



**EFFECTS OF LAND ABANDONMENT ON ANIMAL SPECIES IN
EUROPE: CONSERVATION AND MANAGEMENT
IMPLICATIONS**

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PREFACE

Ecosystems provide multiple services essential to society. These services maintain the Earth in a state that can support life. As has recently been demonstrated by the Millennium Ecosystem Assessment, ecosystem services help maintain the atmosphere in a clean state, provide clean water, control soil erosion, reduce pollution and much more. Our well-being and our future are inextricably linked with those of our ecosystems. Consequently, we need to protect ecosystems and their natural services for future generations. One task of ecosystem science is to provide knowledge for informed decision-making to combat degradation of ecosystems and also to provide guidance for sustainable human practices that impact on ecosystems. To achieve this goal, it is necessary to study ecosystem processes and analyse both the dynamics of nature and, in particular, the interactions with human activities. The European Commission, DG Research has supported multiple research initiatives during the Fifth and Sixth Framework Programmes for Research under the headings “Environment and Sustainable Development” and “Sustainable Development, Global Change and Ecosystems” respectively, with an increasing focus on the integration of natural and social sciences research.

This report presents a paper commissioned by the Concerted Action 'Integrated Assessment of Vulnerable Ecosystems under Global Change' (AVEC), funded under the Fifth Framework Programme, which drew together scientists from eleven European research institutes with the aim of capacity building and establishing a scientific network on the issue of the vulnerability of ecosystem services; It addresses the consequences of land abandonment for ecosystems. In Europe traditional farming is under severe pressure, which will increase in the future. The paper helps to meet the challenge of ensuring a sustainable future, regarding the ecosystem management, as it makes concrete suggestions for policy changes that should be initiated in response to land abandonment. It is thus very timely, giving decision-makers a scientific rationale on which to base their future choices.

The resulting land abandonment is not so high on the policy agenda but will become more prominent in the future. It is hoped that future work towards the sustainable management of European ecosystems might benefit from the AVEC project.

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INTRODUCTION

Ecosystems provide multiple services to humanity and a basic task of ecosystem science is to assist policy-makers in assuring stable future provisions of these services. Towards this goal, the European Commission has supported multiple research initiatives over the last decade, with an increasing focus on the integrated nature of the analysis. This means that, for the purpose of sustainable ecosystem management, it is now considered insufficient to study ecosystem processes while merely pointing towards the “relevance” of findings for future policy. Instead, we must do our best to analyse both the dynamics of nature and their interactions with human activities, while using the highest possible level of scientific rigour in both realms.

The term “ecosystem services” was not immediately welcomed by many scientists involved, because, for them, it carried the notion of materialistic “consumption” rather than the acceptance of nature's intrinsic values. Modern biodiversity conservation, however, fully accepts the human priority of protecting nature in its own right, and it is then only a technical aspect whether the function of maintaining a certain number of species is called a “service” or something else. More so, even the economic value of strict protection of species richness is now frequently recognised. In order to address these issues, the ATEAM¹ Integrated Project (also funded by the European Commission, DG Research, Environment and Sustainable Development Programme under Framework Programme 5), involving a large European consortium of researchers, has focused on addressing ecosystem services and the threats posed to them by using scenarios of changes in the environment (climate, land use) and state-of-the-art assessment tools to study the consequences of change for ecosystem services.

ATEAM scientists quickly recognised that a key to the achievement of their goals was the communication of findings not only to stakeholders (which was a part of the project itself), but also to their colleagues in the natural sciences. To advance this dialogue, a concerted action, AVEC², was initiated, focusing on dedicated workshops, reports and two high-level summer schools. The theme of the present report, the consequences of land abandonment for animal populations, has been studied by a sizeable research community for a while, but AVEC provided the opportunity to discuss these issues in a wider context. An open exchange of findings and ideas about the topic occurred during a workshop on the island of Capri (Italy) on October 11-13, 2004.

The present report, written by Danilo Russo and sponsored by AVEC, provides, perhaps, a more long-lasting resource. For it, Dr Russo has evaluated a large body of recent literature, covering a broad range of animal groups and providing a very differentiated analysis. Based on the findings in the literature, he then investigates the implications for conservation policy. One of his main

¹ Advanced Terrestrial Ecosystem Analysis and Modelling

² Integrated Assessment of Vulnerable Ecosystems under Global Change

conclusions is that the maintenance of high species numbers does not constitute a valid conservation goal per se – instead the ecosystem service concept can be employed usefully here. Furthermore, the analysis works out differently at different scales: both the ecosystem analysis and the conservation policy must consider processes from local to continental scales, with potentially differing conclusions. Evidently, there are ways to manage landscapes effectively for conservation, either by employing techniques that resemble previous land use practices or by ensuring that alternative disturbances may still occur that create open spaces needed by many species. Finally, a particular challenge exists in the case of predators which in the past have been considered to be threats to traditional land use systems – Russo discusses new approaches to manage landscapes that contain resources for these species as well.

We hope that this comprehensive review and the access it provides to a large body of relevant literature will assist both, land managers seeking state-of-the-art information on land abandonment and biodiversity, and scientists who aim to cover the remaining gaps in our understanding.

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Executive summary

Human-maintained semi-natural habitats and landscapes are often characterised by highly diverse animal communities. Such habitats are disappearing following depopulation of rural areas (i.e. land abandonment), and are being replaced by scrublands and forests; the process is causing great concern especially in mountainous areas of Europe and in the north Mediterranean.

This review examines responses of animal communities to land abandonment in the European region, and shows that it mainly harms open habitat or ecotone specialists, which often decline markedly; forest specialists show opposite trends. Responses at the community level include species turnover as well as shifts in relative abundance and diversity, mostly related to changes in vegetation. Biogeography and human history help interpret responses, such as the well-documented “simplification” of the avian communities in the Mediterranean, in which many conservation-dependent species linked with open habitats are replaced by widespread forest ones. Several – but not all – mammal species have benefited from forest expansion, including forest specialists and large predators. For instance, wolf populations increased and re-colonised areas from where they had disappeared: their coexistence with humans in the areas recently occupied is now posing a major challenge to conservationists. To counter species loss linked with land abandonment, policies favouring the survival of traditional farming should be implemented. In abandoned areas, appropriate management – e.g. prescribed burning and grazing – is needed to preserve open habitats and avoid the spread of large wildfires which eventually also harm forest species due to large-scale habitat loss. Future research should focus more on poorly investigated animal groups to avoid management strategies biased towards the best-known species; multi-scale analyses, interactions with other global change processes and detailed modelling are other important aspects needing attention.

1. INTRODUCTION

In recent years the preservation of biological diversity in the vast area of the world devoted to agriculture, pastoralism and silviculture has attracted considerable attention (Ostermann, 1998; Robinson and Sutherland, 2002) as one of the major aspects of biodiversity loss on the global scale (Chapin *et al.*, 2000).

The traditional, low-intensity farming systems of temperate regions give rise to and maintain semi-natural habitats and landscapes which sustain highly diverse biological communities (e.g. Ostermann, 1998; Allen, 2001) and have been defined 'High Nature Value farming' (e.g. Baldock *et al.*, 1996).

Since World War II, the growing demand for high productivity has triggered dramatic changes in farmed areas in Europe as a result of agricultural intensification and land abandonment (Eijsackers and Quispel, 1988; Ostermann, 1998; MacDonald *et al.*, 2000; Robinson and Sutherland, 2002). Intensification, largely encouraged by national and international policies promoting productivity (e.g. Bignal, 1998; Robinson and Sutherland, 2002), has occurred especially in lowland areas. It involves a number of profound changes in farmland management to increase yields, including a massive use of chemicals (synthetic fertilisers, biocides), mechanisation, monoculture, as well as structural changes such as the disappearance of hedgerows, woodland patches, ponds and other structures associated with traditional farming (McLaughlin and Mineau, 1995; Gillings and Fuller, 1998; Ewald and Aebischer, 1999; Stoate *et al.*, 2001; Robinson and Sutherland, 2002). Its impacts on biodiversity have received a good deal of attention at both species and community levels (e.g. Carson, 1962; Tew *et al.*, 1992; Freemark, 1995; Fuller *et al.*, 1995; Bishop *et al.*, 1999; Stoate *et al.*, 2001; Robinson and Sutherland, 2002).

Land abandonment (hereafter abbreviated as LA) is the shift from a given pattern of land use (often extensive farmland) to a less intensive one caused by the reduction of human activity, leading to a recovery of scrubland and eventually forest (e.g. Burel and Baudry, 1994; MacDonald *et al.*, 2000). The post-abandonment vegetation succession, however, may either stop at an intermediate stage (such as scrubland in the Mediterranean) or follow a number of alternative pathways, depending on local abiotic and biotic factors (Petit *et al.*, 2003). The phenomenon has spread in many European areas (e.g. Burel and Baudry, 1994; Luick, 1998; Zervas, 1998; MacDonald *et al.*, 2000; Olsson *et al.*, 2000; Krumalová and Rättinger, 2001; Petit *et al.*, 2003; Romero-Calcerrada and Perry, 2004) where farming proved too costly on account of the difficulty of access, remoteness, poor land quality or the labour intensive requisites of individual farms. It often occurred in mountain areas, where environmental conditions make farming less profitable and no further resource adjustment options are available from the modification of farming practices and farm structure (MacDonald *et al.*, 2000). In North America, LA began to emerge in the second half of the nineteenth century (Burel and Baudry, 1994; Foster *et al.*, 2002; Hall *et al.*, 2002).

With respect to traditional management, intensification and LA represent shifts in opposite directions, respectively towards increased and decreased land utilisation (Ostermann, 1998; Fig. 1).

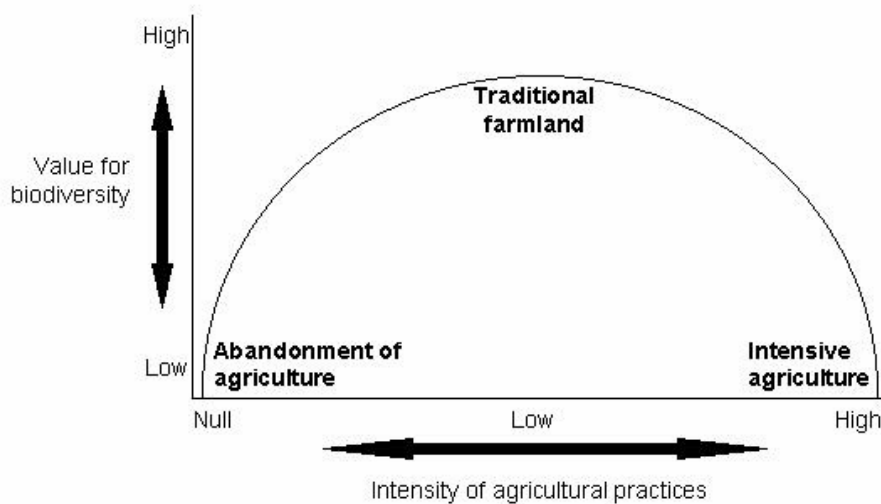


Figure 1. Influence of agriculture polarisation on biodiversity values. Both intensification and land abandonment lead to a decrease in biological diversity; low-polarised, extensive agriculture corresponds to optimal levels of disturbance (and, as a consequence, of heterogeneity) sustaining the highest levels of biodiversity. Modified after Ostermann (2000).

