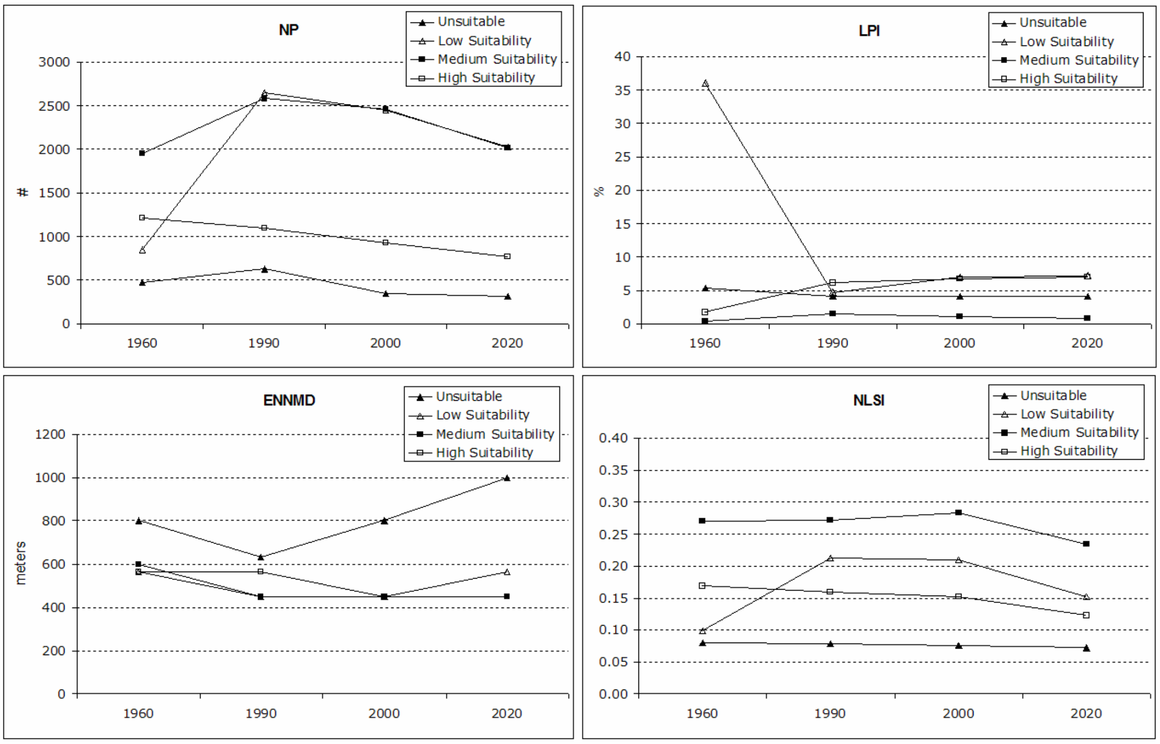

Figure 7. Landscape metrics (NP = Number of Patches; LPI = Largest Patch Index; ENNMD = Euclidean Nearest Neighbor Median Distance; NLSI = Normalized Landscape Shape Index; dimensionless) calculated for the entire study area in the four time frames.

Medium and high suitability areas showed different trends. In 1960, the two classes represented only a minor portion of the study area and were relatively fragmented (Fig. 7). In 1990, PLAND and LPI increased, while NP, NLSI and ENNMD decreased indicating a lower fragmentation. We revealed the same tendency for medium and high suitability areas for both 2000 and 2020.

Overall, by contrasting PAs and the rest of the study area (results not shown), we revealed a greater fragmentation for unsuitable areas and a lower fragmentation of high suitability areas. However, no temporal trends of the landscape metrics were detected between PAs and the rest of the study area.

Validation and sensitivity analyses

The 2020 land-cover change projection was performed 100 times. With just 5 simulations, more than 97.7% of the study area was always classified in the same land-cover class, and after 25 simulations the percentage did not change markedly (96.4%, 96.1% and 96.05% after 25, 50 and 100 simulations, respectively). The remaining areas of uncertain assignation (roughly 4% of the study areas) were small (median size=1ha) and located at the boundaries between land-cover classes.

The Boyce index calculated for 2000 was 0.8, indicating that the DM is sufficiently consistent with the evaluation dataset (bear presence data points).

As indicated by the Cramer’s V (mean value for 1960: 0.78±0.11; 1990: 0.85±0.06; 2000: 0.84±0.07; 2020: 0.82±0.07; all $p<0.001$) all 639 alternative DMs used for sensitivity analysis were similar to the final model.

Discussion

While we checked for validity and/or stability of all the models presented, we obviously had no way of validating the 2020 land-cover projection, which is based on the assumption that the land-use change pattern observed during 1990-2000 will remain constant up to year 2020. While indications provided by the 2020 projection should therefore be interpreted cautiously, the output of our LC projections in year 2020 was very stable already after 20 simulations providing additional support to our analyses. We recognize, however, that development projects (e.g., tourist and ski resorts, roads, wind farms) can drastically change the landscape, even within the limited time frame that we considered in our projection. Nevertheless, our 2020 projected landscape is based on layers (like distance from existing infrastructures, slope, and elevation) which can be considered as proxies for the probability of future developments, thus minimizing the possibility for unforeseen events altering the predicted landscape. In addition, most of the development projects that are currently considered will be implemented in areas of low suitability for the bear and near to current human settings (www.regione.abruzzo.it), and therefore they should not alter significantly the land-use change pattern in areas of high suitability.

The DM for 2000 was validated using field data, and the concordance between locations of bear presence and model predictions indicates that the deterministic approach we used provides a reliable synthesis of the species distribution in the study area. In the absence of proper datasets, no validation was possible for the DMs of the other time frames, but model sensitivity analyses (639 alternative models) showed extremely low departures to changes in habitat suitability scores, further supporting the reliability of the DMs for the scope of this analysis.

Overall, our results suggest that large-scale availability of suitable brown bear habitat is not a major issue for bear conservation, provided that recent and current trends in land-use are maintained. While increasing fragmentation of the natural landscape is continuing today in many developing regions of the world (e.g., Fuller et al. 2004; Sodhi et al. 2004), different trends have been observed in many parts of Europe (Ales et al. 1992; Garcia-Ruiz et al. 1996; Debussche et al. 1999; Falcucci et al. 2007). During the 20th century, traditional agriculture, grazing and forestry activities, following rural depopulation, became increasingly economically non-viable (Debussche et al. 1999; Olsson et al. 2000; Robinson and Sutherland, 2002). As a consequence, in spite of a long history of continuous human impacts, vegetation succession is progressing, particularly in the last few decades, towards forest re-establishment and spread (Laiolo et al. 2004; Falcucci et al. 2007). Accordingly, our analyses show that habitat availability for the Abruzzo brown bear has followed a similar pattern. In 1960, most of the study area was classified as unsuitable or low suitability, with small and fragmented areas of medium or high suitability. In 1990, the situation was different, with an increase of high suitability areas and of their connectivity, implying the possible occurrence of more secure movements throughout the entire study area. At the same time, unsuitable and low suitability areas became smaller and fragmented.

After 1990, we recorded very limited changes in the landscape in terms of land-cover classes and bear habitat suitability, and there appears to be limited possibility for a further increase in suitability up to year 2020. Currently, most of the remaining unsuitable areas are localized on lowlands, where agriculture and urbanization are the dominant features, and human population is not, and most probably will not, decrease. The least-cost-path analysis outlined that natural re-colonization by brown bears of the northern part of the study area is possible, and no major limitation to animal movement appears to be particularly relevant, at least at the landscape scale and according to the variables we modelled. Once more it is important to underline that our results for 2020 do not consider future developments, particularly roads and highways, considered among the most important barriers to bear movements (Swenson et al. 2000). Moreover, our results are tentatively confirmed by the recent presence of bear signs (camera-traps, sightings, scats) in the northern portion of the study area (Mt. Terminillo and M.ts Sibillini National Park; P. Ciucci and P. Forconi pers. comm.), at about 140 km from the PNALM and where the Abruzzo brown bear was considered extinct already by the 1930s (Boitani et al. 2003).

In summary, our models show that according to the land-cover changes that have occurred throughout the Italian peninsula, and in the absence of any habitat restoration intervention, habitat availability will not be an issue for bear conservation in the foreseeable future on the landscape scale. This indication is important in shaping and prioritizing renewed conservation efforts to ensure the survival of the species in central Italy.

However, it is important to underline that our results are valid for a landscape scale approach, and that land-cover and topography do not represent all ecological parameters which affect habitat suitability for bears. The focus of our landscape approach is to analyze major trends in habitat availability throughout the bear range since the 60’s, to project habitat availability for the entire bear population, and also to evaluate the large-scale connections among the different ‘core’ portions of the study area. However, moving from the landscape to the local scale (i.e., sub-population and home range scale), the increase in forests and the decrease in open areas that has been measured across the study areas (Falcucci et al. 2007), might in fact correspond locally to an overall lower trophic production for the bear. An example from the study area is represented by the many abandoned fruit-tree plantations found in many areas of high/medium suitability for the bear. These orchards are gradually changing to forests, a process registered as a positive effect on habitat suitability on the landscape scale, even though, on a local scale, abandoned plantations lose productivity at a rate of 50% every 10 years, reducing food availability for bears in the area. Therefore, we stress that the deterministic approach we followed at the landscape scale should be considered complementary to more fine-grained, inductive modelling at the local level. Such a modelling approach, based on environmental variables more directly linked to habitat productivity, is planned as collection of new radio-telemetry information, currently in progress (Ciucci and Boitani 2006), will produce a representative dataset.

Contrary to previous modelling efforts (Posillico et al. 2004), our approach is intentionally deductive and not based on field data, due to the scarcity of appropriate datasets, as well as to the indirect nature of most of the available information on bear presence and distribution. While regional governments in central Italy urge a spatially-explicit representation of landscape bear suitability to aid in land-use and conservation planning, we preferred to follow a deterministic approach, allowing for a safer but coarser extrapolation of the species-habitat relationships out of the occupied range.

According to our results, the PAs already established provide a reasonable representation of the bear area of occupancy (Maiorano et al. 2006). More than 23% of the study area is already protected, and if we also consider the NATURA2000 network that is being implemented, the percentage of the study area being protected exceeds 38%, making the possibility for additional PAs to be established in the future quite unrealistic. Moreover, PAs host a higher percentage of high suitability areas than the rest of the study area, a situation that most likely, according to our 2020 projections, should persist in the near future. In addition, our least-cost-path analyses suggest that bears can apparently move from one PA to another within the study area using areas with high and medium habitat suitability found outside PAs. Therefore these areas, potentially used as corridors by bears, should be considered as a fundamental component for any conservation strategy.

It is clear, however, that habitat protection alone does not represent per se a sufficient solution for bear conservation. This is clearly indicated by the number of bears accidentally killed and poached inside the PNALM boundaries (Posillico et al. 2002, L. Gentile pers. comm). Fifty-six bears have been found dead in the last 30 years in the PNALM and its buffer area (Wilson and Castellucci 2006), and in many cases (n=21) poaching was the cause of death.

A further limitation of a conservation strategy based solely on PAs is that human-related conflicts in the rest of the territory are not accounted for and managed efficiently, and this has been a severe limitation of the recent conservation policy, especially in light of the foreseeable expansion of the bear population from its core range. Our models show that medium suitability areas, corresponding among others with fruit tree and berry plantations, are more commonly found outside PAs. As these areas are potential feeding grounds for bears, they represent areas of potential conflict with human activities and should be treated accordingly if we want bears ranging outside the PNALM in the future and connecting among different core populations at the landscape scale.

Our results reinforce the indication that the conservation of the Abruzzo brown bear must focus most of its effort on issues other than establishing additional PAs and promoting further habitat restoration. The amount, configuration and connectivity of suitable habitat at the landscape scale seem appropriate to host a larger brown bear population and allow for the natural recolonization of parts of its former range. However, despite the positive trends in habitat suitability we revealed for the past 40 years, the bear population apparently continues to decrease (Wilson and Castellucci 2006). Direct conservation action aimed at reducing human-caused mortality in the core population appears extremely urgent, while, at the landscape scale, the level of connectivity indicated by our model should be preserved at any costs from potential developments or habitat alteration.

Acknowledgments

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References

Ales, R.F., A. Martin, F. Ortega and E.E. Ales. 1992. Recent changes in landscape structure and function in a Mediterranean region of SW Spain (1950-1984). Landscape Ecology 7:3-18.

Boitani, L., S. Lovari and A. Vigna-Taglianti. 2003. Fauna d'Italia. Mammalia III: Carnivora – Artiodactyla. Bologna: Calderini Ed.

Bologna, M.A. and A. Vigna-Taglianti. 1992. Osservazioni sull'areale dell'orso marsicano con particolare riferimento al Gran Sasso e ai Monti della Laga. Hystrix Italian Journal of Mammalogy 5:75-80.

Boscagli, G. 1999. Status and management of the brown bear in central Italy (Abruzzo). In Bears: status, survey and conservation action plan (eds C. Servheen, S. Herrero, and B. Peyton), pp. 81-84. IUCN SSC, Gland, Switzerland.

Bossard, M., J. Feranec and J. Otahel. 2000. The revised and supplemented Corine land-cover nomenclature. EEA. Copenhagen, Denmark.

Boyce, M.S., P.R. Vernier, S.E. Nielsen and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Bulgarini, F., E. Calvario, F. Fraticelli, F. Petretti and S. Sarrocco. 1998.. Libro rosso degli animali d'Italia, Vertebrati. WWF Italia. Roma, Italy.

Ciucci, P. and L. Boitani. 2006. Conservation of large carnivores in Abruzzo. A Research project integrating, species, habitat and human dimension. 2006 Annual Report. Wildlife Conservation Society, New York.

Corsi, F., J. de Leeuw and A. Skidmore. 2000. Modeling species distribution with GIS. In Research techniques in animal ecology: controversies and consequences (eds L. Boitani and T.K. Fuller), pp. 389-434. Columbia University Press, New York.

Corsi, F., E. Dupré and L. Boitani 1999. A large-scale model of wolf distribution in Italy for conservation planning. Conservation Biology 13:150-159.

Debussche, M., J. Lepart and A. Dervieux. 1999. Mediterranean landscape changes: evidence from old postcards. Global Ecology and Biogeography 8:3-15.

Eastman, J.R. 2001. IDRISI3.2 Release 2. Guide to GIS and image processing. Clark Labs, Clark University, Worcester, MA.

Fabbri, M., G. Boscagli and S. Lovari. 1983. The brown bear population of Abruzzo. Acta Zoologica Fennica 174:163-164.

Falcucci, A., L. Maiorano and Boitani. 2007. Changes in land-cover patterns in Italy and their implications for biodiversity conservation. Landscape Ecology 22:617-631.

Febbo, D. and M.Pellegrini. 1990. The historical presence of the brown bear on the Apennines. Aquilo 27:85-88.

Fuller, D. O., T.C. Jessup and A. Salim. 2004. Loss of forest cover in Kalimantan, Indonesia, since the 1997 – 1998 El Niño. Conservation Biology 18:249-254.

Garcia-Ruiz, J.M., T. Lasanta, P. Ruiz-Flano, L. Ortigosa, S. White, C. Gonzalez and C. Marti. 1996. Land-use changes and sustainable development in mountain areas: a case study in the Spanish Pyrenees. Landscape Ecology 11:267–277.

Hirzel, A.H., G. Le Lay, V. Helfer, C. Randin and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199:142-152.

Laiolo, P., F. Dondero, E. Ciliento and A. Rolando. 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. Journal of Applied Ecology 41:294-304.

Johnson, C.J. and M.P. Gillingham. 2005. Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. Journal of Applied Ecology 41:1032-1041.

Maiorano, L., A. Falcucci and L. Boitani. 2006. Gap analysis of terrestrial vertebrates in Italy: priorities for conservation planning in a human dominated landscape. Biological Conservation 133:455-473.

McGarigal, K. and B.J. Marks. 1995. FRAGSTAT. Spatial analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW-GRT-351.

Olsson, E.G.A., G. Austrheim and S.N. Grenne. 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960-1993. Landscape Ecology 15:155-170.

Ott, L., R.F. Larson and W. Mendenhall. 1983. Statistics: a tool for the social sciences. Boston: Duxbury Press.

