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Department of Earth and Environmental Sciences

PH.D. SCHOOL OF ENVIRONMENTAL SCIENCES XXVIII CYCLE



Analysis of species distribution in time and space for wildlife conservation

Ph.D. Dissertation

Candidate: Dr. Massimiliano Luppi

Tutor: Dr. Luciano Bani

Co-tutor: Dr. Valerio Orioli

Ph.D. Thesis abstract

The main aim of my research project is the identification and the application of appropriate modelling methodologies, to case studies concerning species distribution, landscape ecology and habitat quality in areas with a high human impact or land abandonment.

In the first part, I analysed population trends and distributions of breeding birds in Lombardy (Italy), focusing on agro-ecosystem species. I used data derived from a long-term monitoring program and other projects by means of point counts method. Species distribution and abundance were estimated using generalized additive models (GAMs). I assessed the mean annual variation rate for 20 breeding bird species, between 1992 and 2016, applying the discrete population growth model. Moreover, I performed spatial predictions using fitted models in order to build potential distribution maps. Over the whole period, ten species showed a significant decline, while five species showed a significant increased. As extreme values at regional scale, the Skylark showed a significant population decline, losing about the 90% of starting population, while the Common Wood Pigeon population increased about 2000% from 1992.

Afterwards, I evaluated the change of altitudinal distribution of alpine species. I used the response curve shape method to investigate changes in altitudinal distributions of breeding birds over a long-term period (form 1982 to 2015) in the central Alps, and over a medium-term period (from 2006 to 2015) to compare the dynamics occurred in the central and western Alps. During the long-term period, all species exhibited changes in at least one part of their altitudinal distribution. Most woodland species expanded towards higher and lower altitudes, probably stimulated by forest regrowth and/or temperature increase. Almost all alpine grassland species retracted the lower portion of their altitudinal range, moving towards the summit. During the medium-term period, both areas showed an increase in species moving downwards, which confirms the relevance of this apparently contrasting pattern. However, the species and ecological groups of the two areas revealed some differences in altitudinal changes, probably due to the interaction between local and wide-scale processes (i.e. climate change and forest expansion).

In the second and third parts of my PhD thesis, I investigated the role of environment in determining the spatial distribution of butterflies using a multi-scale approach. I analysed the effects of different types of land cover, habitat characteristics, and management actions on butterfly richness and abundance by mean of GAMMs. Land cover models showed that butterfly communities are positively affected by meadows at the local scale, although this effect decreases when the artificial surface increases at the landscape scale. Conversely, arable lands at the local scale had a positive effect when associated with a high level of urbanization. This pattern was probably due to an increase of landscape heterogeneity and an increased presence of semi-natural habitats in peri-urban areas, compared to intensive farmlands. Among habitat variables, the abundance of flowers is the most important driver of both species richness and abundance. In addition, the negative effect of the number of meadow cuts, and the positive effect of the width and height of herbaceous margins along crop fields, highlighted the importance to adopt correct management measures for the conservation of this taxon and the overall biodiversity.

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Chapter 1

Introduction

"It's easy to think that as a result of the extinction of the dodo we are now sadder and wiser, but there's a lot of evidence to suggest that we are merely sadder and better informed."

(Douglas Adams and Mark Carwardine, Last Change to See, 1990)

Conservation biology is a young discipline whose birth is usually attributed to the First International Conference on Conservation Biology held in San Diego, California, in 1978. Conservation history is based on our use of natural resources, but more fundamental is the evolution of our ethical attitudes toward nature and its intrinsic and instrumental values (Callicott, 1990).

Conservation biology is a cross-disciplinary subject lying between basic biological sciences and natural resource sciences (Hunter and Gibbs, 2007). Moreover, it is a mission-driven science with the aim to preserve the remaining natural areas through the study of the mechanisms that underlie natural ecosystems. Thus, it is about biodiversity loss and the methods to minimize it (Macdonald and Service, 2007).