LA has a wide range of social, economical and ecological implications, whose assessment and interpretation are often complex. Adverse effects of LA on animal biodiversity have been reported (e.g. MacDonald *et al.*, 2000): in Southern Europe biodiversity in arable land is more seriously threatened by LA and other land use change than by intensification (Stoate *et al.*, 2001). Likewise, the future of farmland wildlife diversity in Eastern Europe is jeopardised by the high abandonment rate that has followed the fall of communism (Robinson and Sutherland, 2002).

Conservation of many habitats currently regarded as threatened in Europe and listed in Annex I of the EU 92/43 'Habitat and Species Directive' depends on the maintenance of low-intensity, extensive farming practices (Bennett, 1997; Ostermann, 1998). Such habitats occur in over 50% of the European biotopes of special conservation concern identified using the criteria set out in the Directive (Bignal and McCracken, 1996). LA has been recognised as a threat for 33 semi-natural habitat types of Community interest: 26 (10 of which classified as priority habitats) are put at risk by

the decline of pastoralism, six by the termination of grass-cutting and hay-making, and one by the abandonment of harvesting crops (Ostermann, 1998).

So far, the effects of LA on animal species and communities have received much less attention than the impact of intensification: several related issues need further investigation before we can predict the effects of this process on animals and develop adequate management strategies. It could be argued that the loss in animal biodiversity due to LA may be “compensated” by the gain in scrubland and forest species. Moreover, if LA is seen as a return to a more original vegetation and fauna (Preiss *et al.*, 1997), is not the related loss of “human-dependent” biodiversity actually to be welcomed?

The aims of this work are to 1) review current knowledge on wildlife reactions to LA; 2) analyse similarities and discrepancies in the response to LA across species, groups, and landscape types; 3) present some management implications; and 4) identify knowledge gaps to stimulate further studies.

Specifically, this paper will concentrate on Europe – to which most of the literature available for temperate areas refers – where LA is still spreading (MacDonald *et al.*, 2000) and where loss of farmland biodiversity constitutes a particularly important environmental issue (Benton *et al.*, 2003); in the Northern Mediterranean, well studied in respect with LA, the process has been in progress for many areas and has altered historical, human-shaped landscapes. LA in tropical regions – which often concerns areas previously occupied by primary forest that have been abandoned after being logged, cultivated or grazed by cattle – is outside the scope of this paper: the problem of wildlife recovery associated with secondary forest growth has been thoroughly reviewed by Dunn (2004).

2. THE VALUE OF TRADITIONAL FARMLAND FOR ANIMAL BIODIVERSITY

Many animal species often select open, early successional habitats, characterised by low vegetation and simple architecture, such as grassland, steppe and scrubland (e.g. Dafni and O’Toole, 1994; Lockwood, 1997; Tella *et al.*, 1998; Söderström and Pärt, 2000; Moreira, 1999; Pedrini and Sergio, 2001; Henderson *et al.*, 2002). Open habitats occur naturally where topography, soil characteristics and climate prevent the development of tall vegetation, but they also originate from natural disturbance such as wildfires (e.g. Moreira *et al.*, 2001) and wild ungulate grazing (Putman and Moore, 1998). Over the millennia, agriculture, pastoralism and forest harvesting have developed in human communities (Bignal, 1998; Blondel and Aronson, 1999; Olsson *et al.*, 2000), creating and maintaining open habitats through clearing, cutting, logging, fire setting and livestock grazing. Grazing by domestic animals has restricted vegetation re-growth, replacing in many cases the role of wild ungulates, which had been often over-hunted by humans (see e.g. Breitenmoser, 1998; Gaudzinski and Roebroeks, 2000). Except in cases where land is abandoned and then encroached on by vegetation, such habitats may persist for a

long time: some pastures in the eastern Mediterranean have been preserved thanks to continuous livestock grazing for over 5000 years (Blondel and Aronson, 1999). According to the intermediate disturbance hypothesis (Connell, 1979), traditional farming – located half-way along a polarisation (land abandonment-intensive farming) gradient – would produce “optimal” levels of disturbance intensity and frequency, maximising biodiversity (Ostermann, 1998; Fig. 1).

Livestock also provide a significant food source for many animal species, including large carnivores (e.g. Meriggi and Lovari, 1996; Breitenmoser, 1998; Boitani, 2000), scavengers (see e.g. the case of griffon vultures, *Gyps fulvus*; Donázar and Fernández, 1990) and dung-dwelling insects (Lumaret and Kirk, 1987), the latter being in turn important prey for several vertebrates, such as bats (Duvergé and Jones, 2003) and birds (Wilson *et al.*, 1999). A peculiar case is that of cattle egret (*Bubulcus ibis*) commensalism: this bird species often forages among cattle in fields and grassland for the insects stirred up by grazing livestock (Heatwole, 1965; Wahungu *et al.*, 2003), and its range expansion is driven by movements of free-ranging cattle (Petretti, 2003).

The importance of farmed habitats for wildlife varies according to habitat features, patch size and configuration within the landscape, in relation to the species' specialised life strategies and/or perception of the environment (e.g. Wiens and Milne, 1989; Ricklefs, 1990; Mazerolle and Villard, 1999; Summerville *et al.*, 2002). Habitat effects prevail on landscape effects in influencing species richness patterns for those animal taxa characterised by limited mobility and dispersal (Aauri and de Lucio, 2001; Dauber *et al.*, 2003).

Matrix effects (e.g. Miller *et al.*, 1997; Weibull *et al.*, 2000) – depending upon landscape composition and arrangement features of habitat patches – may influence animal distribution, spatial use patterns, foraging behaviour and interspecific relationships (Cronin, 2003; Dauber *et al.*, 2003; Hirsch *et al.*, 2003): therefore, they may be important in determining the diversity of animal communities in farmland. However, because matrix effects are often taxon-specific (Hirsch *et al.*, 2003), species richness supported by a given landscape configuration may differ greatly according to the various species' requirements.

Heterogeneity has been addressed as a significant feature favouring biological diversity: in this respect, it might be regarded as a crucial farmland property (Benton *et al.*, 2003). Even when the species diversity observed for a given animal group seems to be determined by habitat type, this outcome may in fact reflect the influence of within-habitat heterogeneity (Aauri and de Lucio, 2001).

Heterogeneous landscapes allow different animal communities – each linked with a specific habitat – to co-exist (Aauri and de Lucio, 2001), and favour those species requiring ecotones or multiple habitats. Among the latter, examples include: species using separate habitats for different activities, such as foraging, nesting, or roosting (Law and Dickman, 1998; Dauber *et al.*, 2003; Martínez *et al.*, 2003); those requiring different habitats at larval and adult stages, as well as sex-

or age-dependent habitat use patterns (Law and Dickman, 1998; Debinski *et al.*, 2001); and species with daily or seasonal patterns of multiple habitat use (Law and Dickman, 1998).

Species-specific search behaviour and perceptual abilities constrain movements patterns between the various components of the landscape used. For example, vision is employed by many species to follow landmarks (e.g. Graham and Collett, 2002, for ants; Biro *et al.*, 2004 for pigeons, *Columba livia*), and its performance may affect dispersal (as in white-footed mice, *Peromyscus leucopus* under different light conditions; Zollner and Lima, 1999); elevation cactus bugs *Chelinidea vittiger* probably rely on olfaction to navigate as suggested by their tendency to move upwind (Schooley and Wiens, 2003); and, to maintain their orientation during foraging or commuting, several microbats (e.g. Verboom and Huitema, 1997) are likely to employ echolocation (but navigation mechanisms in bats are still poorly understood) to follow linear landscape elements – a flying greater horseshoe bat (*Rhinolophus ferrumequinum*) has been likened to “a person in fog”, its sensory range being only 5-10 metres (Ransome and Hutson, 2000).

Given such constraints, landscape elements may either prevent or facilitate animal movement, and their occurrence and extension determine considerable variation in how “good” a landscape is for a certain species (Mader *et al.*, 1990; Bright, 1998; Hehl-Lange, 2001; Pedroli, 2003). Hedgerow networks (Baudry *et al.*, 2000), well developed in traditional farmland, offer important corridors – as well as valuable habitats – for both invertebrates (Joyce *et al.*, 1999; Nicholls *et al.*, 2001) and vertebrates (Wegner and Merriam, 1990; Hinsley and Bellamy, 2000; Russo *et al.*, 2002).

The timing of traditional agricultural and pastoral practices also induces temporal heterogeneity by influencing changes in habitat features and resource availability over time (Benton *et al.*, 2003) which further influence animal diversity and activity patterns.

Thus LA may cause biodiversity impoverishment by bringing about progressive loss of heterogeneity at several spatial and temporal scales, heading towards progressively denser vegetation, with open habitats and their animal communities confined to sites where steep terrain, shallow soil or natural disturbance occur (Preiss *et al.*, 1997).

3. WINNERS AND LOSERS IN ABANDONED AREAS

Burel and Baudry (1995) highlight the paradoxical nature of the impact of LA on animals. As they put it, “the fear that abandonment of agricultural land will lead to spontaneous succession and a loss of open field species is as widespread as the hope that this trend may provide larger habitats for forest species”. Below, reactions to LA by different animal groups are described: similarities or discrepancies are linked with the group’s natural history and the scale-dependent perception of land use changes, and help understand the consequences of LA for biodiversity (Burel and Baudry, 1995). Special attention will be paid to taxa of particular functional value or conservation significance.

3.1. Invertebrates

Unlike mega-vertebrates (Linnell *et al.*, 2000), invertebrates rarely include “charismatic” species (Hunter, 1996); so, in spite of their functional importance in ecosystems and sensitivity to environmental change, the impact of LA on their conservation status has not received enough attention. In general, vegetation structure seems to be the dominant factor influencing invertebrate community turnover and dynamics, but there are differences among taxa: community turnovers are driven by the level of adaptation of individual species to the degree of shading and vegetation development. Responses to LA are observed in both epigeic (= above-ground) and endogeic (= below-ground) assemblages, resulting in changes in species richness or composition, density and relative abundance.

Earthworm (Lumbricidae) community structure is mainly affected by vegetation structure (e.g. Miles, 1979; 1985), influencing micro-habitat diversity and litter quality upon which these invertebrates depend. In Normandy chalk grasslands, earthworm biomass and density both peaked soon after the termination of grazing; biomass slightly decreased, but density kept increasing, as deciduous woody stages developed (Decaëns *et al.*, 1997). Especially earthworm epigeic assemblages find both a hospitable micro-habitat and high-quality food in the low C:N ratio litter resulting from the development of shrub and deciduous tree cover (Decaëns *et al.*, 1997). Pine wood, however, was characterised by low earthworm biomass and density due to the poor nutrient quality of conifer needles. While species richness remained unchanged in the various vegetation stages, community composition changed drastically (Tables 1, 2). Variation in earthworm biomass according to vegetation dynamics has been recorded in an abandoned region of the French Alps, with a peak at intermediate stages such as fallow land and open forests, in dry and wet areas respectively (Grossi *et al.*, 1995).

The composition of land gastropod communities in Mediterranean France proved sensitive to both vegetation structure at the stand level and abandonment dynamics at the landscape level (Magnin *et al.*, 1995). Vegetation structure controls snail food and shelter availability as well as influencing the micro-climate close to the ground (Magnin *et al.*, 1995). Pastoral abandonment strongly influences species assemblages through both habitat and landscape structure (Tables 1, 2). Grazed areas favour xerophilic, open-space snail species, but are species-poor as they affect negatively shade-loving, litter-feeding and saxicolous taxa; ungrazed grassland and scrubland harbour a higher diversity as they provide snails with within-habitat heterogeneity, i.e. with a range of different niches (Labaune and Magnine, 2002). Snail communities in small open patches are subject to matrix influences, so include shade-loving taxa dispersing from the surrounding woodland, but large open patches prevent colonisation (Labaune and Magnine, 2002). Besides changing habitat structure by grazing, sheep also seem to be important passive dispersers of land snails, influencing population genetic structure (Fischer *et al.*, 1996).