Posillico, M., A. Petrella and L. Sammarone. 2002. Piano preliminare di conservazione dell'orso bruno (*Ursus arctos* L. 1758). Progetto LIFENAT99/IT/006244. Ministero delle Politiche Agricole e Forestali – Commissione Europea, 48 pp.

Posillico, M., A.Meriggi, E. Pagnin, S. Lovari and L. Russo. 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. Biological Conservation 118:141-150.

Randi, E., L.Gentile, G. Boscagli, D. Huber and U.U. Roth. 1994. Mithocondrial DNA sequenze divergence among some west European brown bear (*Ursus arctos* L.) populations. Lessons for conservation. Heredity 73:480-489.

Ray, N. and M.A. Burgman. 2006. Subjective uncertainties in habitat suitability maps. Ecological Modelling 195:172-186.

Robinson, R.A. and W.J. Sutherland. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology 39:157-176.

Sæther, B–E, S.Engen, J.E. Swenson, Ǿ. Bakke and F. Sandegren. 1998. Assessing the viability of Scandinavian brown bear, *Ursus acrtos*, populations: the effects of uncertain parameter estimates. Oikos 83:403–416.

Sodhi, N.S., L.P. Koh, B.W. Brook and P.K.L. Ng. 2004. Southeast Asian biodiversity: an impending disaster. Trends of Ecoogy and Evolution 19:654-660.

Swenson, J.E., N.Gerstl, B. Dahle and A. Zedrosser. 2000. Action plan for the conservation of the brown bear (*Ursus arctos*) in Europe. Nature and Environment 144:1-69.

Taberlet, P., J.E.Swenson, F. Sandegren and A. Bjärvall. 1995. Localization of a contact zone between two highly divergent mitochondrial DNA lineages of the brown bear Ursus arctos in Scandinavia. Conservation Biology 9:1255-1261.

Turner, M.G., R.H. Gardner and R.V. O'Neill. 2001. Landscape Ecology in theory and practice. Pattern and process. New York: Springer–Verlag.

Vigna Taglianti, A. 2003. *Ursus arctos*. Note di sistematica. In Fauna d'Italia. Mammalia III: Carnivora – Artiodactyla (eds L. Boitani, S. Lovari and A. Vigna-Taglianti), pp. 87-92. Calderini Editrice, Bologna:

Walker R. and L. Craighead. 1997. Least-cost-path corridor analysis: analyzing wildlife movement corridors in Montana using GIS. Proceeding of the 1997 ESRI User's Conference.

Wiegand, T., J. Naves, T. Stephan and A. Fernandez. 1998. Assessing the risk of extinction for the brown bear in the Cordillera Cantabrica, Spain. Ecological Monograph 68:539-570.

Wieglus, R.B. 2002. Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biological Conservation 106:381-388.

Wilson, C.J. and C. Castellucci. 2006. The Apennine brown bear and the problem of large mammals in small populations. Ecos 27:75-81.

Woods, J.G., D. Patkau, D. Lewis, B.N.McLellan, M. Proctor and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616-627.

Zedrosser, A., B.Dahle, J.E. Swenson and N. Gerstl. 2001. Status and management of the brown bear in Europe. Ursus 12:9-20.

NOT ONLY ENVIRONMENTAL SUITABILITY: CONSERVATION OF THE ABRUZZO BROWN BEAR REQUIRES MORE

Introduction

Once distributed along most of the Apennines, the Italian endemic Abruzzo brown bear (*Ursus arctos marsicanus*) is now restricted to a limited area in central Italy (Fig. 1) because of habitat loss and direct persecution (legal hunting before 1938 and poaching afterwards; Fabbri et al. 1983; Febbo and Pellegrini 1990). Current population size is unknown, but the number of bears probably does not exceed 40-60 individuals (Boitani et al. 2003), well below what is required for a viable population (Wiegand et al. 1998; Wieglus 2002; but see Sæther et al. 1998).

The subspecies is protected by law and the Abruzzo-Lazio-Molise National Park (PNALM), along with other adjacent protected areas, has been instituted to secure its conservation. The Abruzzo brown bear is considered endangered by the Italian WWF red list (Bulgarini et al. 1998), and critically endangered by the IUCN Red List (L. Boitani pers. com.). Moreover, Swenson et al. (2000) consider the subspecies as highly threatened; CITES includes the Abruzzo brown bear in its Appendix II; the European Community lists the bear in the Bern convention (1979) as strictly protected, and in the Habitat Directive (1992), as endangered.

Today, brown bears in central Italy exist as a remnant, isolated population (Randi et al. 1994) inhabiting 5000–8000 km^2 (Fig. 1). However, the most densely and steadily occupied area is only 1500–2500 km^2 wide, mainly in the PNALM and surrounding areas (Bologna and Vigna-Taglianti 1992; Boscagli 1999; Meriggi et al. 2001; Posillico et al. 2004). Dispersing individuals from this population can be found in other parts of the central Apennines, like the Terminillo area and the M.ts Sibillini National Park, where signs of presence (obtained with camera-traps, sightings, and scats) have been recorded (P. Ciucci and P. Forconi pers. comm.; Fabbri et al. 1983).

Posillico et al. (2004) identified more than 12,000 km^2 of suitable bear habitat in the Apennines and suggested a population density in the core area of 1 bear/50-80 km^2. This implies sufficient habitat for at least 150-240 bears. In fact, the current core bear range is composed mainly of good quality habitat, with extensive ancient beech forest, and earlier studies have indicated that this rich environment could probably support even more than the current densities (Wilson and Castellucci 2006).

Moreover, Falcucci et al. (submitted) showed that according to land-cover changes that occurred throughout the Italian peninsula from 1960, and in the absence of any direct habitat restoration intervention, habitat availability will not be an issue for bear conservation in the foreseeable future (2020) on the landscape scale. However, the Abruzzo brown bear population apparently continues to decrease (Wilson and Castellucci 2006).

Therefore, it is clear that habitat protection alone does not represent *per se* a sufficient solution for bear conservation. This is clearly indicated by the number of bears accidentally killed and poached inside the PNALM boundaries (Posillico et al. 2002, L. Gentile pers. comm). Fifty-six bears have been found dead in the last 30 years (from 1970 to 2005, 88 bears are reported to have been killed, see Castellucci 2004) in the PNALM and its buffer area (Wilson and Castellucci 2006), and in many cases (n=21) poaching was the cause of death.

Direct conservation action aimed at reducing human-caused mortality in the core population appears extremely urgent. Even more important would be a conservation strategy that accounts for and efficiently manages human-related conflicts, not only in the protected areas, but especially in the rest of the territory. This has been a severe limitation of the recent conservation policy, especially in light of the foreseeable expansion of the bear population from its core range (Falcucci et al. submitted).

Most often, researchers have focused on habitat selection and spatial distribution of bear habitats (Posillico et al. 2004; Falcucci et al. submitted) assuming that the identification of areas most frequently occupied by animals represent high quality habitats (Garshelis, 2000). However, this assumption is rarely met (Van Horne 1983; Nielsen et al. 2006) and it is even possible that areas frequented by animals (i.e. areas identified as high quality in habitat models) represent attractive sinks, i.e. areas where resources are abundant and reproductive potential could be high but, at the same time, the risk of mortality is high (Delibes et al. 2001a, 2001b; Naves et al. 2003).

Identifying attractive sinks as high quality habitat would be misleading for management and conservation action. Recognizing this phenomenon within habitat models is therefore crucial for fully representing habitat quality and ultimately for the management of species of conservation concern. Research that identifies mortality sinks, or the opposite secure high-quality sites (source-like habitat), as it relates to human features, terrain, and vegetation, is important if the goal is to maintain future populations of bear.

Although substantial information on the spatial occurrence of bear populations exists, relatively little has been done to examine how spatial factors, especially human-related features, influence human-caused bear mortality in local populations (see however, Johnson et al. 2004; Mattson and Merrill, 2002). It is well accepted that survival, particularly of adult females, is the most important factor shaping population growth and long-term viability of grizzly bear populations (Wiegand et al. 1998; Pease and Mattson, 1999; Boyce et al. 2001). Given the threatened status and the supposed decline of the Abruzzo brown bear population, the identification of mortality sinks (Knight et al. 1988) is crucial to the future conservation of this small population.

Recently, Naves et al. (2003), using only presence-absence data, incorporated both survival and reproduction data into a spatial framework for defining brown bear habitats in northern Spain. Nielsen et al. (2006), using mortality and presence data of adult females, elaborated a framework for identifying attractive sink and source-like habitat for grizzly bears in west-central Alberta, Canada.

Such modeling approaches are attractive management tools for identifying conservation needs because they record attractive sinks and source or secure habitats. Both habitat states provide managers with 2 separate conservation strategies: (1) preservation and protection of existing source and secure areas to impede habitat degradation; and (2) mitigation of sites where habitat conditions are excellent, but risk of mortality is high and manageable (Nielsen et al. 2006).

Following these approaches, our goal was to produce a more realistic habitat model for the Abruzzo brown bear, developing a framework for distinguishing attractive sink and source-like habitats for the subspecies in central Italy. We used presence-only algorithms to model both mortality risk and habitat distribution. Moreover, we developed a framework that can be used to expand the identification of attractive sink and source-like habitats outside of the areas of stable presence for the species. Our model could help to predict the potential distribution of brown bears in the study area, as well as to identify critical areas for the expansion and the conservation of the population.

Study area

Our study area covers 9,940 km^2, corresponding to the entire range of the Abruzzo brown bear (Fig. 1). The boundaries of the study area have been drawn considering the existing protected areas (4 National Parks, 2 Regional Parks, and several other smaller protected areas) where the presence of the bear has been recorded (scats, hair samples, tracks, and camera-traps) in the last 10 years (Parchi News newsletter, October 2006). Where no protected area was present we considered existing roads, rivers and administrative boundaries (all the environmental layers considered are described under the paragraph "Predictor variables").

The study area is dominated by mountains (mean elevation 1,134 m, sd 407 m), and it is covered mainly by deciduous and mixed forest (essentially beech forests).

Within the study area, we distinguished 3 zones: the core area, representing the area where the Abruzzo brown bear has always been present and where it is possible to find the highest densities (1 bear/50-80 km^2, Lorenzini and Posillico 2000); the marginal area, where the presence of the species is not stable and densities are very low (Ciucci and Boitani 2004; Posillico et al. 2004), and two flats areas: the Aterno valley and the Fucino area (Fig. 1).

The core area covers 2,402 km^2, with a mean elevation of 1,220 m (sd 395 m). The marginal area covers 6,381 km^2, with a mean elevation of 1,183 m (sd 391 m). The two areas have similar land-cover characteristics (Table 1), being covered mainly by "natural" land-cover classes (e.g. beech forest, prairies, and oak forest). Also human population densities in the two areas are really similar (core area: mean 0.24, std 2.72 n/km^2; marginal area: mean 0.16, sd 1.86 n/km^2), as is the case for distance to roads (Table 2).

Taken together, the Aterno valley and the Fucino area are significantly different from the rest of the study area, with a different elevation (mean 720m and sd 212m), with a land cover composition that is different from those of the core and marginal areas

(Table 1), and with higher population densities (Aterno: mean 1.96, sd 9.57 n/km^2; Fucino: mean 1.83, sd 9.92 n/km^2) and higher street densities (Table 2) with primary roads being extremely important (Wilks' Lambda = 0.635, $p<0.0001$; test performed over land-cover, distance to roads, elevation and population density measured for 578 random points in the Fucino area plus the Aterno valley and for 3390 random points over the rest of the study area, corresponding to 1 random point per km^2). Thus, we excluded the two areas from any further analyses, given that they are characterized by the development of industrial, commercial, and agricultural activities, which prevent the establishment of a bear population.

Hereafter, when we refer to the study area we are considering only the core and the marginal areas.

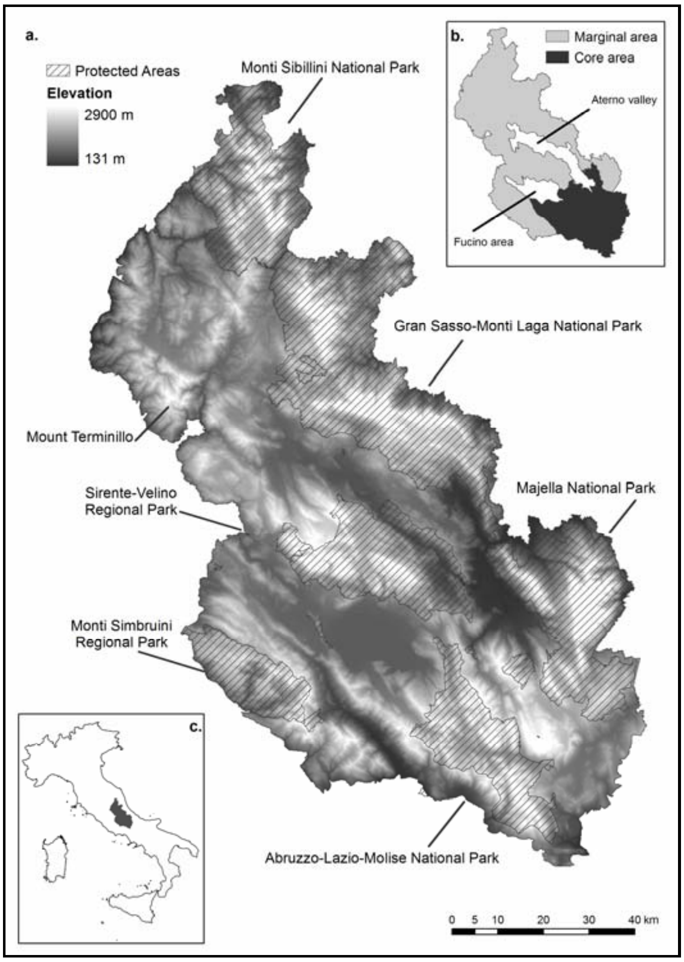

Figure 1. a. Protected areas and elevation in the study area; **b.** Core area, marginal area, Aterno valley and Fucino area; **c.** Location of the study area in Italy.

	Core area	Marginal area	Aterno valley	Fucino area
Artificial	0.7	0.5	5.3	5.4
Intensive agriculture	3.7	4.3	28.3	63.1
Pastures	5.1	2.7	5.1	2.1
Heterogeneous agriculture	4.4	5.8	11.5	13.3
Forest	50.3	53.3	14.1	5.1
Shrubs/erbaceous vegetation	33.6	30.6	35.3	11.0
Open spaces with little or no vegetation	2.3	2.8	0.3	0.0

Table 1. Land-cover composition (given in percentages) for core area, marginal area, Aterno valley, and Fucino area.

	Primary	Secondary	Urban
Core area	1,687 mean 1,490 std	826 mean 720 std	3,028 mean 1,731 std
Marginal area	1,481 mean 1,294 std	794 mean 760 std	2,784 mean 1,780 std
Aterno valley	610 mean 592 std	359 mean 379 std	1,237 mean 813 std
Fucino area	462 mean 426 std	274 mean 245 std	1,384 mean 1,021 std

Table 2: Distance to roads (m) for the core area, the marginal area, the Aterno valley, and the Fucino area.

Materials and Methods

Mortality data

The PNALM Scientific Service kindly provided the dataset on bear mortality. The dataset includes 56 locations acquired from 1980 to 2003. We considered only 27 human-caused mortality records (15 poaching, 3 car accident, 4 train accident, 4 poisoning, and 1 contagious disease). We excluded all the records of natural mortality, mortality for unknown cause, or with no UTM coordinate. Twenty human-caused mortality events out of the 27 considered were registered between May and October, no event was registered in April, and 7 events were registered from November to March. The 27 records considered in the analysis represent independent events; in fact the two closest locations are 353m apart, but occurred in a 2 year time frame.

Presence data

We obtained data on bear presence by merging different datasets. The PNALM Scientific Service provided 1451 points (sightings, tracks and signs) acquired from 1999 to 2003. P. Ciucci provided 125 sightings collected in 2006. The Forestry Service (Ufficio Territoriale per la Biodiversità di Castel di Sangro) provided 304 locations of sampled Abruzzo brown bear hairs (with >95% probability of being bears on a genetic basis) acquired from 2000 to 2003 (Randi et al. 2004). P. Ciucci provided radio-tracking point data for 8 animals (5 females and 3 males; a total of 12,800 fixes) collected from 2005 to 2006. The presence points were distributed over the entire course of the year, with lower numbers during the winter and higher during the summer months.

To ensure spatio-temporal independence, we removed, from each dataset, all the records that were, at the same time, within a distance of 500m and within a time frame of 1 day, obtaining a final database with 5986 points.

We used the first two datasets (sightings, tracks and signs for a total of 1399 points) to build the habitat distribution models because they cover a larger area and a larger time-frame (not only more years but also a more homogeneous coverage of months). We used the other two datasets (hair samples, 239 points, and radio-tracking data, 4348 locations) for the validation process because, even though the number of points is higher if compared to the available sightings, track and signs, the spatial coverage is more limited and the temporal coverage is biased towards May-October.

Predictor variables

To characterize the study area we considered elevation, land-cover, road network, and human population density, for a total of 17 variables. All the layers considered were re-sampled for the analysis using a common origin and 100m cell size.

The digital elevation model (DEM) was provided by the Italian Military Geographic Institute already in ArcGIS raster format, with a cell size of 20m. We used the DEM to calculate the percent slope and we used a Box-Cox transformation in order to normalize both the DEM and the slope.

The CORINE Land Cover (CLC; EC 1993) was provided by the Italian Ministry of the Environment – Directorate for Nature Conservation already in ArcGIS shape-file format. In particular we used the CLC IV level, which has a 66 class legend and a spatial detail comparable to that of a paper map on a scale of 1:100,000.

Only 39 of the original 66 CLC land-cover classes are present in the study area. Artificial classes (6 classes) are very marginal (0.8% of the core area, 0.5% of the marginal area, 1.1% of the entire study area) and have been removed. Human impact has been taken into account using population density and distance to road as described below. We aggregated the remaining 33 land-cover classes into 10 categories relevant for the ecology of the subspecies: intensive agriculture, pasture, heterogeneous agriculture, oak forest, beech forest, broadleaf forest, mixed forest, prairies, moors and barren areas. We also used the CLC to calculate a layer of distance to forest edges, considering oak, beech, broadleaf and mixed forests.

The road network was produced by De-Agostini-GeoNext and TeleAtlas in 2003, distinguishing 8 structural classes. We re-classified roads into three main categories: urban, secondary and primary roads and for each category we calculated a layer of distance to roads.

Human population censuses for 2001 were provided by the Italian Institute of Statistics in ArcGIS shape-file format, distinguishing urban and rural population to the smallest available census unit (comparable to that of a paper map on a scale of 1:10,000).

In order to account for possible errors in the environmental layers, in the bear presence dataset, and in the mortality datasets, and in order to obtain 17 continuous variables we ran a map-algebra focal function over all 17 layers to assign to the central pixel of a circular window (500m radius) the mean value calculated over the entire window for continuous variables, or the count of all cells included in the window and belonging to each category for categorical variables. In all the subsequent analysis, we used the 17 layers resulting from the map-algebra focal function.

To avoid using too highly correlated variables that can create problems in the habitat suitability modeling process we calculated an UPGMA tree with Pearson correlations among the 17 quantitative variables using BioMapper3.2 (Hirzel et al. 2002).

Distribution model

We used environmental niche factor analysis (ENFA; Hirzel et al. 2002) to build the distribution model (DM) for the Abruzzo brown bear.

Starting from a set of environmental variables ENFA extracts all relevant information while discarding the correlation among variables and the background noise. It does so using mathematical tools similar to PCA and calculating new uncorrelated ecological predictor variables. The first of these new variables maximizes the absolute value of the marginality, i.e. the standardized difference between the species mean and the global mean on all the descriptors. The marginality coefficients range from -1 to +1, with positive values indicating a species' optimum higher than the average conditions in the study area, and negative values indicating a lower species' optimum. All the subsequent new variables maximize the specialization, i.e. the ratio of the global variance to the species variance. The specialization coefficients go from -1 to +1, with larger absolute values indicating species with larger niche breadth and smaller absolute values indicating species with smaller niche breadth. To give an overall idea of a species' ecology, the ENFA algorithm calculates also the global marginality and the global tolerance. Both measures range from 0 to 1 and the first gives an idea of how much the species habitat selection is different from the mean habitat conditions that it is possible to find in the study area (the higher the value the higher the difference), the second gives an indication of the species' niche breadth, with 0 indicating a small niche breadth (a "specialist" species) and 1 indicating a large niche breadth (a "tolerant" species). Further details on ENFA can be found in Hirzel et al. (2002).

Even though ENFA has been shown to be robust to the bias produced by species that are not at equilibrium with their environment (Hirzel et al. 2001), it is always advisable to give particular attention to such situations. Thus, we built two different DMs using the same set of 1399 presence locations for both. In particular, we built one model considering only the core area (i.e. the area where the species is present with the highest density and where it can be considered at equilibrium with its environment), and one considering the entire study area (thus including all the areas where the species is expanding its range). The core-area model represents the baseline over which it is possible to compare the study area model.

To verify that the two models describe bear’s habitat selection and habitat suitability in the same way, we measured Pearson correlation between suitability scores in the two and we compared global marginality, global specialization, and relative importance of different environmental variables in the two ENFA analyses.

We reclassified the study area DM into 5 discrete suitability classes (original values ranging from 0 to 100): unsuitable (0), low or marginal suitability (1st quartile of the habitat suitability model values), medium or moderate suitability (2nd quartile), high suitability (3rd quartile), and the optimum suitability (4th quartile).

Human-caused mortality model

We used the same procedure described above to build two models of suitability for human-caused mortality (MM) considering the 27 available mortality locations.

In particular, we built a MM for the core area and a MM for the study area, we calculated Pearson correlation between the two models, and we compared global marginality, global specialization, and the relative importance of the different environmental variables in the two ENFA analyses.

We reclassified the study area MM (original values ranging from 0 to 100) into 5 classes of suitability for mortality: unsuitable (0), low or marginal suitability (1st quartile), medium or moderate suitability (2nd quartile), high suitability (3rd quartile), and the optimum suitability (4th quartile).

Model validation

To evaluate the distribution and the mortality models, we used the Boyce index (Boyce et al. 2002; Hirzel et al. 2006) calculated using the predicted/expected ratios for each suitability class. The index goes from -1 to 1, with negative values indicating an incorrect model, which predicts poor quality areas where presences are more frequent, with positive values indicating a model whose predictions are consistent with the presence distribution in the evaluation dataset, and with values close to zero indicating that the model is not different from a chance model. The index is built calculating the predicted (percentage of validation points falling in the suitability class) vs expected (proportion of the map’s total area occupied by the suitability class) ratio for each suitability class.

In particular we calculated a Boyce index for the 239 hair-sample locations and one for the 4348 radio-tracking presence locations for both the study area DM and the core DM This proviede more confidence in the model results, because we compared the distribution model against two independently collected datasets, and we avoided pooling points collected using different techniques and different time frames.

No independent dataset was available for the validation of the mortality model. Thus we used a jackknife procedure (Fielding and Bell 1997) over the 27 human-caused mortality locations to calculate the Boyce index for both the core MM and the study area MM. Here, the predicted percentages were obtained assigning at each of the 27 points the mortality class calculated with a model built using the remnant 26 locations. The expected percentages were calculated using the MM built with all the 27 mortalities locations.

To evaluate the stability of the final MM we also developed 147 alternative MMs. We realized 27 of these models using 26 points out of the original 27 mortality points; we realized 20 MMs using 20 different sets of 25 randomly selected mortality points (20 couples of points selected at random were excluded from the analyses); we realized 20 MMs using 20 different sets of 24 randomly selected mortality points (20 triplets of points selected at random were excluded from the analyses), and so on till 20 model that were realized with 20 different sets of 20 randomly selected mortality points (20 sets of 7 points selected at random were excluded from the analyses).

Two-dimensional habitat model

We merged the reclassified DM and MM for the study area to obtain the final two-dimensional habitat model for the bear. In particular, we defined 5 habitat states (Fig. 2): unsuitable, primary sink, secondary sink, primary habitat, and secondary habitat. Unsuitable habitat was defined by the combination of unsuitable pixels in the distribution models and any possibility of the mortality model. Secondary sink and secondary habitat were both defined using marginal and moderate suitability in the distribution model but were distinguished according to the mortality model (with higher mortalities giving secondary sinks and lower mortalities giving secondary habitats). Primary sink and primary habitat share high or optimum suitability in the distribution model, but primary sink have high or optimum in the mortality model, while primary habitat has moderate or lower for mortality.

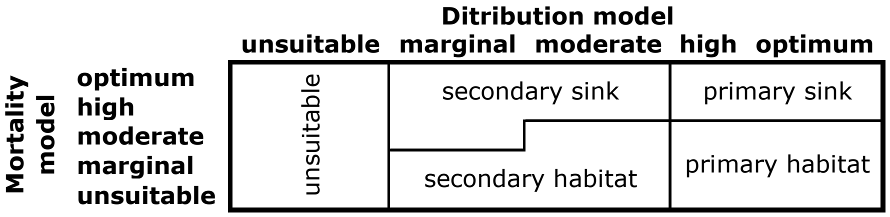

Figure 2. Five habitat state for the two-dimensional model.

Results

Mortality data

Human-caused mortality events are on the average closer to any type of road than all the other mortality events. In particular, there is a significant difference (tested with a Wilcoxon test) between human-caused and the other mortality locations in the distance to main roads (median distances respectively of 1,204m and 2,692m; z=2.3326, *p*=0.0197) and in the distance to urban roads (median distances respectively of 1,612m and 3,228m; z=2.6216, *p*=0.0088), while there is not a significant difference in the distance from secondary roads (median distances respectively of 1,204m and 2,692m; r=1.1058, *p*=0.2688). We also found that human-caused mortality events are located at significantly lower elevations compared to the other mortality events (median elevation respectively of 1019m and 1311m; z=2.9784, *p*=0.0029).

Predictor variables

All the correlation coefficients measured among the environmental variables were lower than 0.6, and only 2 were greater than 0.5: elevation vs secondary road, and beech forest vs distance to forest edge. Thus, considering that ENFA is quite robust even in presence of highly correlated variables (Hirzel et al. 2002), we kept all 17 predictors for DM.

For the MM, we used only 16 predictor variables. We excluded "barren areas" because a preliminary ENFA analysis showed that it is not important to define the environmental characterization of mortality events.

Distribution model

The suitability scores obtained for the study area DM and for the core DM were highly correlated ($r=0.97$; $p<0.0001$) and the ENFA analyses performed for the two models gave extremely similar results, with comparable global marginality and global tolerance values (Table 3), and with comparable marginality and specialization structure (Table 4) indicating that study area DM explains the distribution and ecology of the species in the same way as the core DM.

For the study area DM analysis we kept the first eight factors (the marginality plus the first 7 specialization factors), for a total explained information of 90.7% (Table 3) (100% of the marginality and 81.3% of the specialization). In this case, the marginality factor explained little of the specialization (7%) (Table 4), meaning that the bear niche breadth was not particularly narrow for the variables for which its optimum was the furthest from the average conditions.

The overall marginality value of 0.839 (Table 3) indicates that the Abruzzo brown bear prefers habitat conditions that are different from the mean conditions measured over the study area. In particular beech forests, elevation, distance to primary roads, distance to urban roads, and distance to forest edges are positively selected, while intensive and heterogeneous agriculture, broadleaf forest, and high human population densities are avoided (Table 5).

The tolerance value of 0.576 (Table 3) indicates that the species is not too picky with respect to the environmental conditions that it is possible to find in the study area. However, it is more specialized over intensive and heterogeneous agriculture; oak, broadleaf, and beech forest; prairies and moors.

	Study area-DM	Core-DM	Study area-MM	Core-MM
Explained Information	90.7	90.3	90.8	89.5
Marginality	0.839	0.773	0.757	0.672
Tolerance	0.576	0.606	0.490	0.521

Table 3. Main results of the ENFA analysis for the distribution models and the human-caused mortality models.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
Study area-DM	7%	27%	11%	10%	9%	7%	5%	4%
Core-DM	10%	25%	12%	11%	8%	6%	5%	4%
Study area-MM	22%	22%	19%	10%	9%	---	---	---
Core-MM	26%	22%	14%	10%	7%	---	---	---

Table 4. Percentage of the explained information in each factor of the ENFA analysis for the distribution models and the human-caused mortality models.

Predictor variable	Factor 1[a]	Factor 2[b]	Factor 3[b]	Factor 4[b]	Factor 5[b]	Factor 6[b]	Factor 7[b]	Factor 8[b]
intensive agriculture	-	**	**	***	***	*	***	0
heterogeneous agriculture	--	**	***	0	*******	0	0	**
oak forest	--	****	***	****	***	***	**	****
broadleaved forest	--	***	***	****	0	****	*	0
mixed forest	+	**	**	**	*	**	0	0
beech forest	++++	*****	*****	*****	***	****	***	0
pasture	0	**	**	*	*	*	**	*
prairies	-	*****	****	****	**	****	**	*****
moors	-	***	***	***	*	****	***	***
barren	+	**	**	*	*	**	**	*
distance forest edge	++	0	*	*	*	*	***	******
distance primary road	++++	0	0	0	0	*	0	0
distance secondary road	++	0	0	0	0	0	*	0
distance urban road	+++++	0	0	*	0	0	**	**
population density	--	*	*	***	***	*	*	*
elevation	++++	0	**	*	*	****	*******	*
slope	+	0	*	0	0	0	**	**

[a] Marginality factor. The symbol + means that the bear was found in locations with values higher than average. The symbol – means the opposite. The greater the number of pluses or minuses the higher the difference. 0 indicates small differences.

[b] Specialization factor. The symbol * indicates that the bears occupy a range of values that is narrower than the range available. The greater the number of asterix, the narrower the range. 0 indicates a very low specialization.

Table 5. Correlation between ENFA factors and the environmental variables for the study area distribution model.

Human-caused mortality model

The suitability scores obtained for the core MM and the study area MM were highly correlated (r=0.75; $p<0.0001$) and the ENFA analysis performed for the two models gave similar results, with comparable global marginality and global tolerance values (Table 3), and with comparable marginality and specialization structure (Table 4), indicating that the study area MM describes the distribution of human-caused mortality in the same way as the core MM.

For the study area MM we kept the first five factors, that explain 90.8% (Table 3) of the information available in the original variables (100% of the marginality and 81.6% of the specialization). The marginality factor explained also 22% of the specialization (Table 4), meaning that the bear mortality breadth is relatively narrow for the variables for which its optimum was the furthest from the average conditions.

The overall marginality value of 0.757 (Table 3) indicates that human-caused mortality events occur in environmental conditions that are on average different from the mean values measured in the study area. In particular, human-related mortality events occur mainly in areas with high levels of pasture and broadleaf forests, and in areas with limited presence of prairies, with lower distance to secondary and to urban roads, lower elevation and lower slope (Table 6).

The tolerance value of 0.49 indicates that human-related mortality events are not too specialized in relation to the overall range of conditions that prevail in the study area. However, there is a clear indication that mortality events have a low variance over some of the land-cover categories (oak, broadleaf, and beech forest, prairies, and barren), and for the distance to any type of road, the distance to forest edge, and elevation.

Predictor variable	Factor 1[a]	Factor 2[b]	Factor 3[b]	Factor 4[b]	Factor 5[b]
intensive agriculture	+	*	*	0	0
heterogeneous agriculture	-	*	0	0	*
oak forest	0	***	**	****	*
broadleaved forest	++	*	**	***	**
beech forest	0	**	*****	****	***
mixed forest	+	**	*	**	*
pasture	+++++++	*	0	0	*
prairies	----	****	*	*	******
moors	0	**	0	0	*
barren	-	***	***	***	*
distance forest edge	+	*	******	*****	*
distance primary road	+	*	*	0	**
distance econdary road	--	***	**	***	*
distance urban road	--	***	*	0	*
population density	0	*	0	0	*
elevation	--	*****	0	*	******
slope	---	**	*	**	0

[a] Marginality factor. The symbol + means that the bear was found in locations with values higher than average. The symbol – means the opposite. The greater the number of plusesor minuses the higher the difference. 0 indicates small differences.

[b] Specialization factor. The symbol * indicates that the bears occupy a range of values that is narrower than the range available. The greater the number of asterix, the narrower the range. 0 indicates a very low specialization.

Table 6. Correlation between ENFA factors and the environmental variables for the study area mortality model.