Table 1. Examples of animal species negatively affected by the decline of agricultural or pastoral activity. Some of them may initially benefit from early or intermediate vegetation stages following land abandonment; however, they will be harmed by later stages such as thick scrubland or woodland. Details are given in text.

Group	Species	Source
ANNELIDA OLIGOCHAETA	<i>Lumbricus terrestris</i>	Decaëns <i>et al.</i> , 1997
	<i>Aporrectodea caliginosa</i>	Decaëns <i>et al.</i> , 1997
	<i>Allolobophora icterica</i> (*)	Decaëns <i>et al.</i> , 1997
MOLLUSCA GASTROPODA	<i>Trochoidea geyeri</i>	Labauve and Magnin, 2002
	<i>Trochoidea cylindrica</i>	Labauve and Magnin, 2002
MYRIAPODA DIPLOPODA	<i>Ommatoiulus rutilans</i>	David <i>et al.</i> , 1999
	<i>Glomeris annulata</i> (*)	David <i>et al.</i> , 1999
	<i>Cilindroiulus caeruleocinctus</i> (*)	David <i>et al.</i> , 1999
INSECTA ORTHOPTERA	<i>Leptoiulus belgicus</i> (*)	David <i>et al.</i> , 1999
	<i>Decticus verrucivorus</i>	Guido and Gianelle, 2001
	<i>Chortippus parallelus</i>	Guido and Gianelle, 2001
INSECTA HYMENOPTERA	<i>Euthystira brachyptera</i>	Guido and Gianelle, 2001
	<i>Messor barbarus</i>	Gómez <i>et al.</i> , 2003
	<i>Cataglyphis piliscapus</i>	Gómez <i>et al.</i> , 2003
	<i>Tetramorium ruginode</i>	Gómez <i>et al.</i> , 2003
	<i>Tetramorium semilaeve</i>	Gómez <i>et al.</i> , 2003
	<i>Formica rufibarbis</i>	Gómez <i>et al.</i> , 2003
	<i>Messor scabrinodis</i>	Gómez <i>et al.</i> , 2003
	<i>Formica cunicularia</i>	Gómez <i>et al.</i> , 2003
	<i>Aphaenogaster senilis</i> (*)	Gómez <i>et al.</i> , 2003
	<i>Tetramorium caespitum</i> (*)	Gómez <i>et al.</i> , 2003
INSECTA COLEOPTERA	<i>Lasius niger</i>	Gómez <i>et al.</i> , 2003
	<i>Amara communis</i>	Burel and Baudry, 1994
	<i>Amara lunicollis</i>	Burel and Baudry, 1994
AMPHIBIA	<i>Amara brevicollis</i>	Burel and Baudry, 1994
	<i>Discoglossus sardus</i>	D'Antoni <i>et al.</i> , 2003
	<i>Discoglossus pictus</i>	D'Antoni <i>et al.</i> , 2003
REPTILIA	<i>Bombina variegata</i>	Giovine, 1994
	<i>Podarcis hispanica</i> (*)	Martín and Lopez (2002)
	<i>Psammodromus hispanicus</i> (*)	Martín and Lopez (2002)
	<i>Psammodromus algirus</i> (*)	Martín and Lopez (2002)
	<i>Acanthodactylus erythrurus</i> (*)	Martín and Lopez (2002)
	<i>Lacerta lepida</i> (*)	Martín and Lopez (2002)
AVES	<i>Natrix maura</i>	Perez Mellado, 1991
	<i>Bubulcus ibis</i>	Moreira, 1999
	<i>Gyps fulvus</i>	Donázar and Fernández, 1990
	<i>Aquila adalberti</i>	Moreno and Villafuerte, 1995; Ferrer and Harte, 1997
	<i>Aquila chrysaetos</i>	Pedrini and Sergio, 2001
	<i>Falco naumanni</i>	Tella <i>et al.</i> , 1998
	<i>Perdix perdix hispaniensis</i> (*)	Novoa <i>et al.</i> , 2002
	<i>Tetrax tetrax</i>	Moreira, 1999
	<i>Otis tarda</i>	Moreira, 1999
	<i>Bubo bubo</i>	Penteriani, 1996; Penteriani <i>et al.</i> , 2002
	<i>Melanocorypha calandra</i>	Moreira, 1999
	<i>Calandrella brachydactyla</i>	Moreira, 1999
	<i>Alauda arvensis</i>	Laiolo <i>et al.</i> , 2004a
	<i>Motacilla alba</i>	Laiolo <i>et al.</i> , 2004a
	<i>Saxicola rubetra</i>	Laiolo <i>et al.</i> , 2004a
	<i>Turdus pilaris</i>	Laiolo <i>et al.</i> , 2004a
	<i>Acrocephalus paludicola</i>	Aquatic Warbler Conservation Team, 1999; Flade, 1999; Kloskowski and Krogulec, 1999
	<i>Lanius collurio</i>	Laiolo <i>et al.</i> , 2004a
	<i>Sylvia undata</i>	Moreira <i>et al.</i> , 2001
	<i>Pyrrhocorax pyrrhocorax</i>	Blanco <i>et al.</i> , 1998
	<i>Serinus serinus</i>	Preiss <i>et al.</i> , 1997
	<i>Carduelis cannabina</i>	Preiss <i>et al.</i> , 1997 ; Moreira <i>et al.</i> , 2001; Laiolo <i>et al.</i> , 2004a
	<i>Carduelis carduelis</i>	Preiss <i>et al.</i> , 1997
<i>Carduelis chloris</i>	Preiss <i>et al.</i> , 1997	
<i>Miliaria calandra</i>	Moreira, 1999	
MAMMALIA	<i>Oryctolagus cuniculus</i>	Moreno and Villafuerte, 1995
	<i>Lepus corsicanus</i>	Trocchi and Riga, 2001
	<i>Lynx pardinus</i>	Delibes <i>et al.</i> , 2000

Table 2. Examples of animal species favoured by habitat changes and/or mitigation of human disturbance linked with the decline of agricultural or pastoral activity. Species selecting mid-succession woody vegetation (labelled with an *), although temporarily favoured by abandonment, may eventually decline as forest develops. Details are given in text.

Group	Species	Source
ANNELIDA OLIGOCHAETA	<i>Allolobophora multali</i>	Decaëns <i>et al.</i> , 1997
	<i>Lumbricus castaneus</i>	Decaëns <i>et al.</i> , 1997
	<i>Dendrobaena mammalis</i>	Decaëns <i>et al.</i> , 1997
MOLLUSCA GASTROPODA	<i>Pomatias elegans</i>	Labauune and Magnin, 2002
	<i>Pagodulina pagodula</i>	Labauune and Magnin, 2002
	<i>Vitrea contracta</i>	Labauune and Magnin, 2002
	<i>Urticicola glabellus</i>	Labauune and Magnin, 2002
	<i>Cochlostoma septemspirale</i>	Labauune and Magnin, 2002
	<i>Punctum pygmaeum</i>	Labauune and Magnin, 2002
	<i>Abida polyodon</i>	Labauune and Magnin, 2002
	<i>Xerosecta cespitum</i>	Labauune and Magnin, 2002
	<i>Candidula gigaxii</i>	Labauune and Magnin, 2002
	<i>Zebrina detrita</i>	Labauune and Magnin, 2002
	<i>Solatopupa similis</i>	Labauune and Magnin, 2002
<i>Chondrina avenacea</i>	Labauune and Magnin, 2002	
CRUSTACEA ISOPODA	<i>Porcellio gallicus</i>	David <i>et al.</i> , 1999
MYRIAPODA DIPLOPODA	<i>Glomeris marginata</i>	David <i>et al.</i> , 1999
INSECTA ORTHOPTERA	<i>Pholidoptera griseoaptera</i> (*)	David <i>et al.</i> , 1999
INSECTA HYMENOPTERA	<i>Plagiolepis pygmaea</i>	Gómez <i>et al.</i> , 2003
	<i>Leptothorax racovitzae</i>	Gómez <i>et al.</i> , 2003
	<i>Formica gerardi</i>	Gómez <i>et al.</i> , 2003
	<i>Crematogaster scutellaris</i>	Gómez <i>et al.</i> , 2003
	<i>Camponotus lateralis</i>	Gómez <i>et al.</i> , 2003
	<i>Solenopsis fugax</i>	Gómez <i>et al.</i> , 2003
<i>Aphaenogaster subterranea</i>	Gómez <i>et al.</i> , 2003	
INSECTA COLEOPTERA	<i>Steropus madidus</i>	Burel and Baudry, 1994
	<i>Abaxa ater</i>	Burel and Baudry, 1994
REPTILIA	<i>Vipera latasti</i>	Perez Mellado, 1991
AVES	<i>Columba palumbus</i>	Preiss <i>et al.</i> , 1997
	<i>Dryocopus martius</i>	Mikusi ski, 1995
	<i>Troglodytes troglodytes</i>	Laiolo <i>et al.</i> , 2004a
	<i>Prunella modularis</i>	Laiolo <i>et al.</i> , 2004a
	<i>Erithacus rubecula</i>	Laiolo <i>et al.</i> , 2004a
	<i>Hippolais polyglotta</i>	Preiss <i>et al.</i> , 1997
	<i>Sylvia atricapilla</i> (*)	Preiss <i>et al.</i> , 1997
	<i>Sylvia borin</i>	Laiolo <i>et al.</i> , 2004a
	<i>Sylvia curruca</i>	Laiolo <i>et al.</i> , 2004a
	<i>Sylvia melanocephala</i> (*)	Preiss <i>et al.</i> , 1997
	<i>Phylloscopus collybita</i>	Laiolo <i>et al.</i> , 2004a
	<i>Regulus ignicapillus</i>	Preiss <i>et al.</i> , 1997
	<i>Parus ater</i>	Laiolo <i>et al.</i> , 2004a
	<i>Parus caeruleus</i>	Preiss <i>et al.</i> , 1997
	<i>Parus cristatus</i>	Preiss <i>et al.</i> , 1997
	<i>Parus major</i>	Preiss <i>et al.</i> , 1997
<i>Parus montanus</i>	Laiolo <i>et al.</i> , 2004a	
<i>Fringilla coelebs</i>	Preiss <i>et al.</i> , 1997	
MAMMALIA	<i>Microtus arvalis</i>	Delattre <i>et al.</i> , 1986
	<i>Arvicola terrestris</i>	Delattre <i>et al.</i> , 1988
	<i>Sciurus vulgaris</i>	L. Lapini, <i>pers. comm.</i>
	<i>Muscardinus avellanarius</i>	L. Lapini, <i>pers. comm.</i>
	<i>Hystrix cristata</i>	Bruno and Riccardi, 1995
	<i>Capreolus capreolus</i>	Chenavier <i>et al.</i> , 1997 ; Gortazar <i>et al.</i> , 2000
	<i>Cervus elaphus</i>	Gortazar <i>et al.</i> , 2000
	<i>Sus scrofa</i>	Gortazar <i>et al.</i> , 2000
	<i>Vulpes vulpes</i>	Moreno and Kufner, 1988
	<i>Genetta genetta</i>	Moreno and Kufner, 1988
	<i>Canis lupus</i>	Breitenmoser, 1998; Boitani, 2000
	<i>Ursus arctos</i>	Breitenmoser, 1998
<i>Lynx lynx</i>	Breitenmoser, 1998	

Plant architecture also affects spider (Araneae) assemblages in successional stages by controlling both substrate and micro-climate conditions required by the various species. In a controlled sheep grazing experiment made at the plot level, in five years species gradually accumulated in ungrazed areas on former arable fields; grazing led to simpler assemblages (Gibson *et al.*, 1992).