Model validation

The validation of the study area DM gave a Boyce index = 1 ($p<0.0001$) for both the hair sample locations and the radio-tracking data, indicating that the model is highly consistent with the presence distribution in the two independent evaluation datasets (Table 7).

The jack-knife validation for the study area MM gave a Boyce index = 0.7 ($p=0.1881$); even though the index was not statistically significant (because of the low number of classes and the low number of points) there is a clear indication that the model is consistent with the distribution of human-related mortality events. Moreover, the correlation among the study area MM and the alternative 147 MMs realized with a lower number of points was always really high (mean r=0.837; std=0.115) indicating a high stability of the MM.

DM & MM category	**Hair sample***	**Pi**	**Ei**	**Fi**	**Radio-tracking***	**Pi**	**Ei**	**Fi**	**Mortality events****	**Pi**	**Ei**	**Fi**
Unsuitable	4	0.0167	0.0611	0.2739	22	0.0051	0.0611	0.0828	0	0.0000	0.0571	0.0000
Marginal	23	0.0962	0.2644	0.3640	135	0.0310	0.2644	0.1174	7	0.2593	0.2726	0.9510
Moderate	38	0.1590	0.2075	0.7663	299	0.0688	0.2075	0.3314	6	0.2222	0.2760	0.8050
High	63	0.2636	0.2326	1.1331	910	0.2093	0.2326	0.8996	4	0.1481	0.1740	0.8514
Optimum	111	0.4644	0.2344	1.9815	2982	0.6858	0.2344	2.9261	10	0.3704	0.2202	1.6817

*Boyce Index = 1 $p<0.0001$

**Boyce Index = 0.7; jackknife approach

Pi: predicted proportion of validation points falling in category i

Ei: expected proportion of the map's total area occupied by category i

Fi: Pi/Ei

Table 7. Validation results for the study area distribution and mortality model.

Two-dimensional habitat model

More than 6% of the study area was classified as unsuitable, 31% was classified as a secondary sink, 12% as a primary sink, 16% as a secondary habitat, and 35% as a primary habitat (Fig. 3). No particular difference was measured in the percentages among the core and marginal areas considered independently (Table 8), with the exception of the primary habitat constituting 38.3% of the core area and of secondary sinks constituting 32.3% of the marginal area.

In general, protected areas host few areas classified as unsuitable (Table 8; from 0.4% of PNALM to 7.7% of Velino-Sirente-Duchessa Regional Park), while the areas classified as primary habitat are always dominant (from 64.4% of PNALM to 35.0% of Simbruini Regional Park).

More than 74% of the “barren areas” and more than 59% of “beech forests” are classified as primary habitats, while “agricultural areas” are mainly occupied by totally unsuitable areas (51.2% of intensive agriculture and 45.5% of heterogeneous agriculture are classified as totally unsuitable, Table 8). Secondary habitats occupy large areas of pastures (65.3%) and prairies (35.4%), but are rare in beech (3.5%) and broadleaf forests (5.8%), and in heterogeneous agriculture areas (5.6%). Primary sinks are important over beech (32.01%) and mixed forest (31.2%), but not in all the other land cover categories (from 0.5% of the heterogeneous agriculture to 4.5% of moors). Finally, secondary sinks occur primarily over broadleaf (83.9%) and oak forests (73.7%), and to a lesser extent over intensive and heterogeneous agriculture (41.1% and 47.9%) and over moors (45.1%) (Table 8).

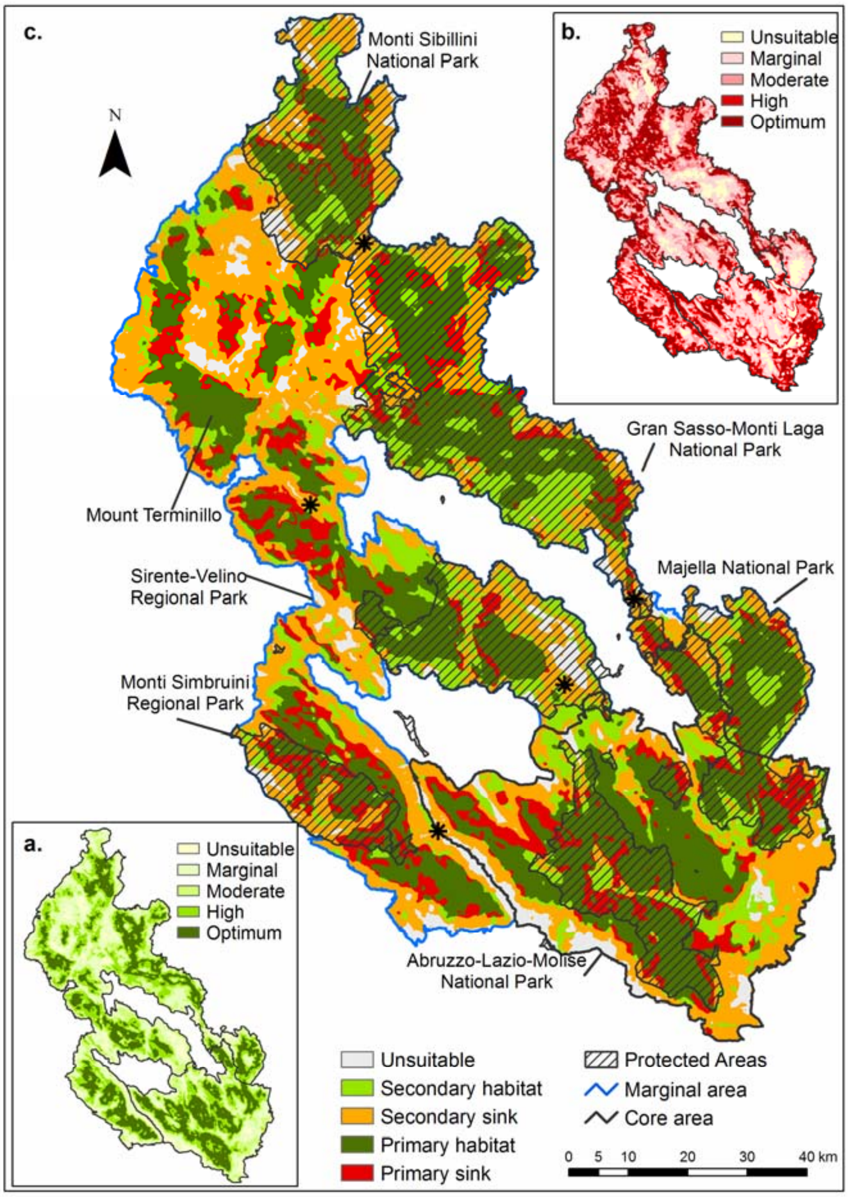

Figure 3. a) Distribution model for the Abruzzo brown bear; **b)** Human-caused mortality model for the Abruzzo brown bear; **c)** two-dimensional habitat model for the Abruzzo brown bear. The asterisks indicate obligate corridors that connect different parts of the study area; from the north and clock-wise: Sibillini NP-Gran Sasso-Laga NP; Gran Sasso-Laga NP-Majella NP; Abruzzo Lazio Molise NP-Silente-Velino RP; Abruzzo Lazio Molise NP-Monti Simbruini RP; Silente-Velino RP-Mt. Terminillo.

		Unsuitable	Secondary habitat	Primary habitat	Secordary sink	Primary sink
a)	**Core**	6.3	15.4	38.3	26.6	13.4
	Marginal	6.0	16.8	33.3	32.3	11.6
b)	**Abruzzo-Lazio-Molise (NP)**	0.4	10.4	64.6	7.8	16.8
	Gran Sasso-Monti Laga (NP)	2.2	21.6	41.7	23.5	10.9
	Majella (NP)	2.1	18.2	46.7	19.5	13.5
	Sibillini (NP)	7.7	16.6	38.1	30.1	7.5
	Simbruini (RP)	4.4	7.8	35.0	28.3	24.4
	Velino-Sirente-Duchessa (RP)	7.7	24.9	35.6	26.5	5.3
c)	**Intensive agriculture**	51.2	6.4	0.4	41.1	0.9
	Heterogeneous agriculture	45.5	5.6	0.4	47.9	0.5
	Pasture	5.4	65.4	14.1	11.1	4.0
	Oak forest	2.7	13.7	5.8	73.7	4.2
	Broadleaf forest	4.6	5.8	2.2	83.9	3.5
	Mixed forest	0.7	9.3	22.9	36.0	31.2
	Beech forest	0.0	3.5	59.2	5.3	32.0
	Moors	2.6	13.0	34.8	45.1	4.5
	Barren areas	0.0	18.0	74.9	4.7	2.4
	Prairies	1.0	35.5	45.9	16.3	1.3

Table 8. Percent composition of the 5 habitat state values for a) marginal and core area, b) protected areas (NP=national park, RP=regional park), and c) land-cover categories.

Discussion

The approach we suggest with our analyses is based on the consideration that every evaluation of habitat quality should be explicitly linked with demographic features, such as reproduction and mortality (e.g., Hall et al. 1997; Thomas and Kunin 1999). In fact, survival can vary among different habitats and human-related landscapes, and relying on animal occurrence alone for the assessment of habitat quality is questionable. One risk is that of promoting habitats that are effectively attractive sinks where occupancy and reproduction may be high, but survival is low (Delibes et al. 2001a).

This is particularly true for species of large carnivores (i.e. species with relatively low reproductive and natural mortality rates) living in a human dominated landscape, where human-caused mortality (poisoning from pesticide and pollution, contagious diseases, direct killing, etc.) can be the main factor regulating survival (Weaver et al. 1996; Woodroffe 2000; Ferreras et al. 2001; Treves and Karanth 2003). In this context, it is clear that "classical" habitat suitability models (either based on presence-absence or on presence only approaches; see Posillico et al. 2004; Falcucci et al. submitted) cannot be of great help for developing a biologically-sound conservation strategy.

The Abruzzo brown bear is classified as highly endangered (Bulgarini et al. 1998; Boitani L. pers. comm.) and habitat loss is often pointed out as one of the main factors affecting the species (Lorenzini et al. 2004). However, Falcucci et al. (submitted) show that habitat availability should not represent the main focus for its conservation, because human-related mortality, together with habitat connectivity and conflicts with human activities, are probably the main causes for the steady decline that the Abruzzo brown bear is experiencing (Lorenzini et al. 2004; Posillico et al. 2004; Wilson and Castellucci 2006).

However, habitat-specific demographic parameters are lacking, as is the case for many species, and waiting for such data to be collected might result in documenting species decline rather than providing a recommendation for their conservation. No doubt, it is important to collect long-term life history databases based on field studies, but it is also important to fully exploit existing data sources to develop short-term conservation/management plans. What is available is spatially explicit information on animal occupancy and on mortality locations.

Naves et al. (2003) and Nielsen et al. (2006) have demonstrated that these datasets can be successfully used to identify attractive sink habitats, as well as secure habitats building a separate distribution model for presence (a surrogate for reproduction) and mortality. This approach can be especially useful when the factors that determine the different demographic processes differ substantially. Both Naves et al. (2003) and Nielsen et al. (2006) developed their models using logistic regression, but Naves et al. (2003) used only presence data together with two different sets of predictors (one set of environmental variables used for the presence model and one set of human-related variables for the mortality model), while Nielsen et al. (2006) used presence points to model species presence and mortality points to model species mortality.

In the case of the Abruzzo brown bear it is not possible to use a logistic regression approach, because Hirzel et al. (2001) have demonstrated that GLMs, contrary to ENFA, are badly affected in the case of species that are not at the equilibrium with their environment. Thus we developed two ENFA models, one for presence and the other for mortality and we developed a framework that can be used to combine the two models in a final two dimensional habitat model. In particular, we divided the study area in two subsets, a “core” area where the presence of the species can be at equilibrium with its environment, and a marginal area, where the species is expanding its range. The development of the presence and of the mortality models for the core area do not create any particular problem from a theoretical point of view. However, presence-only and presence/absence models are difficult to extrapolate outside the area in which they have been developed because they are based on the comparison between the locations where the species has been observed (presence or mortality location in our case) and the available habitat. Although a model can accurately predict habitat suitability (or mortality) inside the study area, exporting the model to another place can be very tricky. The same species can be highly marginal if the study area has a large extent and includes many different regions, but it will show almost no marginality if the study area fits closely to its spatial distribution (Hirzel et al. 2002).

In this paper, we compared the distribution and mortality models developed for the core area with the ones developed for the entire study area. We showed that the values of global marginality and tolerance for both the distribution and the mortality model are very similar for the two areas, as it was expected given the environmental homogeneity of the study area.

In particular, considering the distribution model, the global marginality calculated for the entire study area is greater than that calculated for the core area alone while the tolerance for the study area is smaller (Table 3), indicating that the marginal area, although very similar to the core, generalized the environmental characteristics of the study area (Table 1) making the species more selective and with a narrower niche breadth.

Considering the mortality model, the interpretation is complicated by the fact the killing events are only 27 and thus their ecological characterization is weaker, as indicated by a larger differences among marginality and tolerance calculated for the core area and for the total study area (Table 3). Moreover, the 27 mortality locations represent not only mortality points but also presence points, making more difficult the interpretation of the ENFA factors that accounts for both.

In order to account for possible errors in the environmental layers, in the bear presence points and in the mortality datasets, and in order to obtain continuous variables we used a focal function to assign to the central pixel of a circular window (500m radius) the mean value over the window for continuous variables, or the count of cells in the window belonging to each category for categorical variables. The choice of the window radius is mainly due to logistic reasons (pixel size of the original layers, errors associated with locations, practicality of the analyses, etc); however, it is important to underline that 500m corresponds roughly to the average distance (457m ± 152m) covered in 2 hours by a bear (average calculated over the 8 animals monitored with radio-collars) and thus represents a biologically sound approximation of the individual awareness of the surrounding territory.

Both the presence and the mortality model were validated positively. The presence model was perfectly validated using two independent datasets, collected using different techniques, different time frames, and different sampling scheme, and both sets gave extremely good results. The jackknife validation performed for the mortality model gave results somewhat weaker, but still the Boyce index was really high if we consider that the mortality model has been built using only 27 points. Moreover, the trials performed with a lower number of points, clearly demonstrated the stability of the model.

Validating the final 2-dimensional model would require extensive datasets on population parameters, and especially on natality and mortality, and no such dataset is still available. We assume that given the positive validation of the presence and of the mortality models, also our final source-sink model is reliable sufficiently to be used as support for management and conservation of the Abruzzo brown bear. However, it is important to underline that other factors different from those included in the model may be responsible for the decline of the subspecies. Different authors have suggested that increased tourist pressure (Zunino 1981), increased numbers of wild boars (*Sus scrofa*) competing with the bears for food (Fabbri et al. 1983) and perhaps the decline of traditional farming, which used to provide additional food for the bears (Wilson and Castellucci 2006) may all contribute to the decline.

Conclusion and management indications

Using our model it is possible to obtain useful insight for management and conservation of the Abruzzo brown bears. An interesting possibility is that of developing a long term management plan based on the results of our model. For example, our model can clearly help managers to identify the critical points for dispersal of the bear northward. In fact, it is possible to identify a series of obligate corridors that connect different parts of the study area but are characterized by the presence of primary or secondary sinks (Fig. 3). Particularly significant is the connection between the Gran

Sasso-Laga NP and the Sibillini NP, mainly classified as a secondary sink: the area is part of the Tronto valley, with many inhabited areas and with important transportation structures connecting Rome with the Adriatic coast. The connection between the PNALM and the Silente-Velino RP is characterized by extensive secondary habitats and does not pose particular problems. Much more difficult is the situation for the connections characterizing the western part of the study area (from the PNALM to the Monti Simbruini RP and going north towards the Silente-Velino RP and the Mt. Terminillo area) where large primary and secondary sink areas (mainly linked to human-related factors) characterize the landscape.

We recommend that all the stakeholders involved in bear conservation in central Italy consider our two-dimensional model. In particular, any industrial or otherwise destructive development should be avoided in areas of critical habitat, even if the bear is not yet present with a stable population. As an alternative, restoration of primary sinks should be considered to ensure no net-loss of primary habitat for the species. On the contrary non suitable habitat could be managed without strict conservation rules.

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References

Boitani, L., S. Lovari and A. Vigna-Taglianti. 2003. Fauna d'Italia. Mammalia III: Carnivora – Artiodactyla. Bologna: Calderini Ed.