Saprophagous assemblages of Mediterranean subterranean macroarthropods, i.e. millipedes (Diplopoda) and woodlice (Isopoda), respond very sensitively to changes in vegetation structure occurring with LA, so that different vegetation stages are characterised by quite different species composition and relative abundance (Tables 1, 2; David *et al.*, 1999). Open grassland communities, dominated by *Ommatoiulus rutilans*, differ markedly from the final woodland stages, where *Glomeris marginata* and *Porcellio gallicus* prevail. *G. marginata* and *P. gallicus* also co-exist at intermediate vegetation stages, and a third – *Glomeris annulata* – may be abundant in situations of sufficient shrub cover. *O. rutilans* are also favoured by sheep droppings on which they feed. After an initial increase from grassland to intermediate succession steps, diversity of subterranean macroarthropod communities declines towards the final (woodland) stage: the diversity peak observed in semi-open situations is due to the occurrence of species associated with the different vegetation patches as well as the presence of ecotonal species. It can be concluded that increasing tree cover favours woodland specialists, but threatens open and shrubby habitat specialists, as well as ecotone dwellers.

In abandoned meadows of the Southern Italian Alps, different Orthoptera species were found to select micro-habitats according to vegetation composition, mostly to meet their oviposition requirements (Guido and Gianelle, 2001). *Decticus verrucivorus* mainly used mown open meadows, declining progressively along the abandonment gradient and disappearing in the last stages; *Chortippus parallelus*, although present at all stages, also declined in the later ones (Table 1). Numbers of both species are favoured by mowing, as they lay eggs beneath the soil surface where high temperatures, important for hatching, are reached in open spots. *Euthystira brachyptera* also showed some preference for lightly managed meadows and early successional stages, while *Pholidoptera griseoptera*, laying eggs in bark crevices or rotten wood, was linked with mid-successional forested stages (Table 2). Although LA may show some short-term positive effects on Orthoptera communities, replacement of meadows with woodland would eventually lead to a dramatic loss of these insects (Guido *et al.*, 1998): none of the four species mentioned occurs in the mature woodland, which would become the only habitat in the absence of management. The diversity of orthopteran communities has been found to depend upon habitat heterogeneity at different spatial scales in Greece too: management options including livestock grazing, which ensures forest heterogeneity by maintaining open patches in forests and grassland, are recommended to conserve Orthoptera communities (Kati *et al.*, 2004).

Different responses to LA are known for bees and ants (Hymenoptera). Due to their complex ecological requirements and dispersal capabilities, bees prove sensitive to both habitat and matrix

effects (e.g. Dauber *et al.*, 2003) and may form rich assemblages in patchy, open landscapes. In the Mediterranean, although jeopardised by industrial agriculture, solitary bee species are favoured by traditional farmland and patchy scrubland, where they find many nesting and foraging opportunities; such conditions are rare in the final succession (oak woodland) stages, where fewer species occur (Dafni and O'Toole, 1994; Blondel and Aronson, 1999).

Because of their involvement in several key ecological processes, ants have been proposed as bioindicators of land use change, particularly in agro-ecosystems (Peck *et al.*, 1998). Mediterranean ant richness and abundance increase as the land is abandoned, and peak at the woodland stage (Gómez *et al.*, 2003). However, forest ant species characterised by high mobility still rely on mosaics to select habitats other than forest, where high-quality breeding conditions may be found all year round (du Merle *et al.*, 1978). Ant assemblage dynamics is related to the increasing vegetation complexity from cultivated or grazed sites to woodland, characterised by the occurrence of different species (Tables 1, 2; Gómez *et al.*, 2003). Analyses made by functional group (*sensu* Andersen, 1995) showed that Opportunists and Hot-climate Specialists (respectively associated with environmental stress and arid conditions) both decline in abundance and, for the latter group, in species richness; meanwhile, richness and abundance increase in "Generalized Myrmecinae" (with generalised foraging and breeding needs), Cryptics (mainly nesting and feeding within soil and litter) and Cold-climate Specialists (Gómez *et al.*, 2003). Ants are active seed dispersers by myrmecochory (in this case seeds are specifically adapted to ant dispersal) and dyszoochory (accidental seed dispersal as a by-product of predation; see e.g. Buckley, 1982). In the Mediterranean, dyszoochory may influence vegetation dynamics in recently abandoned fields: proportions of both harvester ants and dyszoochorous plants peak in younger old-fields, and decline along the successional gradient (Wolff and Debussche, 1999).

From the 1920s to 2002, in the French Pyrenees, butterfly (Lepidoptera) species richness increased following partial abandonment (some traditional farms were maintained in the landscape). All initial species persisted and three (*Carterocephalus palaemon*, *Hetropterus morphaeus* and *Araschnia levana*) of the further 12 species observed may have extended their range thanks to an open woodland increase (Corke, 2003).

On sandy soils in southern England, species diversity of the phytophagous beetles Curculionoidea and Chrysomeloidea (Coleoptera) has been found to decrease with secondary succession from recently ploughed and harrowed fields to birch woodland (Brown and Kalff, 1986). In the North Mediterranean, the diversity of epigeic beetle communities relies on landscape heterogeneity (Romero-Alcaraz and Ávila, 2000); woodland expansion causes a turnover in carabid assemblages, excluding the species that dominate grazed or cultivated patches and favouring forest specialists (Tables 1, 2; Burel and Baudry, 1994). Bramble patches developing in abandoned spots have been found to help beetle dispersal, acting as stepping stones: they are colonised by forest species moving from nearby woodland or hedgerows to invade newly

abandoned areas (Burel and Baudry, 1994; 1995). Contrasting evidence is available about whether beetle responses are driven by either changes in vegetation structure (as found by Waliczky (1991) and Burel and Baudry (1994) for predator, phytophagous and polyphagous species), or composition (see Brown and Kalff (1986) for phytophagous curculionids and chrysomelids). In central Finland, Carabidae diversity declined in response to structure changes in a forest succession gradient following clear-cutting (Koivula *et al.*, 2002): species richness was initially high, due to invading open habitat species, then it decreased following canopy closure; forest species, scarce or absent at younger stages, became progressively abundant.

Dung beetles – important in recycling organic matter and preserving pasture quality – are jeopardised by agriculture intensification (Hutton and Giller, 2003). Although their response to abandonment has not been specifically analysed, they depend upon habitat patchiness and grazing mammals, so may potentially be harmed by LA.

3.2. Amphibians and reptiles

The impact of LA on amphibians and reptiles has been largely neglected: Delbaere (2002) states that although these vertebrates do not seem to be strictly linked with farming, this is not supported by data. In fact, structures associated with traditional farming, such as livestock drinking holes or troughs and other small water bodies, are crucial for amphibian conservation and may also favour some reptiles, such as *Natrix maura* (Table 1; Perez Mellado, 1991). Dry-stone walls are often found in traditionally farmed landscapes to mark property boundaries, and are used by amphibians for both aestivation and hibernation. Where extensive livestock breeding has declined, loss of small unused water bodies which tend to fill up with sediments and vegetation (Bressi and Stock, 1999; Scoccianti, 2001), harms threatened species such as the painted frog (*Discoglossus pictus*), the Tyrrhenian painted frog (*D. sardus*) and the yellow-bellied toad (*Bombina variegata*) (Giovine, 1994; D'Antoni *et al.*, 2003), and contributes to depress population genetic variation by isolating breeding sites.

High conservation value reptiles are found in semi-natural habitats threatened by LA, such as calcareous grasslands and Hungarian and Spanish steppes (Delbaere, 2002). Mediterranean scrubland is also a major reptile habitat (e.g. D'Antoni *et al.*, 2003). Nonetheless, although shrub spreading in recently abandoned areas may have a short-term positive impact on scrubland reptiles, in the long term human disturbance is needed to preserve suitable habitats as it counters forest growth. Even scrubland reptiles such as several lizards will finally be harmed by the expansion of thick scrubland or forest, since they need open sites for thermoregulation (Martín and Lopez, 2002). In dehesas, old quarries – from which stones for rural constructions used to be extracted – offer shelter to high numbers of snakes and lizards (Perez Mellado, 1991). However, *Vipera latasti* occurring in dehesas has undergone a strong decline due to both direct persecution and alteration of the original Mediterranean woodland (Perez Mellado, 1991)

3.3. Birds

The sensitivity of birds to spatial and temporal environmental changes (e.g. Kushlan, 1993; Fuller et al., 1995; Blair, 1999; Reynaud and Thioulouse, 2000) has made them a favourite indicator of the ecological consequences of land use change in farmland (Ormerod and Watkinson, 2000), including LA (e.g. Farina, 1997; Preiss *et al.*, 1997; Moreira *et al.*, 2001; Suárez-Soane *et al.*, 2002). By dispersing fleshy-fruited plant species, birds also influence vegetation changes spatial and temporal dynamics following LA (Clergeau, 1992).

At the species level, birds of prey are interesting models for several reasons: many of them are open habitat foragers (Tworek, 2002); respond sensitively to land use change (Newton, 1979); occupy high positions in the food chain; have large home ranges and a long life. Moreover, the precarious conservation status of many raptors makes them a priority target for habitat management.

Among bird communities viewed on a broad geographical scale, the well-studied Mediterranean avifauna offers a unique opportunity to explore how biogeography and human history – both particularly complex in this region (Blondel and Aronson, 1999) – may influence current animal community structure and dynamics, helping to interpret responses to LA and predict future scenarios.

This section a) reviews the impact of LA on habitats important to birds; b) focuses on birds of prey as valuable indicator species; and c) analyses the Mediterranean bird communities as a special case-study.

3.3.1. Birds and habitat changes

Farmed systems have an overwhelming importance for avifauna (Tucker and Evans, 1997): European semi-natural landscapes support 173 priority bird species of which *ca* 20% have an unfavourable conservation status because their populations are small or declining (Nagy, 2002). Many endangered birds are open-habitat specialists (e.g. Blanco *et al.*, 1998; Tella *et al.*, 1998; Wolff *et al.*, 2001; 2002) and are often defined as “farmland birds” since their conservation relies on the availability of human-maintained steppes and grassland, put at risk by LA (Delgado and Moreira, 2000; Moreira, 1999; Nagy, 2002).

For example, in Mediterranean upland areas all partridge species depend upon early successional habitats, so are affected by the growth of vegetation and the decline in livestock grazing (Génard and Lescourret 1990; Bernard-Laurent and de Franceschi 1994; Papaevangelou *et al.*, 2001). Breeding Pyrenean grey partridges (*Perdix perdix hispaniensis*) were found to select scrubland (Novoa *et al.*, 2002): in spring, successful breeders used sparse (20-40%) and open (40-60%) scrublands more frequently than the unsuccessful ones, and in summer the former used open

habitats much less than the latter. To maintain the mosaic of dense and open scrubland required by the species in the long term, grazing and management are needed (Novoa *et al.*, 2002).

Pastoral abandonment in Alpine landscapes has been found to increase overall avian diversity, but it impacts endangered grassland species depending upon grazed pastures (Laiolo *et al.*, 2004a; Table 1): the negative effects were mostly observed at lower altitude (i.e. below the timberline), where vegetation changes are most significant.

The decline in livestock grazing and agricultural practices have also been recognised as a factor for the disappearance of large open sedge and *Cladium* fen mires progressively overgrown by shrubs: this has resulted in a loss of breeding habitat for the globally threatened aquatic warbler *Acrocephalus paludicola* (Aquatic Warbler Conservation Team, 1999; Flade, 1999; Kloskowski and Krogulec, 1999).

As expected, the replacement of open habitats with scrublands or forests favours forest bird species (Table 2): for example, LA and afforestation may help explain the expansion of the European range in central and Western Europe and downward altitude shift in the black woodpecker (*Dryocopus martius*) recorded during the last century (Mikusi ski, 1995; Bologna, 2002).

In some cases, abandonment of forestry practices may be detrimental to bird conservation too. In South Scandinavia, the ca. 500 year-old oak-hazel woodlands, managed to produce hay, nuts and timber and to keep grazing livestock in autumn, risked dying out over the last century: those still managed traditionally sustain many breeding bird species and are especially important for migrants, while neither of these features is found for totally abandoned forest sites (Hansson, 2001). In other situations, however, abandoned forests prove valuable for bird biodiversity: unmanaged, regenerating beech-wood stands support higher bird richness, abundance and diversity than managed ones, primarily thanks to the higher dead tree availability, which provide several species with invertebrate prey as well as suitable nesting or roosting conditions (Laiolo *et al.*, 2004b).

In agricultural mosaics, the value of different habitat factors in determining the occurrence of breeding birds differs according to the species' ecological strategy, so that maintaining a diversity of habitat within the landscape is the best way for maximising bird diversity (Moreira *et al.*, 2001; Tworek, 2002; Laiolo *et al.*, 2004a). The effects of LA on bird diversity will largely depend on the scale of the phenomenon, for it may either encourage or depress habitat diversity. Landscape homogeneity is a likely outcome when large areas are abandoned, and this will be detrimental to bird conservation (e.g. Nagy, 2002).

Within the landscape mosaics, habitats such as cultivated land and, secondarily, deciduous woodland may contribute considerably to regional bird diversity (Farina, 1997; Preiss *et al.*, 1997; Moreira *et al.*, 2001). However, further habitats within the mosaic, although used by a less speciose community, may still be crucial for some species (Delgado and Moreira, 2000) due to

their specialist or multiple-habitat needs. In a rural area of north-western Portugal subject to abandonment, low scrublands produced by recurrent fires hosted the least diverse bird community of all occurring habitats, but still proved important for narrow-niche taxa such as the Dartford warbler (*Sylvia undata*), the common linnet (*Carduelis cannabina*) and the European goldfinch (*C. carduelis*), and for foraging birds of prey (Moreira *et al.*, 2001).

A special form of abandonment with repercussions on avifauna is the ending of salt production in the salt pans, whose traditional management determines the availability of shallow, saline water. A case-study from Spain (Paracuellos *et al.*, 2002) showed that abandonment reduced shallow, salty pools and increased deeper water with lower salinity and a higher productivity. For several species, it had a positive effect: waterbird community diversity increased as the changed conditions favoured diving foragers, while many of the original species still persisted in the remaining shallow, salty water. However, especially the abundance of some large species foraging in the interior and deeper zones of shallow salty lagoons – including greater flamingos (*Phoenicopterus ruber*), avocets (*Recurvirostra avosetta*) and black-tailed godwits (*Limosa limosa*) – declined since their preferred habitat was drastically reduced. Thus although saltpan abandonment is generally favourable to birds, some form of management (such as controlled seawater flooding) would be advisable to contrast the negative effects described (Paracuellos *et al.*, 2002).

3.3.2. Birds of prey

The end of farming practices affects several raptor species on account of the loss of open foraging grounds and of the reduced availability of preferred prey. Crop abandonment is harmful to the globally threatened lesser kestrel (*Falco naumanni*): in Spanish pseudo-steppe this raptor selects field margins and cereal fields for foraging, while abandoned fields and scrublands are avoided (Tella *et al.*, 1998). Likewise, in the Kazakhstan steppe, the Saker falcon (*Falco cherrug*) shows a lower breeding success where vegetation re-growth due to the disappearance of nomadic grazing has reduced availability of its choice prey, *Spermophilus* ground squirrels (Watson and Clarke, 2000).

Grasslands are major foraging habitats in alpine regions for the golden eagle, *Aquila chrysaetos* (e.g. Haller, 1988). In the central-eastern Italian Alps, nest spacing correlated positively with the amount of woodland occurring within foraging ranges (i.e. fewer nesting birds occurred in more forested areas): according to the current rate of loss of grassland due to LA and afforestation, a 5-9% density decline is expected in the next 20 years (Pedrini and Sergio, 2001). Pedrini and Sergio (2001) point out that this long-term effect might be currently masked by counteracting factors such as increasing food supply and reduced persecution.

The imperial eagle (*Aquila adalberti*) – the most endangered European bird (Ferrer and Harte, 1997) – depends on rabbits as its main prey (e.g. González *et al.*, 1990), and the decline in their abundance throughout the eagle range has been related to LA (Moreno and Villafuerte, 1995).

Furthermore, although adult eagles use more forested habitats (González *et al.*, 1990), non-irrigated fields, pastures and cultivated farmland scattered with oaks and olive trees are important habitats for dispersing immature birds, so that the conservation of these extensively managed landscapes should be promoted (Ferrer and Harte, 1997). A high rabbit availability and the preservation of traditional farmed landscapes are also beneficial to other sympatric eagle species, such as Bonelli's eagle, *Hieraaetus fasciatus* (Moreno and Villafuerte, 1995; Ferrer and Harte, 1997).

In a Mediterranean area of Spain, breeding densities of tree nesting raptor species (booted eagle, *Hieraaetus pennatus*; short-toed eagle, *Circaetus gallicus*; buzzard, *Buteo buteo*; and goshawk, *Accipiter gentilis*) were best predicted by woodland cover, but were also associated positively with extensive agricultural land use, at a small (9 km²) scale for *H. pennatus* and *C. gallicus*, and at a larger scale (100 km²) for both *H. pennatus* and *B. buteo* (Sánchez-Zapata and Calvo, 1999). The length of edge between forest and extensive agriculture was a good descriptor for breeding density, particularly at the 100 km² scale (Fig. 2), explaining a high variation proportion for *H. pennatus* and *C. gallicus*, which both rely on edge and open habitats for foraging (Sánchez-Zapata and Calvo, 1999).

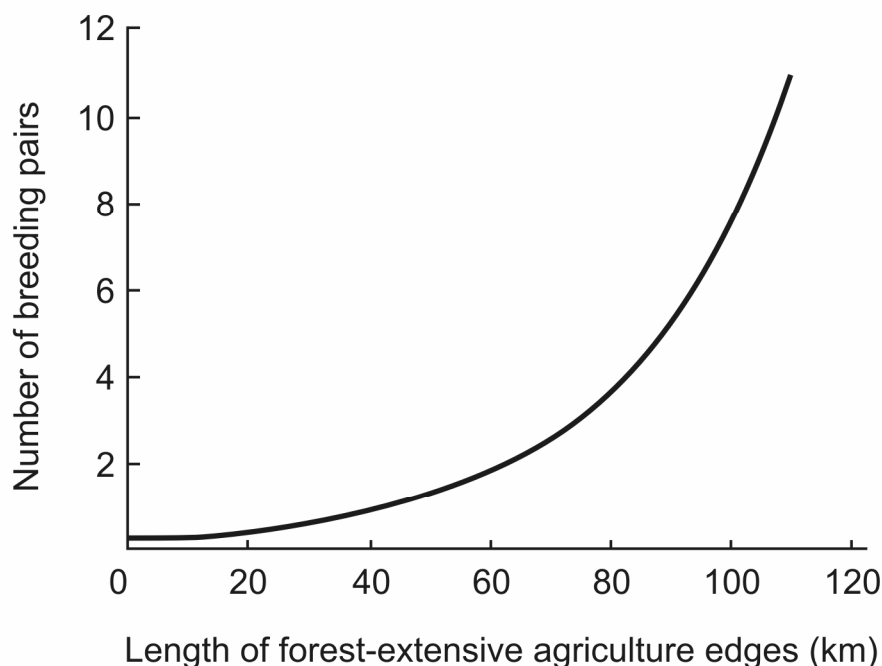


Figure 2. The relationship occurring between the length of forest-extensive agriculture edges and number of breeding pairs of *Hieraaetus pennatus*, a forest raptor species, at the 100 km² scale. The species greatly relies on edge and open habitats for foraging (Modified after Sánchez-Zapata and Calvo, 1999).

The abandonment of agricultural upland in the Italian Apennines has been addressed as a major cause, together with electrocution, for the population crash of an apex predator from the Strigiformes, the eagle owl (*Bubo bubo*), which has undergone a 70% *ca.* decrease in the last 20-30 years in the Abruzzo region (Penteriani, 1996). Clearings in beech woodlands – formerly maintained for livestock breeding and agriculture and progressively disappearing with rural depopulation – used to offer a high-quality foraging habitat for this species in mountainous areas and sustained important prey-species such as hares and partridges (Penteriani, 1996) at sites structurally suitable for nesting but otherwise providing scarce food.

In Mediterranean France, density, diet and breeding performances within the same *B. bubo* population from two nearby areas were examined (Penteriani *et al.*, 2002): an upland, abandoned area with reduced open land and landscape diversity, and a lowland area where habitats such as croplands, pastures and fallow lands were still largely available. Since the 1930s, myxomatosis caused a strong decline in rabbits – a major prey for owls – and in both areas owls switched to smaller prey. However, when exploiting lower-quality, more forested hunting habitats, the owls in the upland (highly specialised in preying on rabbits) foraged less efficiently and shifted to a less diverse diet than those in the lowland, so that their density and productivity fell and egg-laying was delayed.

3.3.3. Mediterranean bird communities and land abandonment

Mediterranean landscape heterogeneity is crucial to sustain highly diverse avian assemblages (Farina, 1995; 1997; Preiss *et al.*, 1997; Aauri and de Lucio, 2001; Moreira *et al.*, 2001). Such assemblages include many autumn migrants on their refuelling stops as well as overwintering species (e.g. Farina, 1995), both dominant among the myriad of migrants crossing the Mediterranean Basin twice a year (Blondel and Aronson, 1999).

Mediterranean forest bird species are in most cases also found elsewhere in Europe, with few exceptions (Blondel and Farré, 1988; Covas and Blondel, 1998): as a result, forest expansion following LA has been found to “simplify” the avifauna. The increase in forest cover that came about between 1979 and 1992 in an abandoned area of Mediterranean France favoured mainly non-Mediterranean forest species such as tits (*Parus* spp.), firecrests (*Regulus ignicapillus*) and the common chaffinches (*Fringilla coelebs*) at the expense of those associated with open habitats and low scrublands (Preiss *et al.*, 1997; Tables 1, 2). In an area in Spain located on the border between the Eurosiberian and Mediterranean regions (Suàrez-Seoane *et al.*, 2002), the response of bird communities observed along an abandonment gradient was linked with the bird species’ biogeographical origins as well as with complexity of habitat structure associated with the vegetation stage. After an initial decline in the “tomillar” stage (abandoned cropland with low, scattered shrubs), bird diversity recovered through tall scrubland (“matorral”) to forest. Trends of Eurosiberian and Mediterranean species proved similar in winter (due to absence of summer tree-

dwelling migrants), but in the breeding season the former showed a considerable diversity increase from cultivated fields to forest, while the latter were not affected by the succession stage. Unlike densities of Mediterranean species, those of Eurosiberian species often correlated positively with vertical vegetation structure, demonstrating a preference for shrubby or wooded habitats.