Bologna, M.A. and A. Vigna-Taglianti. 1992. Osservazioni sull'areale dell'orso marsicano con particolare riferimento al Gran Sasso e ai Monti della Laga. Hystrix Italian Journal of Mammalogy 5:75-80.

Boscagli, G. 1999. Status and management of the brown bear in central Italy (Abruzzo). In Bears: status, survey and conservation action plan (eds C. Servheen, S. Herrero, and B. Peyton), pp. 81-84. IUCN SSC, Gland, Switzerland.

Boyce, M.S., B.M. Blanchard, R.R. Knight and C. Servheen. 2001. Population viability for grizzly bears: a critical review. International Association of Bear Research and Management, Monograph Series Number 4:39.

Boyce, M.S., P.R. Vernier, S.E. Nielsen and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281–300.

Bulgarini, F., E. Calvario, F. Fraticelli, F. Petretti and S. Sarrocco. 1998. Libro rosso degli animali d'Italia, Vertebrati. WWF Italia. Roma, Italy.

Castellucci, C. 2004. Tata Urze, L'Orso Bruno dell'Appennino Centrale. Gruppo Ecologico Appennino Centrale, Edizioni Grafitalia, Sora, Italy.

Ciucci, P. and L. Boitani. 2004. Protocollo per il campionamento genetico non invasivo. PNALM, Pescasseroli, Italy.

Delibes, M., P. Gaona and P. Ferreras. 2001a. Effects of an attractive sink leading into maladaptive habitat selection. American Naturalist 158:277–285.

Delibes, M., P. Ferreras and P. Gaona. 2001b. Attractive sink, or how individual behavioural decisions determine source-sink dynamics. Ecology Letters 4:401–403.

EC (European Community) 1993. CORINE land cover technical guide. Report EUR 12585EN. Office for Publications of the EC, Luxembourg.

Fabbri, M., G. Boscagli and S. Lovari. 1983. The brown bear population of Abruzzo. Acta Zoologica Fennica 174:163-164.

Falucci, A., L.Maiorano, P. Ciucci, E. O. Garton and L. Boitani. Submitted. Land-cover change and the future of the Abruzzo brown bear: a perspective from the past. Oryx.

Febbo, D. and M. Pellegrini. 1990. The historical presence of the brown bear on the Apennines. Aquilo 27:85-88.

Ferreras, P., P. Gaona, F. Palomares and M. Delibes. 2001. Restore habitat or reduce mortality? Implications from a population viability analysis of the Iberian lynx. Animal Conservation 4:265-274.

Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Garshelis, D.L. 2000. Delusion in habitat evaluation: measuring use, selection, and importance. In Research techniques in animal ecology: controversies and consequences (eds L. Boitani and T.K. Fuller), pp. 111-164. Columbia University Press, New York.

Hall, L. S., P. R. Krausman and M. L. Morrison 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173–182.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199:142-152.

Hirzel, A. H., J.Hausser, D. Chessel and N. Perrin. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83:2027–2036.

Hirzel, A.H., V. Helfer and F. Métral. 2001. Assessing habitat-suitability models with a virtual species. Ecological Modelling 145:111–121.

Johnson, C.J., M.S.Boyce, C.S. Schwartz and M.A. Haroldson. 2004. Modeling survival: applications of the multiplicative hazards model to Yellowstone grizzly bear. Journal of Wildlife Management 68:966–978.

Knight, R.R., B.M. Blanchard and L.L. Eberhardt. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. Wildlife Society Bulletin 16:121–125.

Lorenzini, R. and M. Posillico. 2000. DNA fingerprinting and brown bear conservation in Abruzzo – central Italy. Italian Journal of Zoology 67:326–327.

Lorenzini, R., M. Posillico, S. Lovari and A. Petrella. 2004. Non-invasive genotyping of the endangered Apennine brown bear: a case study not to let one’s hair down. Animal Conservation 7:199-209.

Mattson, D.J. and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. Conservation Biology 16:1123–1136.

Meriggi, A., O. Sacchi, U. Ziliani and M. Posillico. 2001. Definizione dell’areale potenziale di cervo sardo, muflone e orso bruno. In Progetto di monitoraggio dello stato di conservazione di alcuni mammiferi particolarmente a rischio della fauna italiana (ed. S. Lovari). Ministry of the Environment, Department for Nature Conservation, Rome, Italy.

Naves, J., T.Wiegand, E. Revilla and M. Delibes. 2003. Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. Conservation Biology 17:1276–1289.

Nielsen, S.E., G.B. Stenhouse and M.S. Boyce 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation 130:217-229.

Pease, C. M. and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. Ecology 80:957–975.

Posillico, M., A.Meriggi, E. Pagnin, S.Lovari and L. Russo. 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. Biological Conservation 118:141-150.

Posillico, M., A. Petrella and L. Sammarone. 2002. Piano preliminare di conservazione dell'orso bruno (*Ursus arctos* L. 1758). Progetto LIFENAT99/IT/006244. Ministero delle Politiche Agricole e Forestali – Commissione Europea, 48 pp.

Randi, E., L. Gentile, G. Boscagli, D. Huber and U.U. Roth. 1994. Mithocondrial DNA sequenze divergence among some west European brown bear (*Ursus arctos* L.) populations. Lessons for conservation. Heredity 73:480-489.

Randi, E., M. Pierpaoli, G. Potena, L. Sammarone, I. Filippone, A. Petrella and M. Posillico. 2004. Relazione Finale sul Conteggio della Populazione, sullo Status Genetico e Demografia/Dinamica della Populazione. LIFE Project Report, Corpo Forestale dello Stato, Sangro, Italy.

Sæther, B–E, S. Engen, J.E. Swenson, Ǿ. Bakke and F. Sandegren. 1998. Assessing the viability of Scandinavian brown bear, Ursus acrtos, populations: the effects of uncertain parameter estimates. Oikos 83:403–416.

Swenson, J.E., N. Gerstl, B. Dahle and A. Zedrosser. 2000. Action plan for the conservation of the brown bear (*Ursus arctos*) in Europe. Nature and Environment 144:1-69.

Thomas, C. D., and W.E. Kunin. 1999. The spatial structure of populations. Journal of Animal Ecology 68:647–657.

Treves, A. and K.U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491-1499.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Weaver, J.L., P.C. Paquet and L.F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky mountains. Conservation Biology 10:964-976.

Wiegand, T., J. Naves, T. Stephan and A. Fernandez. 1998. Assessing the risk of extinction for the brown bear in the Cordillera Cantabrica, Spain. Ecological Monograph 68:539-570.

Wieglus, R.B. 2002. Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biological Conservation 106:381-388.

Wilson, C.J. and C. Castellucci. 2006. The Apennine brown bear and the problem of large mammals in small populations. Ecos 27:75-81.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3:16-173.

Zunino, F. 1981. Dilemma of the Abruzzo bears. Oryx 16:153-156.

LARGE SCALE DISTRIBUTION MODEL OF A NATURALLY EXPANDING SPECIES: THE CASE OF THE ITALIAN WOLF

Introduction

The wolf (*Canis lupus*) originally occupied most of the European continent. Human persecution, deforestation and the decrease of natural prey caused a sharp decline in wolf populations. By the 18th and 19th century the species was present with large populations in the Balkans and eastern Europe, but it was eradicated from most of Western Europe, with small and isolated populations surviving in Spain, Portugal and Italy (Boitani 2003).

The Italian wolf population has been recognized as a valid sub-species (*Canis lupus italicus*) both on a morphological grounds (Nowak and Federoff 2002; Boitani et al. 2003; Nowak 2003; Siracusa and Lo Valvo 2004) and on a genetic basis (Boitani et al. 2003; Lucchini et al. 2004). Lucchini et al. (2004), using a Bayesian coalescent model, indicate that wolves in Italy underwent a decline that was stronger and longer than elsewhere in Europe, suggesting that the population has apparently been isolated for thousands of generations south of the Alps, probably for the last 18,000 years (i.e. since the last glacial maximum).

Italian wolves disappeared from the Alps by the late 1800s and drastically declined in peninsular Italy (Boitani 2003). In 1973 no more than 100 wolves were still present, inhabiting only 3-5% of their original range in Italy, primarily in rugged mountains (Zimen and Boitani 1975). Nevertheless, the Italian wolf never went extinct, making recovery possible (Boitani 1992; Boitani and Ciucci 1993). Legal protection, expansion of natural prey populations, and decreases in human density in many rural areas contributed to the recovery of the species (Falcucci et al. 2007), so that by 1983 the Italian peninsula hosted about 220 wolves (Boitani 1984). Ciucci and Boitani (1991) estimated an annual population increase of 7% from 1973 to 1988 that can be translated into the estimated number of 600 wolves presently living in Italy (Boitani 2003). Moreover, in 1992 the species recolonized the French Alps and in 1996 the presence of Italian wolves was confirmed for Switzerland on a genetic basis (Valière et al. 2003).

At the international level the wolf is included in several conservation agreements (IUCN Red List, IUCN Wolf Conservation Agreement, CITES, Bern Convention, Habitat Directive, etc.; see Boitani 2000 for a review), while at the national level all the countries sharing their boundaries over the Alpine range (Italy, France, Switzerland, Germany, Austria, and Slovenia) consider the species as fully protected in their national legislation, even if the level of enforcement is different (Boitani 2000, 2003).

The recolonization of the Alpine range has obviously many positive consequences from a conservation point of view, but it raises also a number of social conflicts, especially with livestock production activities (Breitenmoser 1998; Weber 2003). Ecological conditions and husbandry in the Alps have been substantially altered since the large carnivores were eradicated, and the potential for conflicts has diminished. However, on numerous occasions Italian wolves have preyed upon livestock over the Alpine range. In Switzerland 100 sheep were killed in 1995-1996, another 40 sheep (together with 2 poached wolves) were found dead in 1998-1999, and a total of 425 domestic animals have been killed by wolves from 1999 to 2003 (Glenz et al. 2001; Weber 2004). In the Italian Alps more than 900 sheep were killed by wolves from 1999 to 2004 (De Biaggi et al. 2005) and numerous damages have been registered in France. To this it should be added that Alpine stockmen have lost any tradition of coexistence with large predators and wolves have become a negative symbol for restrictive conservation measures (Breitenmoser 1998).

All these events caused fierce contention between parties interested in wolf conservation and livestock breeders, especially in Switzerland (Glenz et al. 2001) and in France (WWF-France 2003). In Switzerland, for example, lagislation was introduced in 2001 permitting the shooting of any wolf believed to have killed at least 50 sheep over a four month period, or 25 in a single month. The number has been subsequently lowered to 35 sheep over a four month period, and it is probably going to be lowered further. Moreover, the Swiss delegation to the Bern convention proposed (unsuccessfully) a delisting of the wolf from “strictly protected” to “protected”, a change that if accepted would have allowed for the regulated hunting of the species (Report by the Secretariat on possible control of the wolf (*Canis lupus*) in the Grisons Canton – Switzerland;

Strasbourg, 10/23/2003; available online at http://www.lcie.org/Docs/Regions/Alps/COE%20wolf%20control%20in%20Switzerland%202003.pdf).

In this context it is clear that the conservation of the Italian wolf requires a transboundary approach with coordinated management of the species across borders, considering the entire distribution of the subspecies from the Apennines to the entire Alpine range, also considering areas where the species is not yet present with stable populations (Boitani 2000). Clearly it is important to obtain a clear and detailed idea of the actual and potential distribution of the species, that can be used for conflict management and conservation actions. The appropriate tool in this context is a spatially explicit distribution model that potentially depicts the distribution of the species in the greatest possible detail and that is validated using field data.

In this paper we provide a spatially explicit model depicting the present distribution together with the potentialities for recolonization of the remnant parts of the Alpine range (Corsi et al. 1999a).

For this purpose we developed a method that integrates different types of modeling techniques (ecological niche factor analysis, Pearson's planes of closest fit and deductive habitat model) to provide a spatially explicit model of wolf presence and potential distribution. We used a detailed dataset on wolf presence, on prey-species presence, and on the environmental characteristics of the study area. Our model should contribute to the design of a trans-boundary conservation plan for the species considering Italy, France, Switzerland, Germany, Austria, and Slovenia, a necessary condition for a successful management of wolves in Europe (Boitani 2000).

Materials and methods

Environmental variables

To characterize the landscape of the study area (Fig. 1) we used the CORINE Land Cover 2000 (CLC2000, version 8/2005) available for download from the European Environmental Agency website (http://dataservice.eea.europa.eu/dataservice/default.asp). The dataset cover the 25 European Community countries at an original scale of 1:100,000, using 44 classes of the 3rd level CORINE nomenclature (Bossard et al. 2000).

We used for Switzerland the land cover data available from GEOSTAT produced by the Federal Swiss Statistics Office with a cell size of 100mX100m, with an original legend of 69 land-cover classes and updated to 1998. The integration of the CLC2000 and of GEOSTAT was operated following Nippel and Klingl (1998), producing a final dataset covering the entire study area with a cell size of 100mX100m and with 15 land-cover classes corresponding to the 2nd level CORINE nomenclature (Bossard et al. 2000).

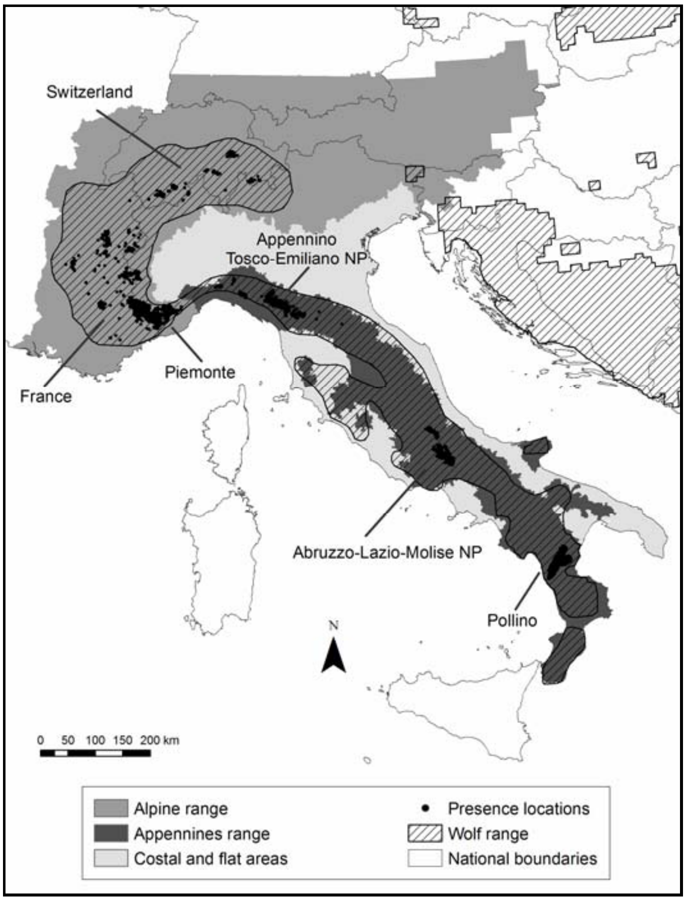

Figure 1. Study area and the three sub-regions considered: Alps, Apennines and flat areas and coastal plains. The points of presence for the wolf used in the analyses are shown. The boundaries of the three sub-regions follow Falcucci et al. (2007) for the Italian part of the study area; the boundaries of the alpine region outside Italy were obtained combining the study area defined by Corsi et al. (1998b) with the Swiss national boundaries and with the Alps Convention (1991; www.convenzionedellealpi.org). Wolf range obtained from LCIE.

We obtained from the European Environmental Agency website (http://dataservice.eea.europa.eu/dataservice/default.asp) a dataset on human population density (inhabitants/km^2) based on 2001 population censuses and covering the entire study area with the exception of Switzerland with a cell size of 100mX100m (Gallego et al. 2001). To cover the Swiss territory we used the data on human population available from the GEOSTAT database (1997 censuses, cell size 100mX100m).

We used a digital elevation model (DEM) derived from the USGS/NASA Shuttle Radar Topographic Mission (SRTM). The CIAT (International Center for Tropical Agriculture) have processed this dataset to provide seamless continuous topography surfaces. Areas with regions of no data in the original SRTM data have been filled in using interpolation methods (Jarvis et al. 2006). This dataset is currently distributed free of charge (http://srtm.csi.cgiar.org/) with a 90mX90m cell size and a vertical error smaller than 16m. We resampled the DEM using the same cell size and grid origin already used for the land-cover and the population datasets and we used the DEM to calculate the percent slope.