Why are there so few typically Mediterranean forest species? During glacial periods, Western Palearctic floras and faunas found their *refugia* in the Mediterranean, expanding northwards in the inter-glacial phases (e.g. Huntley, 1988; Taberlet *et al.*, 1998; Blondel and Aronson, 1999). Boreal bird species never left the deciduous oak forests once widespread in the Mediterranean, and contact between northern and southern forest bird communities was maintained, preventing the occurrence of allopatric speciation in the Basin. In Mediterranean areas where forests could not develop due to climate and soil features, however, scrublands formed throughout the Pleistocene, setting the scene for speciation of open-space specialists such as warblers (genus *Sylvia*), mostly endemic to the region (Blondel *et al.*, 1996).

Fire is an important environmental disturbance in the Mediterranean (e.g. Blondel and Aronson, 1999). It may be valuable to open space-dwelling bird species because it generates suitable habitat (Preiss *et al.*, 1997; Blondel and Aronson, 1999; Moreira *et al.*, 2001). However, colonisation of recently burnt patches by such specialists is accomplished by short-distance dispersal, so it depends on the pre-fire occurrence of suitable habitat in the landscape (Brotons *et al.*, 2005). By reducing the availability of such source-habitat in the landscape, LA may decrease the chances that open patches created *ex novo* by recent perturbations such as fire will be successfully colonised.

On the other hand, fire might be considered harmful for forest birds since it fragments forest cover (e.g. Smith and Hellmann, 2002). However, in a Mediterranean landscape of Spain the fire-shaped scrubland mosaic surrounding forest fragments had no detectable isolation effect on forest bird populations, whose species richness was enhanced by irregular fragment shape, a factor generally regarded as deleterious for forest species (Herrando and Brotons, 2002). Hence, although forest birds in the Mediterranean appear sensitive to patch size and so vulnerable to habitat loss, other influences of fire have negligible effects on them, probably as a result of adaptation of bird communities achieved through rarefaction or extinction of interior forest species and persistence of those performing well in patchy landscapes (Tellería and Santos, 1999; Herrando and Brotons, 2002). Catalanian forest fragments embedded in a fire-generated shrubland matrix and segments of continuous forests of equal area showed similar species richness but differed in species composition and relative abundance (Brotons *et al.*, 2004a): fragments proved important for some species, further remarking the importance of landscape heterogeneity to support bird diversity.

3.4. Mammals

In southern Europe, LA has favoured a number of mammal species (Table 2), including ungulates (Chenavier *et al.*, 1997; Gortazar *et al.*, 2000), probably the crested porcupine, *Hystrix cristata* (Bruno and Riccardi, 1995) and some large carnivores, as discussed below. However, population declines in response to vegetation closure have been recorded in others (Table 1), such as lagomorphs – typically dwelling in open habitats – and their predators (Moreno and Villafuerte, 1995): in the mountains of central-southern Italy, agriculture abandonment is regarded as a threat to the endemic Italian hare, *Lepus corsicanus* (Trocchi and Riga, 2001).

Due to their high mobility and multiple habitat use patterns, responses by most mammals are well revealed at the landscape level. For example, although roe deer (*Capreolus capreolus*) are favoured by the increased availability of close forest following LA, landscape selection is directed towards heterogeneous areas with some openings (Grossi *et al.*, 1995).

Several carnivores, like frugivorous birds and ants, are not simply influenced by LA, but may themselves influence vegetation succession in abandoned areas by disseminating fleshy-fruited shrub species (e.g. Aronne and Russo, 1997).

Small mammals (insectivores and rodents) are sensitive to land use changes, which affect distribution, habitat use, community composition, relative abundance and demography (Moreno and Kufner, 1988; Delattre *et al.*, 1999; Tattersall *et al.*, 2001; Millán de la Peña *et al.*, 2003). In north-east Italy, arboreal rodents such as the red squirrel (*Sciurus vulgaris*) and the common dormouse (*Muscardinus avellanarius*) have been favoured by forest expansion (L. Lapini, *pers. comm.*). Responses also concern population dynamics: in the French Jura mountains, LA has mainly seen the conversion of arable land into permanent grassland, determining a rise in outbreak frequency of grassland rodents such as common (*Microtus arvalis*) and water voles (*Arvicola terrestris*) – a phenomenon which may well have ecological and economical implications, for the spreading rodents may damage other habitats such as forests and cultivated land (Delattre *et al.*, 1986; 1988). Both the amplitude of *M. arvalis* population variation and the duration of the abundance phases are controlled by the grassland-to-agricultural land ratio in the landscape. Outbreaks may occur when the ratio is high, and are further encouraged by forest absence or scarcity (Delattre *et al.*, 1992; Girardaux *et al.*, 1994; Delattre *et al.*, 1999). Moreover, wider population fluctuations occur in *M. arvalis*, the bank vole (*Clethrionomis glareolus*) and the yellow-necked mouse (*Apodemus flavicollis*) where forest cover is scarce (Girardaux *et al.*, 1994). Landscape composition and structure could influence population dynamics mainly by favouring different predator species: the specialised predators, frequent in open habitats, would destabilise rodent populations, whereas the opportunistic ones found in forests would have a regulating effect (Girardaux *et al.*, 1994; Delattre *et al.*, 1999).

No study has specifically addressed the impact of LA on bats. However, their eco-morphological specialisation based on foraging habitat structure (Norberg and Rayner, 1987; Vaughan *et al.*,

1997) and roosting requirements can drive changes in activity patterns and community composition as vegetation re-grows. Although intensive farming is often deemed harmful to bats (Stebbing, 1988), extensively managed habitats may be valuable to foraging bat communities (Wickramasinghe *et al.*, 2003). Rural areas also offer roosting opportunities to synanthropic species (Kunz, 1982), and cattle troughs in mountainous areas are used for drinking by rich species assemblages (Russo and Jones, 2003). Open habitats and clearings favour large species hunting on the wing (Vaughan *et al.*, 1997; Patriquin and Barclay, 2003) as well as those seizing prey from the ground or grass (e.g. the greater and lesser mouse-eared bats, *Myotis myotis* and *M. blythii*; Arlettaz, 1999). Pastures interspersed with tree patches and hedgerows are the preferred foraging habitat for the threatened greater horseshoe bat (*Rhinolophus ferrumequinum*); cattle-browsed hedgerows provide this species with optimal perches from which to hang during “sit-and-wait” foraging, and livestock dung provides food by supporting dung beetles (Duvergé and Jones, 2003). Unlike *R. ferrumequinum*, other rhinolophids more strictly dependent on woodland for feeding (Bontadina *et al.*, 2002; Russo *et al.*, 2002), as well as woodland specialist foragers from other families (e.g. the brown long-eared bat, *Plecotus auritus*: Entwistle *et al.*, 1996) may benefit from forest re-growth, as may species roosting in tree cavities (Russo *et al.*, 2004). However, intermediate stages such as scrubland support limited bat activity and few foraging species (Russo and Jones, 2003), and offer few roosting opportunities.

In recent centuries predation upon livestock and game has brought large carnivores into conflict with humans, who have progressively destroyed their forest habitats. Wild ungulate prey have either declined or disappeared due to habitat loss, over-hunting and competition by livestock (Breitenmoser, 1998). Predators have re-directed their hunting activity to domestic animals, and suffered massive persecution as a consequence. By the middle of last century, for example, wolf (*Canis lupus* L., 1758) populations had dwindled drastically, and the animal had been eradicated in much of Europe (e.g. Breitenmoser, 1998). Larger populations survived only in the Balkans and in the East, along with small yet viable ones in the Mediterranean (Boitani, 1992; 2000). Since then, however, the trend has been strikingly reversed: eastern populations have spread westwards and even re-colonised the Scandinavian peninsula (Wabakken *et al.*, 2001; Vilà *et al.*, 2003), while the Italian population (Fig. 3) has expanded northwards, re-occupying the western Alps and reaching Switzerland and France (Glenz *et al.*, 2001; Valière *et al.*, 2003). This is due to several factors: an increase in wild ungulate prey (in some regions determined by re-introduction), legal protection of large carnivores, a new favourable attitude towards wildlife (Boitani, 1992), and rural depopulation and the consequent decline of human activities (Brangi and Simonetta, 1998; Blondel and Aronson, 1999; Boitani, 2000; Bologna, 2002).

Human disturbance and prey abundance determine habitat quality for large carnivores (Boitani, 2000; Swenson *et al.*, 2000). In several areas, depopulation has mitigated human-wolf conflict – still the major cause of wolf mortality – by reducing contact between them. LA has resulted in

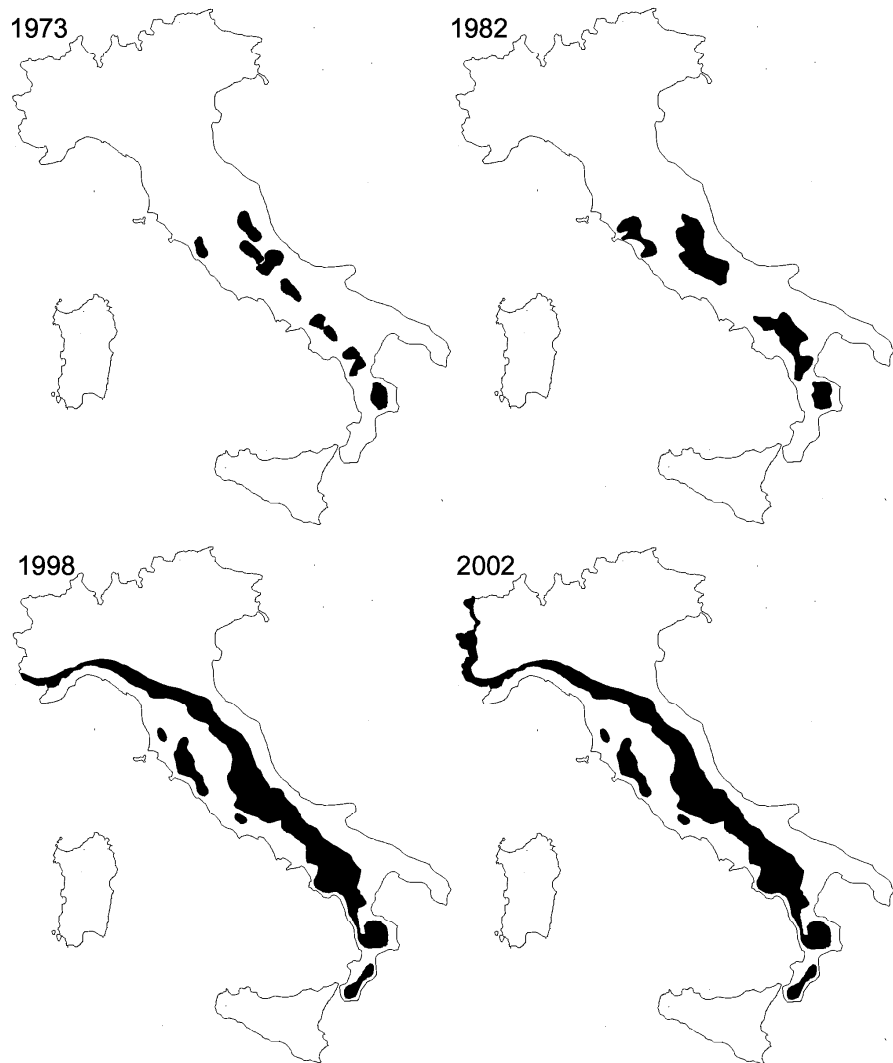


Figure 3. Range expansion of Italian wolves (*Canis lupus*) in 1973-2002. Forest cover increase, greater prey availability and reduced human disturbance are the land abandonment-related factors which help explain the wolf recovery in Italy as well as elsewhere in Europe. Modified after Zimen and Boitani (1975), Boitani and Fabbri (1983), Ciucci and Boitani (1998) and Genovesi and Dupré (2002).

increasing availability of vegetation cover, helping wolves take shelter from people (Boitani, 2000). Forest re-growth has also indirectly favoured wolves (Meriggi and Lovari, 1996) by sustaining larger ungulate prey populations (Chenavier *et al.*, 1997; Gortazar *et al.*, 2000). Such factors may have locally increased population size, encouraging dispersal (through improvement of corridor quality) and colonisation of newly available territories. Similar consequences of LA in mountain regions may have also influenced positively the brown bear, *Ursus arctos*, and Eurasian lynx *Lynx*

lynx, which have reappeared in areas where they had once been extirpated (Breitenmoser, 1998). A contrasting situation exists, however, for the Iberian lynx, *Lynx pardinus* (the world's most endangered Felid species; Delibes, 1999). Habitat disturbance maintains the scrubland-woodland mosaics harbouring its main prey, rabbits (Moreno and Villafuerte, 1995). In the past, traditional farming in mountain areas maintained such habitat mosaics. The current increase in scrub density following LA has reduced suitable habitat, and populations of both rabbits and their feline predator are shrinking (Delibes *et al.*, 2000). Incidentally, in Doñana National Park, the same vegetation change causing this decline has probably favoured generalist predators (common genet, *Genetta genetta* and red foxes, *Vulpes vulpes*) by increasing availability of other prey species such as the wood mouse, *Apodemus sylvaticus* (Rau *et al.*, 1985).

According to a recent study (Lozano *et al.* 2003), habitat preferences in Mediterranean populations of European wild cats (*Felis silvestris*) differ from those identified in the north, where forest conservation is advocated to preserve the remaining cat populations (Stahl and Artois, 1991; Hemmer, 1999). In northern Europe scrublands are rare, so *F. silvestris* shelters and rests in forests and hunts in open habitats. Instead, in Mediterranean Spain the species mainly selects landscape mosaics of scrubland for sheltering and hunting, and pastures offer further hunting grounds (Lozano *et al.*, 2003). If these findings are confirmed for other Mediterranean areas, southern populations might be harmed, rather than favoured, by LA when this leads to the loss of scrubland-pasture mosaics.

4. CONSERVATION IMPLICATIONS

4.1. Conservation targets and strategies in land abandonment

Most studies mentioned in the present paper highlight a considerable impact of LA on many animal species, affecting above all open-habitat specialists. The process concerns many areas of great significance for wildlife, such as 609 of the Important Bird Areas identified by BirdLife International, mostly located in Central and Eastern Europe, as well as in mountainous and coastal regions (Nagy, 2002; Fig. 4). However, LA also favours some animal groups, and setting conservation objectives and management strategies is not a simple task.

Animal richness and/or diversity have been commonly adopted as the main indicators in assessing the effect of land use change, but they cannot constitute the main targets in habitat management. In fact, mere increase in taxonomic unit numbers is undoubtedly a naïve conservation objective. To give an example, although the gain in forest bird species following LA may determine an increase in diversity of avian assemblages, it will not “compensate” for the loss of open-habitat species, as forest birds, which in many cases do not need specific habitat requirements other than some kind of forest, are often characterised by a lower conservation value (Pons *et al.*, 2003, Laiolo *et al.*, 2004a). Preserving endangered species is not enough, however, as the important ecosystem services (Chapin *et al.*, 2000) provided by many common species and their keystone role cannot

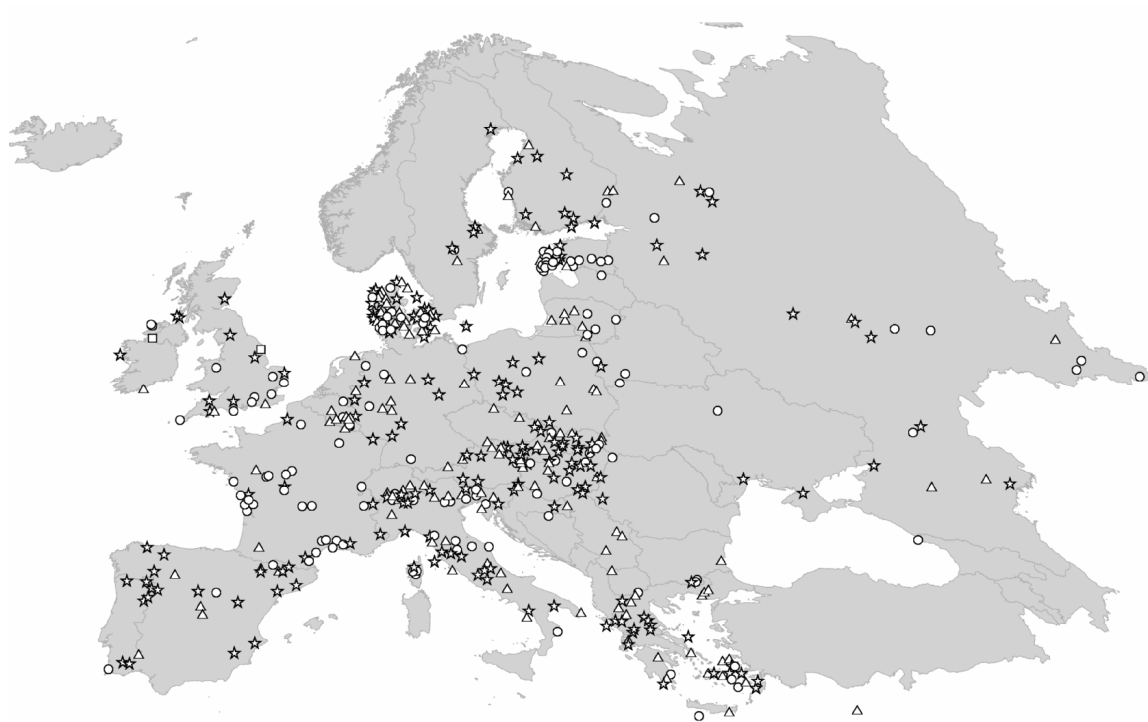


Figure 4. Important bird areas currently jeopardised by land abandonment, from Nagy (2002). Symbols indicate sites under ○ high, ☆ intermediate and △ low risk; □ symbols correspond to sites where risk has not been quantified (reprinted with permission from the author and the Council of Europe).

be ignored. A broad community perspective is also needed: although generally common, species acting as key prey for high-order consumers (e.g. several lagomorphs and rodents) may decline with the increasing complexity of vegetation structure following LA, having dramatic effects on their predators (e.g. Delibes *et al.*, 2000; Penteriani *et al.*, 2002).

The criticism concerning conservation focused on “umbrella species” (Simberloff, 1998) and overlooking the needs of other groups, also applies to the management of animal communities in abandoned landscapes: for example, although in dehesas traditional land clearance is recommended to favour Spanish imperial eagles (*Aquila adalberti*), it may harm lizard communities which rely on some bush cover (Martín and Lopez, 2002).

The differences in responses observed in both invertebrates (see e.g. Kiss *et al.*, 2004 for land snails) and vertebrates (Suàrez-Seoane *et al.*, 2002; Lozano *et al.*, 2003) according to biogeographical origins and local population behaviour suggest caution in applying the knowledge acquired in a given region to models and management strategies developed elsewhere.

4.2. Scale of analysis and management

Scale is a crucial factor to be taken into account in surveys, analyses, models, and management plans: data collected only at patch or plot level are completely inappropriate in dealing with highly mobile, landscape-dependent species, and may lead to misinterpretation even in considering sedentary, habitat-dependent species. Thus although tall vegetation encroachment may cause extinction of open space specialists at habitat level, species with limited spatial requirements which respond sensitively to the degree of openness – such as millipedes and woodlice (David *et al.*, 1999) – will persist in any given vegetation matrix as long as small patches of different vegetation are maintained. Likewise, although the rare open habitat-dwellers among Mediterranean land snail communities such as *Trochoidea geyeri* are favoured in grazed areas, they are not put at risk by reduction in this habitat as far as even small suitable patches persist in the landscape (Labaune and Magnin, 2002).

Landscape is thus often the most appropriate level at which to detect biodiversity trends, record species distribution, assess spatial variation and take management decisions (e.g. Luoto *et al.*, 2003). The extent of the area abandoned and the former characteristics of the landscape – including forest cover and land use intensity – determine whether LA will depress, or enhance, beta diversity of animal communities, since the process may either decrease or increase the range of habitats available. In the latter case, open habitat specialists will still feature in the landscape, while further opportunities are offered to species depending on forest and edge habitats. In mountain areas where forest was already widespread, further forest expansion driven by LA has had harmful effects on animal diversity; but animal communities in landscapes that are more intensively used, dominated by open habitats, probably benefit from LA (MacDonald *et al.*, 2000).

This helps explain why the set-aside measures prescribed by the European Union Agricultural Policies have proved beneficial to wildlife in lowland areas characterised by intensive agriculture (e.g. Sotherton, 1998), while in others, such as hilly or mountain landscapes already subject to rural depopulation, they have mostly proved detrimental (Trocchi and Riga, 2001).

The resulting landscape structure and configuration are likely to have subtle effects on animals, often difficult to predict, controlling factors such as habitat connectivity, fragmentation, edge size and shape.

On the other hand, micro-habitat effects may be important too, particularly for species with a limited mobility: for example, resilience to low fire regimes of Mediterranean gastropods is ensured by micro-refuges allowing shade-loving and mesophilous species to survive even repeated fires and persist in otherwise inhospitable habitats (Kiss *et al.*, 2004). Likewise, small vegetation patches saved from prescribed burning are used by *A. sylvaticus* to escape the fire and subsequently re-colonise the burnt areas (Monimeau *et al.*, 2002). The maintenance of Orthoptera diversity too is facilitated by the occurrence of adjoining small patches, and even species selecting

mown areas need nearby abandoned patches to shelter in during and after mowing (Guido and Gianelle, 2001).

Although rarely carried out, multi-level analyses of spatial requirements may reveal otherwise undisclosed selection patterns and help develop effective management measures (e.g. Sánchez-Zapata and Calvo, 1999; Thompson and McGarigal, 2002; Martínez *et al.*, 2003; Russo *et al.*, 2004). They may go some way to reducing the bias of “human-centred” perspective, for it must always be borne in mind that organisms’ perception of habitats and landscapes may be quite different from the way we define them.

4.3. Managing abandoned land for animal conservation

Finding strategies that strike a balance between biodiversity conservation and productivity, as well as meeting the social and cultural demands of rural human communities, is among the major objectives of modern farmland ecology (Altieri, 1995). Obvious as it may seem, the best way to avoid species loss connected with LA is to preserve traditional farmland (e.g. Moreira *et al.*, 2001) by supporting it and making it more profitable, developing adequate policies to pursue this objective. Agri-environment programmes have been locally applied to prevent land abandonment (Buller and Brives, 2000), but much remains to be done. The main challenges are to withstand the overwhelming competition of industrial agricultural production, save the local knowledge which has allowed people and farmland biodiversity to coexist harmoniously for centuries, and give the young generation good reason to resist the lure of urban society and carry on their fathers’ activity. Consideration of how these challenges can be met has huge social and economical implications and is beyond the scope of this paper, but from an ecological perspective it is worth stressing that the “optimal” heterogeneity patterns found in extensive farmland, so important for conservation, are extremely difficult to reconstruct. In fact, the complex set of farmland spatial and temporal variables, and their intricate multivariate interactions (Benton *et al.*, 2003), make it difficult to design or manipulate each feature in order to enhance biodiversity (Bignal, 1998). This might partly explain the reported failure of specific strategies designed to mitigate the impact of intensive agriculture on wildlife (Kleijn *et al.*, 2001).