We obtained a dataset on roads and railroads from the Digital Chart of the World (DCW; http://www.maproom.psu.edu/dcw/). DCW is an Environmental Systems Research Institute (ESRI) product originally developed for the US Defense Mapping Agency, using data updated to 1993 and a 1:1,000,000 scale. We used DCW data to obtain a layer of the Euclidean distance from transportation network, using a 100mX100m cell size and the same grid origin already used for land-cover and population density.

We built a dataset on the presence of prey species (*Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus*, *Rupicapra rupicapra*) using deductive distribution models developed inside each species' distribution range (Mitchell-Jones et al. 1999). To develop the distribution models, we obtained species-habitat relationships from Maiorano et al. (2006) and, following their approach, we considered as areas of presence for each species only the cells inside the distribution range classified as highly or medium suitability.

In order to account for possible errors in the environmental layers and in the presence location, and in order to obtain 16 continuous variables (distribution of 4 ungulates, human population, DEM and slope, distance to transportation network, 8 land-use/land-cover classes) we run a map-algebra focal function over all 16 layers to assign to the central pixel of a circular window (500m radius) the mean value calculated over the entire window for continuous variables, or the count of all cells included in the window and belonging to each category for categorical variables. We used in all the subsequent analysis the layers resulting from the map-algebra focal function.

To avoid using too highly correlated variables that can create problems in the habitat suitability modeling process we calculated an UPGMA tree with Pearson correlations among all the layers using BioMapper3.2 (Hirzel et al. 2002).

Data on species presence

We obtained data on wolf presence merging many different databases and covering the entire range presently occupied by the Italian wolf (Fig. 1) for a total of 7,111 point localities. For the Pollino area we obtained point location of rendez-vous (24 points collected from 1999 to 2003) and radio-tracking fix (8 packs for a total of 2,400 fix collected from 1999 to 2003) from Ciucci et al. (2005a). For central Italy we obtained sightings, tracks, scats of wolves from the Abruzzo, Lazio and Molise National Park Scientific Service (a total of 272 points collected from 1999 to 2003). Getting to northern Italy, W. Reggioni (Appennino Tosco-Emiliano National Park) provided rendez-vous sites (10 points collected from 2002 to 2003) and genetically-identified-scat locations (571 points collected from 2000 to 2004) along the northern Apennines. Ciucci et al. (2005b, c) provided GPS-collar fix (618 points collected from 2004 to 2005) for one male that moved from the northern Apennines to the Southern Alps (we considered only points referred to areas of stable presence). We obtained wolf scat locations from the Italian alpine range (1,558 points collected from 1999 to 2001) from the Progetto Interreg II – Regione Piemonte. For the French Alps, we obtained genetically identified wolf scat locations (447 points collected from 1995 to 2001; Duchamp et al. 2003) and sightings, track and scats (440 points collected before 2000; Corsi et al. 1999b) For Switzerland, we obtained point location (311 points collected from 1999 to 2004) of sightings, tracks, scats, dead animals and of livestock killings from JM Weber (unpublished data) and Weber (2005).

We obtained the distribution range for the species over the study area from LCIE (www.lcie.org).

Distribution model for the Apennines

We used environmental niche factor analysis (ENFA; Hirzel et al. 2002) to build the distribution model (DM) for the Italian wolf in the Apennines (Fig. 1) that represent the area of stable presence of the species (Boitani et al. 2003). The model was developed using all the 4,127 points available in the Apennines and 14 environmental variables. In particular, we considered the distribution of 3 ungulate species (*Rupicapra rupicapra* was excluded from the analyses because it is not present in the Apennines), DEM, slope, distance to transportation network, human population and 7 land-use/land-cover classes. We excluded the land-use/land-cover class “artificial” because it was highly correlated ($r=0.81$, $p<0.0001$) with human population density that we retained. Also the distribution of *Sus scrofa* was highly correlated with intensive agriculture ($r=-0.7795$, $p<0.0001$) but we retained the species in the analyses because of its importance as a prey species for the wolf (Boitani et al. 2003), also considering that ENFA has been proved robust to correlated variables (Hirzel et al. 2002).

Starting from a set of environmental variables ENFA extracts all relevant information while discarding the correlation among variables and the background noise. It does so using mathematical tools similar to PCA and calculating new uncorrelated ecological predictor variables. The first of these new variables maximizes the absolute value of the marginality, i.e. the standardized difference between the species mean and the global mean on all the descriptors. The marginality coefficients range from -1 to +1, with positive values indicating a species’ optimum higher then the average conditions in the study area, and negative values indicating a lower species’ optimum. All the subsequent new variables maximize the specialization, i.e. the ratio of the global variance to the species variance. The specialization coefficients go from -1 to +1, with larger absolute values indicating species with larger niche breadth and smaller absolute values indicating species with smaller niche breadth. To give an overall idea of a species’ ecology, the ENFA algorithm calculates also the global marginality and the global tolerance. Both measures ranges from 0 to 1 and the first gives an idea of how much the species habitat selection is different from the mean habitat conditions that it is possible to find in the study area (the higher the value the higher the difference), the second give an indication of the species' niche breadth, with 0 indicating a small niche breadth (a "specialist" species) and 1 indicating a large niche breadth (a "tolerant" species). Further details on ENFA can be found in Hirzel et al. (2002).

Distribution model for the Alps

ENFA has been shown to be robust to the bias produced by species that are not at the equilibrium with their environment (Hirzel et al. 2001), but it remains a problem extrapolating the distribution model outside of the area that constitute the core of the distribution for the target species, in areas that may contain landscape configurations not found where presence points are available (Osborne and Suàrez-Seoane 2002; Rotenberry et al. 2002).

One possible solution is that of using modeling techniques as the Mahalanobis distance (Clark et al. 1993; Corsi et al. 1999a), which relay only on presence points and do not depend on the area that is defined as available. Concisely, the Mahalanobis distance is the standardized difference between the values of a set of environmental variables for any point and the mean values for those same variables calculated from all points at which a species was detected and that represent the optimum conditions for the presence of the species (Corsi et al. 1999a; Dunn and Duncan 2000; Rotenberry et al. 2002, 2006). Therefore, any deviation from the habitat conditions measured in correspondence to the points of presence (i.e. any deviation from the optimal habitat), is translated into lower similarity values. However, it is important to note that, if the assumption above is not met, lower similarity values will be found even for deviations in a biologically positive direction (Clark et al. 1993; Knick and Rotenberry 1998; Rotenberry et al. 2002; Browning et al. 2005).

When we are not able to define a biological optimum using the available points of presence (as in the case of species that are expanding their range over areas with different ecological characteristics), modeling techniques based on dissimilarity to an optimum condition may not be the ideal solution (Rotenberry et al. 2002, 2006). Instead, identifying a minimum set of basic requirements may be more appropriate. Rotenberry et al. (2002, 2006) propose a modification of the Mahalanobis distance (the partitioned Mahalanobis distance) that consists in partitioning the distance into *k* separated components, each representing an independent set of relationships between a species' distribution and the environmental variables. The basic assumption is that a species is present at a point only if the values of some of the environmental values at the point satisfy some basic requirement that is important for that species (Rotenberry et al. 2002). In other words we want to identify a constant relationship in a species distribution, i.e. that part of the variables that remain constant over all species occurrences. In this respect, components that have a relatively high variance are less likely to be informative, because they are not restrictive over the species distribution.

The analysis is similar to a principal component analysis. If we perform a PCA of the occupied habitat we obtain a set of new independent axes of which the first accounts for the maximum amount of variation in the original variables, the second is orthogonal to the first and accounts for the maximum remaining amount of variation in the original variables, and so on. In a conventional PCA we focus on the first components, those with the highest eigenvalues and with larger variances. However, what we are interested in are the components with low variances, those with the smallest non-zero eigenvalues (Rotenberry et al. 2002).

The Mahalanobis distance (and the partitioned Mahalanobis distance) approximately follows a X^2 distribution under multinormal assumptions, and thus it can be rescale to range from 0 to 1 (p-values), being interpreted as analogous to a posterior probability resulting from a Bayes discriminant function or logistic regression (Dunn and Duncan 2000; Rotenberry et al. 2006). More details on the partitioned Mahalanobis distance approach and on the mathematical background can be found in Dunn and Duncan (2000) and Rotenberry et al. (2006).

Following the approach briefly outlined above, we developed a distribution model for the Italian wolf in the Alps using 2,673 presence points (the 311 points of presence available for the Swiss Alps were considered only in the validation process) and 13 environmental variables: distribution of 4 ungulates, DEM, slope, distance to transportation network, human population and 5 land-use/land cover classes (we merged agricultural land-use classes into a single class considering the extremely low incidence of these classes along the Alps). To calculate the partitioned Mahalanobis distance we modified the supplementary SAS code made available by Duncan and Dunn

(2001) and Rotenberry et al. (2006). In particular, we used the available code to calculate the partitioned Mahalanobis distance and to transform the distance into p-values. We performed a PCA on a correlation matrix derived from 13 environmental variables measured at 2,673 points where the species has been detected. To choose the number of components to retain for the analyses we followed the procedure outlined by Browning et al. (2005) and Rotenberry et al. (2006): we performed a bootstrap procedure to obtain a measure of the stability of the PCA results and find out the reliability of the smallest eigenvalues. In particular, we created 1,000 random samples of 2,138 presence points (80% of the points used to build the model) and we run a PCA analysis for each one of the random samples. Over the 1,000 PCA analyses we measured all the components that were computationally unstable (i.e. components associated with a 0 eigenvalue) and that were excluded from further analyses. Then, we examined the eigenvalues table obtained with the PCA performed over all 2,673 points to find potential breaks in the distribution that could suggest a number of components to retain for the analyses. Then for each possible set of components, we calculated the partitioned Mahalanobis distance model and the respective p-values. To choose among the possible models associated with the different sets of components, we calculated the median p-value over the 311 points available for Switzerland and, using a jackknife procedure, the mean p-value for the 2,673 points used to build the model, and we chose the model that gave the highest median values (Rotenberry et al. 2006), i.e. the model that provided the best performance.

Distribution model for flat areas and coastal plains

The presence of the species inside this sub-region is not stable and it is heavily regulated by interaction with human activities that can completely determine the survival of the animals living in the area (Boitani et al. 2003). Moreover, no point of presence was available outside of the Alps and the Apennines and thus, it was not possible to use any inductive habitat distribution modeling technique.

However, the ecology of the species is particularly well known (Boitani et al. 2003; Mech and Boitani 2003) and thus we used the species-habitat relationships obtained from Maiorano et al. (2006) and the available environmental layers to build a deductive species distribution model (sensu Corsi et al. 2000).

Models validation

To evaluate the ENFA distribution model we used the Boyce index (Boyce et al. 2002; Hirzel et al. 2006) calculated using the predicted/expected ratios for each suitability class. The index goes from -1 to 1, with negative values indicating an incorrect model, which predicts poor quality areas where presences are more frequent, with positive values indicating a model whose predictions are consistent with the presences distribution in the evaluation dataset, and with values close to zero indicating that the model is not different from a chance model. The index is built calculating the predicted (percentage of validation points falling in the suitability class) vs expected (proportion of the map's total area occupied by the suitability class) ratio for each suitability class. Given that no independent dataset on wolf presence was available for the Apennines the Boyce index was calculated through a cross-validation procedure over the same set of points used to build the model. In particular we divided the points of presence into 10 sets of random points using the evaluation tool available in BioMapper3.2 (http://www2.unil.ch/biomapper/).

The distribution model for the Alps was validated calculating the median p-values for the points of presence available for Switzerland and (through a jackknife procedure) for the points of presence used to build the distribution model as described in the paragraph above.

No presence point was available outside of the Alps or the Apennines and thus no validation was possible for the deductive distribution model. However, Maiorano et al. (2006) and Maiorano et al. (in press) have positively validated the species-habitat relationships that we used over the Italian peninsula, and thus our model can be considered extremely reliable.

Results

Distribution model for the Apennines

To build the distribution model for the Apennines we kept the first 5 factors from the ENFA analysis (the marginality factor plus the first 4 specialization factors), for a total explained information of 98.5% (100% of the marginality and 97% of the specialization). The marginality factor explained 62% of the specialization, indicating that the niche breadth for the wolf over the Apennines was narrow for the variables for which its optimum was further from the mean conditions that characterize the sub-region (Table 1).

Predictor variable	**Factor 1[a] (62%)**	**Factor 2[b] (16%)**	**Factor 3[b] (10%)**	**Factor 4[b] (6%)**	**Factor 5[b] (4%)**
Roe-deer	+++	0	0	0	0
Red-deer	+	0	0	0	0
Wild boar	++	**	*	*	******
DEM	+++++++	0	0	0	0
Distance to transportation network	+++	0	0	0	0
Intensive agriculture	--	****	*****	****	***
Permanent crops	-	*******	***	***	***
Pastures	0	*	**	*	*
Heterogeneous agriculture	--	***	****	*****	****
Forests	+++	***	*****	******	****
Scrub and/or herbaceous vegetation	++	**	***	****	***
Open space with little or no vegetation	0	*	**	*	*
Population	-	***	**	0	0
Slope	+++	0	0	0	0

[a] Marginality factor. The symbol + means that the bear was found in locations with values higher than average. The symbol – means the opposite. The greater the number of plusesor minuses the higher the difference. 0 indicates small differences.

[b] Specialization factor. The symbol * indicates that the bears occupy a range of values that is narrower than the range available. The greater the number of asterix, the narrower the range. 0 indicates a very low specialization.

Table 1. Correlation between ENFA factors and the environmental variables in the Apennines.

Overall, we measured a global marginality of M=1.2 and tolerance of T=0.18, showing that wolf's habitat in the Apennines differs drastically from the mean conditions in the sub-region. In particular, if compared to the study area, the species selected areas with higher elevation, higher slope, higher distance from transportation networks, higher presence of ungulates, and higher coverage in natural land-use/land-cover classes, while agricultural land-use/land-cover classes, as well as areas with higher population densities, were counter-selected (Table 1).

Large and continuous areas of high suitability are present especially in the central and northern Apennines, while in southern Apennines the area with high suitability are limited and more fragmented (Fig. 2). An important gap in the distribution of the higher suitability values can be found in correspondence to the boundaries of Campania, Basilicata and Puglia, where the connection among central and southern Apennines is limited to a few small areas. Particularly low is the suitability in all the major valleys, where human pressure is higher, and towards the margins of the Apennines, especially in the south.

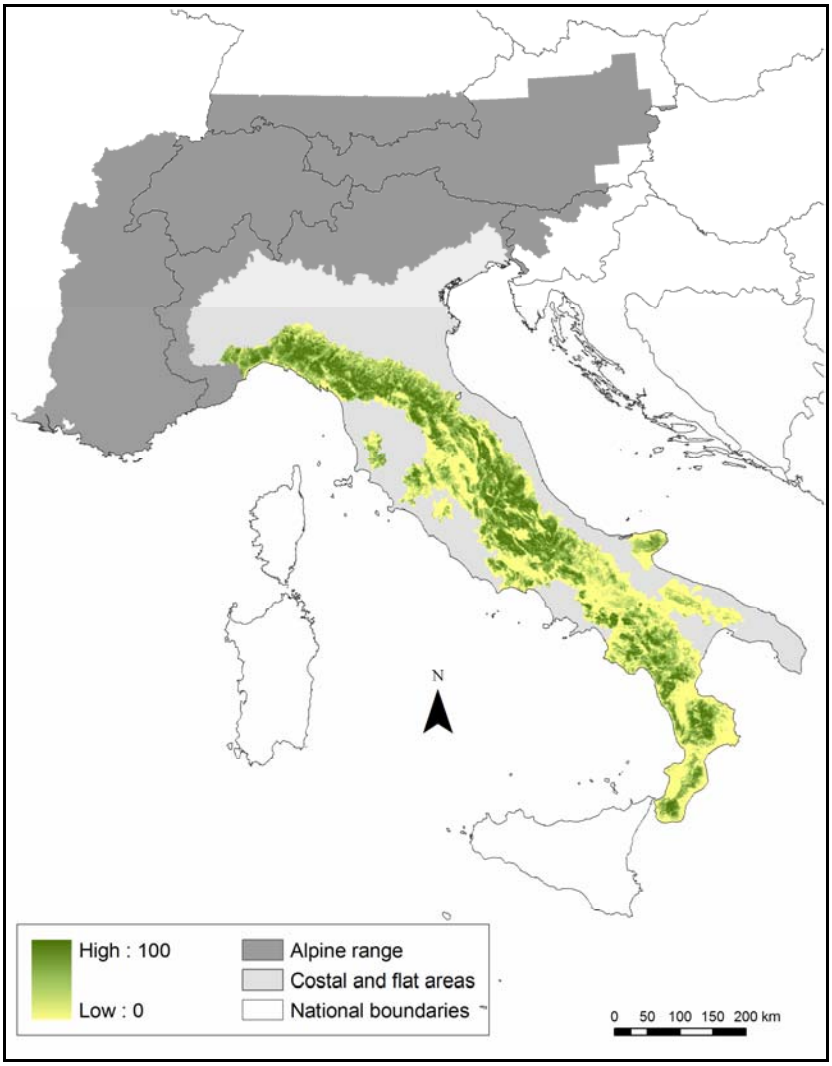

Figure 2. Distribution model for the wolf in the Apennines.