It is now generally agreed that biodiversity conservation cannot be guaranteed by relying on protected areas only: preservation of traditional land use outside parks is an excellent way to enact the ‘Benefits beyond boundaries’ approach advocated by the 2003 IUCN World Parks Congress (Pedroli, 2003). On the other hand, natural parks, often located in mountain regions where LA has largely occurred (MacDonald *et al.*, 2000), have generally devoted little if any effort to preserving traditional farm practices, so that forest species richness has increased at the expense of open habitat specialists, as reported for bird communities (Pino *et al.*, 2000). Extensive farming should be encouraged both within parks – zoning is an excellent tool in this respect (Primack, 1998) – and

in their surroundings to ensure its complementary role in biodiversity preservation at a regional scale (Pino *et al.*, 2000).

Where traditional practices have disappeared, open habitats may be maintained through active management, including prescribed burning and grazing (Moreira *et al.*, 2001). Prescribed burning has been used to counter vegetation encroachment and to recover grassland suitable for livestock farming (e.g. Monimeau *et al.*, 2002; Pons *et al.*, 2003). In the Mediterranean, biological communities are adapted to fire (Blondel and Aronson, 1999): the scale and the return rate at which fires occur, however, may determine whether they favour or threaten animal communities. The random occurrence of localised fires in a sufficiently large area has been found to ensure the persistence of all bird species in the landscape (Prodon *et al.*, 1987; Moreira *et al.*, 2001). A dynamic equilibrium is reached between bird community structure and its spatially and temporally stochastic environment, which constitutes a fire-determined “moving mosaic” of grassland, scrubland and forest (Blondel and Aronson, 1999), encouraging the occurrence of metapopulation dynamics in open habitat specialists which will colonise the new open spaces created by fire from nearby suitable patches (Brotons *et al.*, 2005). Pons *et al.* (2003) highlight the value of grassland with shrubs created by single or repeated burning for bird species of conservation concern in the French Pyrenees; in an agricultural area of Minho (Portugal), grazing and prescribed burning are also recommended to preserve habitat mosaics important for birds (Moreira *et al.*, 2001). Different responses to prescribed burning have been reported for some animal groups besides birds (e.g. Ford *et al.*, 1999; Brand, 2002; Monimeau *et al.*, 2002). Fire as a management practice is still often regarded as quite invasive (e.g. Petretti, 2003). Detailed knowledge (Pons *et al.*, 2003) is needed to evaluate responses according to animal group and geographical area in order to identify the most sustainable spatial scale and schedule to adopt (Brand, 2002).

Besides creating spaces suitable for open-habitat and ecotone specialists, small-scale fires avoid the occurrence of large fires by breaking fuel continuity in the homogeneous, highly-inflammable scrublands of abandoned, scarcely inhabited regions, where fire is less likely to be extinguished by people (Blondel and Aronson, 1999). In this scenario, even the advantages of tall vegetation growth may be heavily reduced by a higher likelihood of large-scale fires (Herrando and Brotons, 2002) which destroy many of the habitats favoured by forest species, replacing them with homogeneous low scrublands characterised by species-poor communities (Moreira *et al.*, 2001; Fig. 5). Although prescribed burning proves useful to control shrubs, additional measure such as grazing are needed to avoid vegetation encroachment in the cleared areas (Moreira *et al.*, 2001).

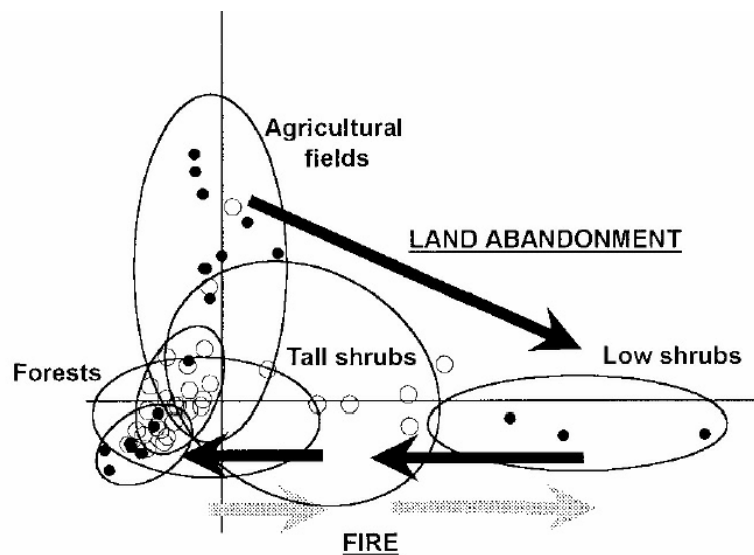


Figure 5. Plot of the first two axes from a Correspondence Analysis of the bird species versus sites matrix for the bird community studied in a Mediterranean rural area in the Minho region (Portugal) after Moreira *et al.* (2001). The large ellipses encompass sites within each of the six land use types examined. Filled circles indicate species with narrow niche breadth (specialists), open circles those with broad niche breadth (generalists). Low scrublands hosted few species, but were important for *Sylvia undata*, *Carduelis cannabina* and *C. carduelis* (corresponding to the three filled circles in the “Low shrubs” ellipse). Further details on species are given in Moreira *et al.* (2001). Black arrows illustrate the land use changes driven by land abandonment; grey arrows those determined by fire. (Figure 4 in Moreira *et al.* (2001), reprinted with kind permission of Springer Science and Business Media.)

4.4. Managing human-predator relationships

The range expansion of predators, partly due to rural depopulation, is a welcome yet challenging development for conservationists. Steps to cope with this new situation should involve several participants, including farmers, hunters, the media, ecologists and policy makers, and action should take into account both local issues and the trans-national scale of management problems (see e.g. Boitani, 2000; Swenson *et al.*, 2000; Breitenmoser *et al.*, 2000). Although humans have driven large carnivores to extinction in much of Europe and still threaten their survival, livestock farming has played a role in sustaining predator populations where wild prey was scarce, especially in Southern Europe (e.g. Meriggi and Lovari, 1996; Lovari *et al.*, 1996). In the Iberian peninsula, wolves still rely largely on livestock (Boitani, 2000; Moreira *et al.*, 2001). In such cases, the livestock-predator co-existence may still be desirable for conservation (Boitani, 2000), making loss compensation of special importance; reintroduction of prey species is advisable to mitigate the

predator's economic impact (Meriggi and Lovari, 1996). Pasture management and improvement in mountainous areas is another important issue for carnivore conservation as it favours the prey of large mammals (Boitani, 2000).

It is now widely agreed that prevention and information are needed to mitigate human-predator conflicts, since loss compensation cannot be the only response (Boitani, 2000; Swenson *et al.*, 2000). Prevention methods (limited flock numbers, use of guard dogs, sheltering livestock at night or in foggy conditions) are still in use where farmers and large carnivores traditionally co-occur, but in recently re-colonised areas these practices no longer exist (Sagor *et al.*, 1997; Boitani, 2000, Swenson, 2000), making livestock much more vulnerable and damage considerable. This evokes harsher reactions on the part of the public to the appearance of predators (Breitenmoser, 1998), and confirms the value of rural cultures in conservation.

5. THE WAY FORWARD IN RESEARCH

Although a number of studies have dealt with the effect of LA on animals, this review highlights several gaps in our knowledge. First, not all animal groups have received equal attention: birds have represented the most popular study subject, but caution is needed in extrapolating findings on these vertebrates to other animal groups, and it is inappropriate to take a bird-biased approach to landscape management. Second, a lot of attention has been focused on single species or taxonomic groups, but a broader focus should be adopted to reveal between-group interactions as well as identify coherent responses in different animal taxa; this might make it possible to select appropriate surrogate taxa for rapid assessment of faunal trends in abandoned landscapes (e.g. Sauberer *et al.*, 2004). Several community-level aspects deserve attention, such as those of the current food-web ecology, whose importance in farmed systems has been widely recognised (Smeding and de Snoo, 2003): species loss due to LA may not only concern keystone species, but also weak interactors, which may crucially buffer consumer-resource oscillations and decrease the statistical risk of extinction (Worm and Duffy, 2003). Third, to detect responses effectively, i.e. to increase the chance of matching the spatial scale with the organism's actual perception, more use should be made of multi-scale analyses. As pointed out in a recent symposium on Mediterranean landscapes and Vertebrates (Brotons *et al.*, 2004b), the concept of "fragmentation", successfully applied elsewhere, may be insufficient and perhaps misleading in the Mediterranean, and only approaches and models suited to the peculiar properties of the region can fully reveal the consequences of land use shifts for animals.

GIS applications and modelling are powerful tools for analysing the effects of LA on animals and making predictions (Petit *et al.*, 2003). To date, even simple models of habitat suitability for animal species in LA scenarios are few and far between (e.g. Sánchez-Zapata and Calvo, 1999; Pedrini and Sergio, 2001). Although vegetation paths have been extensively modelled for several geographical areas (see Petit *et al.* (2003) for a comprehensive review on this topic), models

analysing animal responses, dispersal and colonisation patterns, and plant-animal interactions – to mention some of the main issues – offer a promising yet little developed field. Set-aside too may offer the opportunity to analyse faunal responses to habitat change over time (e.g. Tattersall *et al.*, 2000) and help model the early stages of LA in various geographical contexts.

A further poorly explored frontier is represented by the potentially strong interactions between LA and other global change phenomena, such as global warming, whose ecological effects have received a great attention in the last years (McCarty, 2001; Walther *et al.*, 2002, Root *et al.*, 2003). Several impacts of global warming on animal species have been discerned, including shifts in distribution and abundance (Warren *et al.*, 2001; Parmesan and Yohe, 2003), changes in phenology, breeding performances (Crick *et al.*, 1997; Roy and Sparks, 2000; Stevenson and Bryant, 2000) and in body mass (Smith *et al.*, 1998; Yom-Tov, 2001). However, determining whether, and if so to what extent, land use changes (Warren *et al.*, 2001), and specifically LA, may act as a confounding factor by either masking or simulating climate effects on the above mentioned variables is not an easy task. For instance, altitudinal shifts in birds may be determined by habitat changes rather than climate change (Archaux, 2004). Given the strong influence of ambient temperature on animals, global warming may certainly influence the latter's thermal physiology (e.g. Janzen, 1994; Clarke, 2003). However, the increased vegetation cover linked with LA too may influence microclimate by affecting ground insolation and providing shelter through increased vegetation cover: especially for ectotherms, this may have implications for behavioural thermoregulation and will result in different distributions of sun- and shade loving taxa.

Clearly, global warming may in some cases reinforce the impact of LA: for instance, a global warming-determined upwards altitude shift of the timberline might increase the rate of open habitat loss and threaten even more seriously animal communities in mountainous landscapes (Pedrini and Sergio, 2001). Moreover, higher ambient temperatures and drought might encourage the occurrence of large-scale fires in abandoned areas, with major repercussions on animal conservation.

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