Distribution model for the Alps

The bootstrap procedure (1,000 runs performed over 1,000 random samples of 2,138 presence points) outlined that the structure of the PCA analysis is absolutely stable. All the 1,000 runs gave the same eigenvalue structure and in no case we registered a 0 eigenvalue. Thus all the 13 components of the PCA were retained in the analyses.

The eigenvalue table obtained from the PCA performed with all the 2,673 presence points (Table 2) showed a clear structure. In particular, we identified 4 possible partitioning corresponding to the main "breaks" existing in the distribution of the eigenvalues, breaks that can be identified looking at changes in the order of magnitude of the eigenvalues. A first possible partition is obtained considering only the last component (*k*=13), a second possible partition is obtained considering only the last 3 components (*k*=11), a third possible partition is obtained considering the last 8 components (*k*=6), and the forth possible partition is obtained considering all the 13 components (*k*=1, corresponding to the "full" Mahalanobis distance).

Principal Component (k)	**Eigenvalue**	**Proportion of total variance**
1	4.634084	0.3565
2	2.191383	0.1686
3	1.352785	0.1041
4	1.125078	0.0865
5	1.027765	0.0791
6	0.751528	0.0578
7	0.720061	0.0554
8	0.505953	0.0389
9	0.346079	0.0266
10	0.206080	0.0159
11	0.090868	0.0070
12	0.047104	0.0036
13	0.001232	0.0001

Table 2. Results of PCA on a correlation matrix of 13 environmental variables assessed at 2,673 points where wolves were detected in the Italian and French Alps.

For each of the 4 models considered we calculated a median p-value for the points of presence located in Switzerland (median p-value=0.061 for *k*=1; median p-value=0.036 for *k*=6; median p-value=0.016 for *k*=11; median p-value=0.593 for *k*=13) and for the points of presence used to build the model (median p-value=0.862 for *k*=1; median p-value=0.812 for *k*=6; median p-value=0.857 for *k*=11; median p-value=0.888 for *k*=13). We selected as our final distribution model for the Alps, the one obtained considering only the last component (Fig. 3), i.e. the one that gave the highest median p-value in both cases.

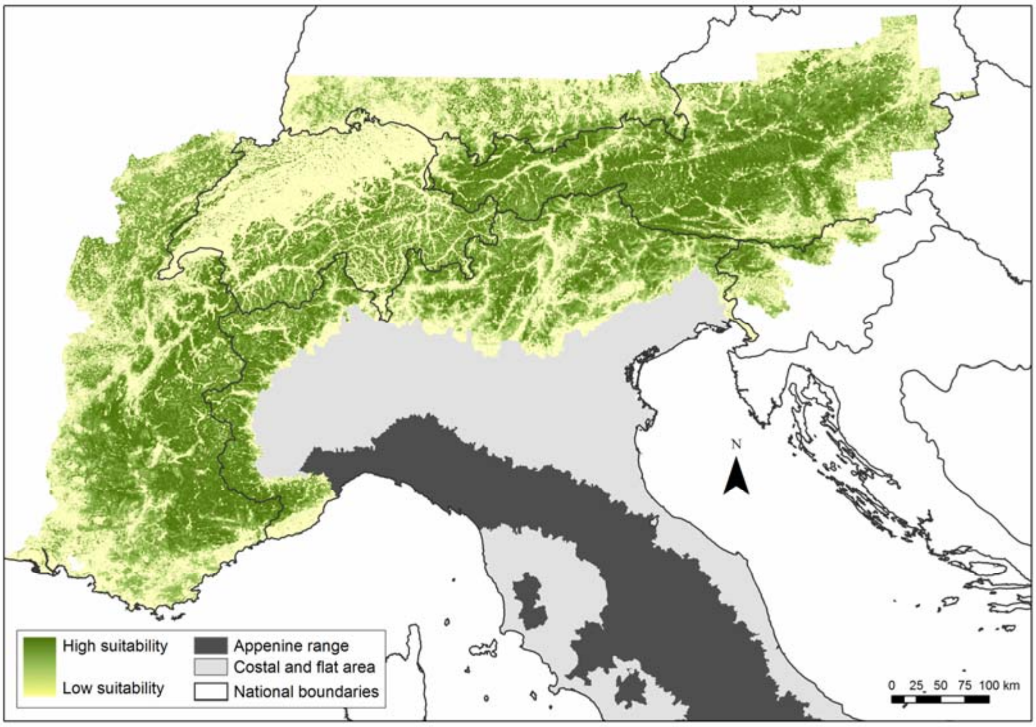

Figure 3. Distribution model (*k*=13) for the wolf in the Alps.

Considering the last eigenvector, the variables that more than other influence the distribution of the species along the Alpine range are the natural land-use/land-cover classes, followed by the presence of roe-deer, by human population density and by agricultural land-use/land-cover classes.

Overall, the western Alpine range (both the Italian and the French part) are characterized by the presence of large highly suitable areas, especially towards the southern part of the study area. The central Alpine range, particularly in Italy and Switzerland are characterized by the presence of smaller areas with high suitability values, and the same is true for the Jura Mountains in Switzerland, and particularly for central Switzerland, where the suitability for the wolf is almost zero. The eastern Alpine range (Italy, Austria, and Slovenia) presents really high suitability values distributed in large continuous areas, with important gaps existing in correspondence to the major valleys.

Distribution model for flat areas and coastal plains

The deductive distribution model (Fig. 4) outline that the areas suitable for the presence of the species in peninsular Italy outside of the Apennines are extremely limited and fragmented. Usually they are located at the boundaries of the study area (i.e. towards the Alps and towards the Apennines), with a few exceptions in Southern Italy (Basilicata and Naples' neighborhoods), in central Italy (both south and north of Rome), and especially in Tuscany, where it is possible to find the largest contiguous suitable areas.

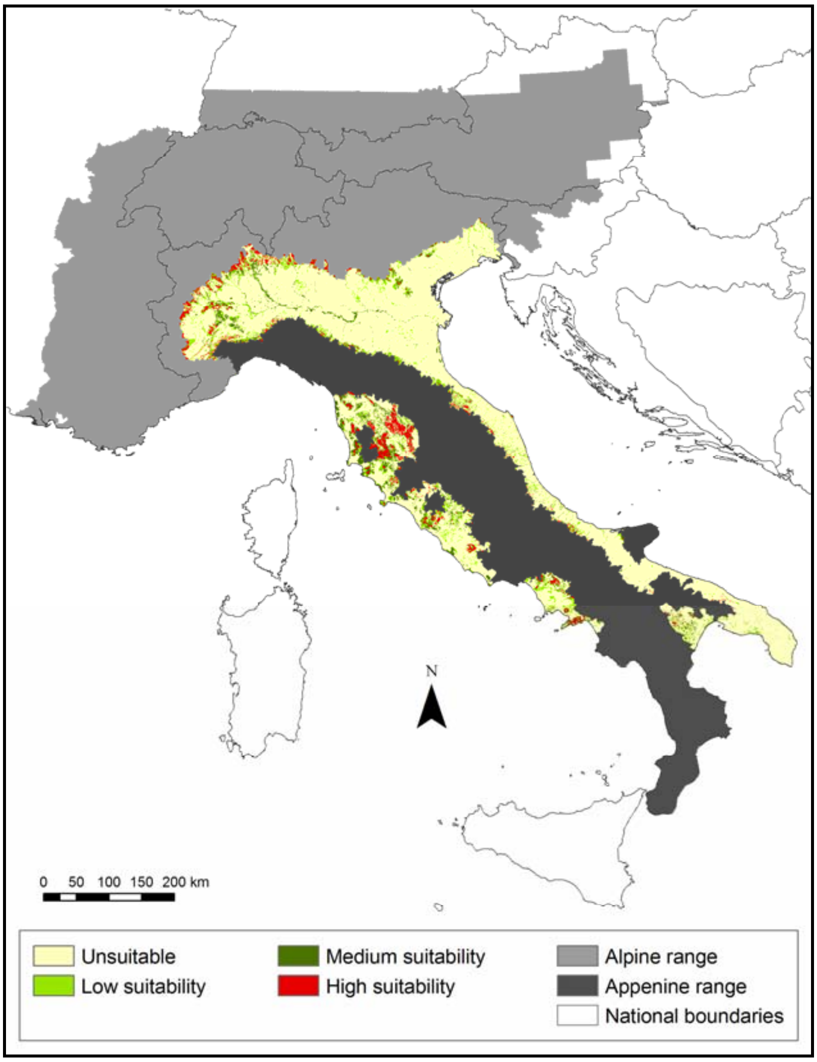

Figure 4. Distribution model for the wolf in flat areas and coastal plains.

Models validation

The validation of the distribution model for the Apennines gave a Boyce index = 0.88 (±0.15), indicating that the model is highly consistent with the available points of presence for the wolf.

The validation of the distribution model for the Alps showed that both the points of presence used to build the model and the points of presence available for Switzerland are classified with a high median p-value (median p-value=0.593 for points of presence in Switzerland; median p-value=0.888 for points of presence in the Italian and French Alps). The lower median p-value obtained for Switzerland can be explained considering that also localities of livestock killings have been included in the dataset, and we cannot safely assume that these sites represent areas of high suitability for the species.

Discussion

Many different habitat suitability models for the wolf have been realized throughout the world, usually giving rise to many controversies (Mladenoff et al. 1995, 1999; Massolo and Meriggi 1998; Mladenoff and Sickley 1998; Carroll et al. 2003; Mech 2006a, b). Just considering our study area, at least two large scale habitat suitability models have already been presented. Corsi et al. (1999a) provided a large scale model of wolf distribution based on limited information. In particular, they developed a model on the potential distribution of the species across the entire Italian territory using presence locations distributed along the Apennines only. Their model did not address the problems related to expanding the habitat suitability model outside of the areas where points of presence have been collected and where the ecology of the species may be different (Osborne and Suàrez-Seoane 2002; Rotenberry et al. 2002, 2006; Browning et al. 2005) but they simply used the same technique and the same points to predict both the present distribution and the potential distribution. Moreover, to develop their model, Corsi et al. (1999a) did not consider the distribution of prey species, one of the most important features to determine the occurrence of stable wolf populations (Mech and Peterson 2003).

Glenz et al. (2001) developed a predictive distribution model for the wolf in Switzerland. They developed a logistic-regression model to predict the presence of the species. However, since no point of presence was available for their study area, they obtained the regression parameters from data collected in the northern Apennines, thus completely ignoring the potential problems related to the ecological differences among the two study areas.

Even considering all the possible limitations, the models presented by Corsi et al. (1999a) and by Glenz et al. (2001) represented an important step for the conservation of the Italian wolf. However, our distribution model (Fig. 5) should represent a significant improvement over the old ones. First of all, the data availability on Italian wolves and on habitat variables has increased exponentially in the last decade. Second we presented significant theoretical improvements over the original modeling technique. Last, but not least, we developed our distribution models considering not only Italy, but all the countries potentially interested by the presence of the species, creating a seamless spatial model.

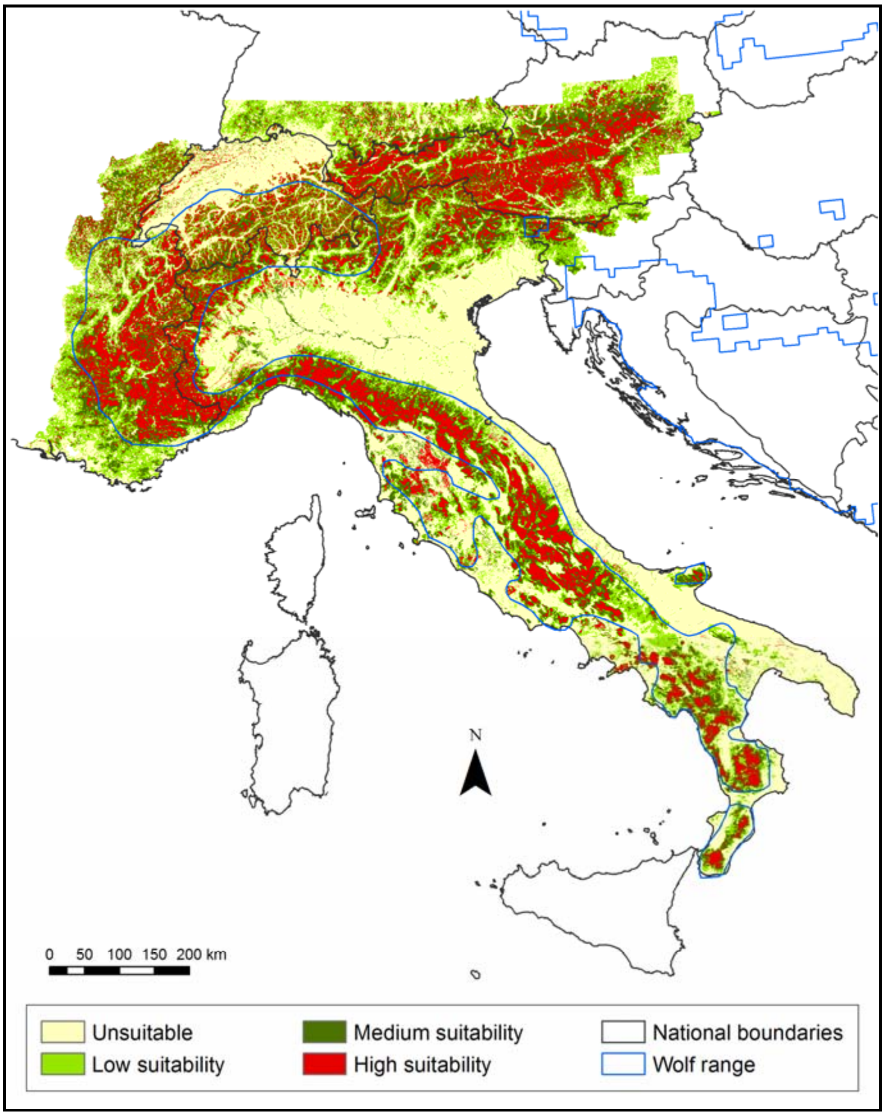

Figure 5. Seamless distribution model for the wolf in the study area. The results of the 3 modeling approaches in the 3 sub-regions of the study area were clumped together following the legend of the deductive model. For the ENFA and the partitioned Mahalanobis model we obtained 4 suitability classes based on quartiles. Wolf range obtained from LCIE.

An important point of our modeling approach is related to the subdivision of the study area into sub-regions. Osborne and Suàrez-Seoane (2002) have suggested that in some instances it is important to partition the data before performing a large scale habitat suitability model in order to account for possible differences in the way animals respond to habitats in different parts of their range. Here we expand this proposing that also the modeling technique should change following the natural subdivision that is possible to find in large study areas. In our case, Falcucci et al. (2007) clearly identified important sub-regions dividing Italy into areas where land-use/land-cover composition is different, where the socio-economic context is different, and where the changes in land-use/land-cover are different.

Thus, we adapted our modeling technique to the data available and to the characteristics of the 3 sub-region, and we used two inductive distribution models (sensu Corsi et al. 2000) for the Alps and the Apennines and a deductive distribution model (sensu Corsi et al. 2000) for the flat areas and coastal plains.

A deductive distribution model was the only possible approach for the flat areas and coastal plains, where the wolf is not present with stable populations and where no point of presence was available for the analyses. However, the wolf is probably, among carnivore mammals, the species with the highest number of studies on its ecology and behavior (Mech and Boitani 2003) and thus it is possible to build a biologically reasonable deductive model.

The choice of the types of inductive models to be developed for the Alps and the Apennines was mainly guided by the available data and by ecological considerations. Considering the Apennines, the number of points of presence available for the modeling exercise was really high (more than 4,000 points) but no point of absence was available. Thus we choose the ENFA approach that is basically a use/availability approach, and that has been proven more robust than others (like GLM) if the species is not at the equilibrium with its environment (Hirzel et al. 2001), something that cannot be assumed safely for the wolf in Italy. The model for the Apennines was positively validated.

The modeling exercise for the Alpine range presented particular difficulties. In fact, the Italian wolf is present with stable populations only in France and, at least in part, in Switzerland. Both presence-only and presence/available modeling techniques are difficult to extrapolate outside the area in which they have been developed because they are based on the comparison between the locations where the species has been observed and the available habitat. Although a model can accurately predict habitat suitability inside the study area, exporting the model to another place can be very tricky. The same species can use the available resources in different ways going from one place to another (Hirzel et al. 2002).

Falcucci et al. (see previous chapter) have developed a framework that can be used to extend ENFA models outside of the area of stable presence of a species. However, their framework can be used with success only when it is possible to individuate a clear and well defined study area and when the study area can be considered ecologically homogeneous. In the case of the expansion of the Italian wolf over the Alpine range, the ecological conditions that the species encounter are completely different among the Alps and the Apennines (Falcucci et al. 2007) and, furthermore, it is impossible to delineate objectively an area of available habitat for the expansion of the species.

Rotenberry et al. (2002, 2006) have proposed a modeling technique (partitioned Mahalanobis distance) that can be used to build distribution models outside of the original study area or when the environment is changing. Here we propose the use of the same model to predict species occurrence outside of the presently occupied range.

Conclusions

The Large Carnivore Initiative for Europe (LCIE; www.lcie.org) has a clear and simple mission: "To maintain and restore, in coexistence with people, viable populations of large carnivores as an integral part of ecosystems and landscape across Europe". As one of the main points to help towards their mission, the LCIE network is now preparing a set of guidelines for the development of large-carnivores management plans at the population level (L. Boitani pers. comm.). The background of this action is that large carnivores are highly mobile organisms that move over very large areas and that cannot be managed effectively in small areas. As a result, in the European context, a single population can easily span several different nations and thus species-specific conservation planning should be considered transboundary. This is clearly the case of the Italian wolves, that can be easily divided into 2 main populations, one occupying in peninsular Italy (the Apennines and the flat areas and coastal plains) and one occurring along (and currently expanding through) the Alpine range (Fabbri et al. 2007).

As for 2006, the Italian wolf is present in Italy, France, and Switzerland, and given the high mobility of the species (two Italian wolves have been genetically traced in the Pyrenees) it is easy to predict a natural expansion eastward (Germany, Austria, Slovenia and Croatia). In a long term strategy, it is not realistic to propose that the wolf must be protected in all areas where the species is present or that the species can potentially recolonize. Wolf presence, in fact, may also be incompatible with some types of economic activities and, since it is not advisable to leave wolf management to individual reactions (i.e. poachers and shepherds protecting their flocks), it is extremely important to plan for the best possible integration of human activities and wolf conservation (Boitani 2000).

In such a context it is clear the importance of our distribution model that can be used to depict present distribution as well the possible expansion of the population, it can be used as a planning tool to help in the management of fragmentation of suitable habitat, or in the management of conflicts with human activities, or in the planning of conservation strategies.

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References

Boitani L. 1984. Genetic considerations on wolf conservation in Italy. Bollettino di Zoologia 51:367-373.

Boitani L. 1992. Wolf research and conservation in Italy. Biological Conservation 61:125-132.

Boitani L. 2000. Action plan for the conservation of the wolves (*Canis lupus*) in Europe. Nature and Environment 113:1-84.

Boitani L. 2003. Wolf conservation and recovery. Pp.317-340 in Mech LD and L Boitani (Editors). Wolves: behavior, ecology, and conservation. The University of Chicago Press.

Boitani L and P Ciucci. 1993. Wolves in Italy: critical issues for their conservation. Pp. 75-90 in Promberger C and W Schröder (Editors). Wolves in Europe: current status and perspectives. Munich Wildlife Society, Ettal, Germany.

Boitani L, S. Lovari and A. Vigna Taglianti. 2003. Fauna d'Italia: Mammalia. III Carnivora – Artiodactyla. Vol. XXXVIII, Calderini Ed., Bologna. 434 pp.

Bossard M, J. Feranec and J. Otahel. 2000. CORINE land cover technical guide: addendum 2000. EEA, Copenhagen.

Breitenmoser U. 1998. Large predators in the Alps: the fall and rise of man's competitors. Biological Conservation 83:279-289.

Browning D.M., S.J. Beaupré and L. Duncan. 2005. Using partitioned Mahalanobis $D^2(k)$ to formulate a GIS base model of timber rattlesnake hibernacula. Journal of Wildlife Management 69:33-44.

Carroll C., M.K. Phillips, N.H. Schumaker and D.W. Smith. 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. Conservation Biology 17:536-548.

Ciucci P. and L. Boitani. 1991. Viability assessment of the Italian wolf and guidelines for the management of the wild and a captive population. Ricerche di Biologia della Selvaggina 89:1-58.

Ciucci P., A. Falcucci and L. Boitani. 2005a. Habitat characteristics of wolf rendez-vous sites in the southern Apennines, Italy. Poster presented at: Frontiers of Wolf Recovery: Southwestern US and the world. International Wolf Center, Colorado Springs, Colorado, 1-4 October 2005.

Ciucci P., L. Maiorano and L. Boitani. 2005b. Long-distance wolf dispersal from Italy to france revamps the need for transboundary wolf management plans. Poster presented at: Frontiers of Wolf Recovery: Southwestern US and the world. International Wolf Center, Colorado Springs, Colorado, 1-4 October 2005.

Ciucci P., L. Maiorano, M. Andreani, W. Reggioni and L. Boitani. 2005c. Dispersione a lungo raggio di un lupo dall'Appennino settentrionale alle Alpi Marittime: movimenti, comportamento spaziale ed eterogeneità ambientale. V Congresso Italiano di Teriologia, Arezzo 10-12 November 2005.

Clark J.D., J. Dunn and K.G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57:519-526.

Corsi F., E. Duprè and L. Boitani. 1999a. A large scale model of wolf distribution in Italy for conservation planning. Conservation Biology 13:150-159.

Corsi F., I. Sinibaldi, L. Boitani, C. Braschi, A. Falcucci, L. Maiorano, M. Ravagli and F. Sforza. 1999b. Large Carnivore Conservation Areas in Europe, Draft Discussion Paper for the Large Carnivore Initiative, IEA. Technical report for CEE.

Corsi F., J. de Leew and A. Skidmore. 2000. Modeling species distribution with GIS. Pp. 389-434 in: Boitani L. and T.K. Fuller (eds). Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York.

De Biaggi E., L. Boitani, F. Marucco, E. Avanzinelli, A. Gazzola, A. Tropini, S. Dalmasso, C. Passalacqua and S. Ricci. 2005. Progetto lupo – Regione Piemonte. Report 2005.

Duchamp C., T. Dahier, B. Lequette, P. Taberlet, Y. Léonard, P. Rouland and E. Marboutin. 2003. News about the wolf status in France: 2002-2003 update. Pp 14-15 in Weber J.-M. (Editor). Wolf monitoring in the Alps, 2nd Alpine Wolf Workshop, Boudevilliers. 17-18 March 2003.

Duncan L. and J.E. Dunn. 2001. Partitioned Mahalanobis D^2 to improve GIS classification. Paper 198-26 in Proceedings of the Twenty-sixth Annual SAS® Users Group International Conference. Cary, NC: SAS Institute Inc.

Dunn J.E. and L. Duncan. 2000. Partitioning Mahalanobis D2 to sharpen GIS classification. Pp. 195–204 in Brebbia C.A. and P. Pascolo (eds). Management information systems 2000: GIS and remote sensing. WIT Press, Southampton, UK.

Fabbri E., C. Miquel, V. Lucchini, A. Santini, R. Caniglia, C. Duchamp, J.-M. Weber, B. Lequette, F. Marucco, L. Boitani, L. Fumagalli, P. Taberlet and E Randi. 2007. From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (*Canis lupus*) population. Molecular Ecology 16:1661-1671.

Falcucci A., L. Maiorano and L. Boitani. 2007. Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Landscape Ecology 22:617-631.

Gallego J. and S. Peedell. 2001, Using CORINE Land Cover to map population density. Towards Agri-environmental indicators, Topic report 6/2001 European Environment Agency, Copenhagen, pp. 92-103.

Glenz C., A. Massolo, D. Kuonen and R. Schlaepfer. 2001. A wolf habitat suitability prediction study in Valais (Switzerland). Landscape and Urban Planning 55:55-65.

Hirzel A.H., J. Hausser, D. Chessel and N. Perrin. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83:2027–2036.

Hirzel A.H., V. Helfer and F. Métral. 2001. Assessing habitat-suitability models with a virtual species. Ecological Modelling 145:111–121.

Jarvis A., H.I. Reuter, A. Nelson and E. Guevara. 2006. Hole-filled seamless SRTM data V3. International Centre for Tropical Agriculture (CIAT), available from http://srtm.csi.cgiar.org.

Knick S.T. and J.T. Rotenberry. 1998. Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance statistic. Journal of Agricultural, Biological, and Environmental Statistics 3: 311-322.

Lucchini V., A. Galov and E. Randi. 2004. Evidence of genetic distrinction and long-term population decline in wolves (*Canis lupus*) in the Italian Apennines. Molecular Ecology 13:523-536.

Maiorano L., A. Falcucci and L. Boitani. 2006. Gap analysis of terrestrial vertebrates in Italy: priorities for conservation planning in a human dominated landscape. Biological Conservation 133:455-473.

Maiorano L., A. Falcucci, E.O. Garton and L. Boitani. In press. Contribution of the Natura2000 network to biodiversity conservation in Italy. Conservation Biology, in press.

Massolo A. and A. Meriggi. 1998. Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. Ecography 21:97-107.

Mladenoff D.J., T.A. Sickley, R.G. Haight and A.P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern great lakes region. Conservation Biology 9:279-294.

Mladenoff D.J. and T.A. Sickley. 1998. Assessing the potential gray wolf restoration in the northern United States: a spatial prediction of favorable habitat and potential population levels. Journal of Wildlife Management 62:1-10.

Mladenoff D.J., T.A. Sickley and A.P. Wydeven. 1999. Predicting gray wolf landscape recolonization: logistic regressionmodels vs. new field data. Ecological Applications 9:37-44.

Mech D.L. and R.O. Peterson. 2003. Wolf prey relations. Pp. 131-160 in Mech L.D. and L. Boitani (eds). Wolves: behavior, ecology, and conservation. The University of Chicago Press.

Mech L.D. and L. Boitani (eds). 2003. Wolves: behavior, ecology, and conservation. The University of Chicago Press.

Mech, L.D. 2006a. Prediction failure of a wolf landscape model. Wildlife Society Bulletin 34, 874–877.

Mech, L.D. 2006b. Mladenoff et al. rebut lacks supportive data. Wildlife Society Bulletin 34, 882–883.

Mitchell-Jones A.J., G. Amori, W. Bogdanowicz, B. Kryštufek, P.J.H. Rejinders, F. Spitzenberger, M. Stubbe, J.B.M Thissen, V. Voralìk and J. Zima. 1999. The atlas of European mammals. Pyser Natural History, London, UK.

Nippel T. and T. Klingl. 1998. Swiss land use in the European context: integration of Swiss land use statistics with CORINE Land Cover. Swiss Federal Statistical Office and Swiss Agency for the Environment, Neuchâtel.

Nowak R.M.. 2003. Wolf evolution and taxonomy. Pp. 239-258 in Mech LD and L Boitani (eds). Wolves: behavior, ecology, and conservation. The University of Chicago Press.

Nowak R.M. and N.E. Federoff. 2002. The systematic status of the Italian wolf *Canis lupus*. Acta Theriologica 47: 333-338.

Osborne P.E. and S. Suàrez-Seoane. 2002. Should data be partitioned spatially before building large-scale distribution models? Ecological Modelling 157:249-259.

Rotenberry J.T., S.T. Knick and J.E. Dunn. 2002. A minimalist approach to mapping species habitat: Pearson’s planes of closest fit. Pp. 281–289 in Scott J.M., P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W. Wall and F.B. Samson (eds). Predicting species occurrences: issues of scale and accuracy. Island Press, Washington, D.C., USA.

Rotenberry J.T., K.L. Preston and S.T. Knick. 2006. GIS-based niche modeling for mapping species’ habitat. Ecology 87:1458-1464.

Siracusa AM and M Lo Valvo. 2004. Confronti craniometrici tra lupi (*Canus lupus*) dell’Italia continentale e della Spagna: primi dati. Histrix - Italian Journal of Mammalogy 15:31-38.

Valière N., L. Fumagalli, L. Gielly, C. Miquel, B. Lequette, M.L. Polle, J.-M. Weber, R. Arlettaz and P. Taberlet. 2003. Long-distance wolf recolonization of France and Switzerland inferred from non-invasive genetic sampling over a period of 10 years. Animal Conservation 6:83-92.

Weber J.-M. 2003. Wolves monitoring in the Alps. KORA report 18:29 pp.

Weber J.-M. 2004. Monitoring loup 1999 – 2003. KORA report 27:28 pp.

Weber J.-M. 2005. Loup (*Canis lupus*). Pp. 40-49 in Zimmerman F., A. Molinari-Jobin, J.M. Weber, S. Capt, A. Ryser, C. Angst, C. Breitenmoser-Würsten and U. Breitenmoser (eds). 2005. Monitoring der raubtiere in der Schweiz. Kora report 29.

WWF-France. 2003. Le loup en France en 2003: analyse et propositions au parlement et au governement. WWF-France/Group Loup France.

Zimen E. and L. Boitani. 1975. Number and distribution of wolves in Italy. Zeitschrift für Säugetierkunde 40:102-112.

CONCLUSION

Large carnivores are quickly coming back in Italy. The Italian wolf is now widespread throughout Italy and is quickly recolonizing the Alpine range. The Abruzzo brown bear is still surviving in central Italy, despite all its problems. The lynx is possibly present in central Italy (coming from illegal releases and thus it is almost impossible for now to now exactly where the animals are, from which populations are they coming, if they are still surviving) and the jackal is colonizing the eastern alpine range.

The results that I obtained with my land-use/land-cover change analysis outlined that habitat availability for these species should not be a problem, even in the future. Using my models, it is possible to predict that the wolf is going to colonize the entire alpine range (even if with some difficulties in the central/Swiss Alps) and that the Abruzzo brown bear, if saved from direct persecution, should return to occupy its entire 1900 distribution range.

The problem that will probably remain in Italy is linked to the fragmentation of management and conservation for the two species. In fact, local and regional authorities (for the bear) and national authorities (for the wolf) all have a say in the management of the two species and different strategies are adopted on the two sides of too many boundary lines, without any consideration of the biological population being interested.

The Large Carnivore Initiative for Europe (www.lcie.org) is trying to remediate to this situation, creating European action plans for each species and introducing at the European level the concept of transboundary management for biological populations. At the national level the Action Plan for the Conservation of the Abruzzo brown bear (Piano d'Azione per la Tutela dell'Orso Marsicano – PATOM) has been signed (April 2006) from all the local, regional, and national authorities and parties that are interested in the conservation of the sub-species, and this should provide a framework for a coordinated and (hopefully) a biologically sound management.

It is necessary now that these important political initiatives are translated into practical actions on the ground. I hope that with my work I have provided the necessary background and the scientific framework into which political actions can be implemented. A first, important result has already been achieved: using my double-layer model for the Abruzzo brown bear Luigi Boitani and Paolo Ciucci have been able to stop the development of a wind-power plant into a primary habitat for the species.