These aims are of great importance considering the general decline in biodiversity that is observed globally (Ceballos et al., 2015) and in Europe (de Heer et al., 2005). One major drivers of biodiversity loos is destroying habitats and causing landscape change because of urbanization, intensification of agricultural practices and land abandonment in marginal areas.

An urgent need is to know the distribution in time and space of animal populations to understand the processes at the basis of ecosystems and to define appropriate management practices of habitats that can also allow to the human dominated areas to contribute to biodiversity conservation. A key role is played by statistical techniques (i.e. models) that allow from samples to define wider distribution patterns considering the link with the available environmental variables (Margules and Pressey, 2000).

In Ecology, the researches often use bio-indicators, i.e. species or group of species which encompass the ecological needs of most of the species present in the community that needs to be protected (Lambeck, 1997). Bio-indicators should have a number of qualities including a well-documented ecology, a demonstrated sensitivity to different environmental conditions and should be easy to identify and monitor, and be popular amongst the general public (Donald et al., 2002; van Swaay and Warren, 2012).

Birds and butterflies are widely monitored groups and are often used as indicators of the effects of agricultural intensification or land abandonment on biodiversity (Donald et al., 2001; Öckinger et al.,

2006; Reif, 2013; Sirami et al., 2008; Suárez-Seoane et al., 2002; Van Dyck et al., 2009). In Europe two indexes have been created to monitor changes of biodiversity in agricultural landscapes: the Farmland Bird Indicator and the European Grassland Butterfly Indicator. The first index is based on the population trends of up to 37 bird species that are common and characteristic of European farmland landscapes. According to it, bird populations have reduced by around 25% in 25 European countries since 1990 (Eurostat, 2012). The second index is based on the population trends of 17 butterfly species in 19 countries. This indicator showed that since 1990 till 2011 butterfly populations have declined by almost 50%, indicating a dramatic loss of grassland biodiversity (Van Swaay et al., 2013).

The main driver of these declines is the change in land use, due to agricultural intensification in lowlands and land abandonment in mountains. Furthermore, climate change could act independently of habitat loss (Franco et al., 2006; Renwick et al., 2012; Thackeray et al., 2016) or in synergy accentuating the negative effect on biodiversity (Chamberlain et al., 2016; Settele et al., 2008).

One of the aspects linked to the intensification of agricultural practices is the growing use of pesticides. In 1963, Rachel Carson published the book *Silent Spring*, considered the first popular attempt to warn the world about the impact of pesticides on biodiversity and in particular on birds. Now you are talking about *Second Silent Spring* (Krebs et al., 1999) and *Silent Summer* (Maclean, 2010) in describing the decline being recorded in latest decades of wildlife. Recent studies are highlighting the growing role of some pesticides (i.e. neonicotinoids) in the decline of populations of many invertebrates (e.g. bees, butterflies; Gilburn et al., 2015; Pisa et al., 2015) and of farmland birds (Gibbons et al., 2015; Hallmann et al., 2014).

The Common Agricultural Policy (CAP), the main instrument of agricultural policy in the European Union, has led to an intensification of agricultural practices supported by capital grants with a loss of hedgerows and other non-productive land (Donald et al., 2002; Henle et al., 2008). Moreover, many marginal agricultural land (i.e. less productive or less accessible regions) due to their low profitability have been abandoned (Stoate et al., 2009). Both agricultural intensification and land abandonment, which can co-exist in the same landscapes, has had severe adverse effects on farmland biodiversity (Donald et al., 2006; Stoate et al., 2001).

Agri-environment schemes (AESs) are a key element for the integration of environmental concerns into the Common Agricultural Policy and they are designed to encourage farmers to protect and enhance the environment quality on their farmland. AESs existed across the EU since 1992, but became compulsory under the 2003 CAP reform. Management practices within AESs represent the only available mechanism to reduce declines in biodiversity over large areas in farmland (Vickery et al., 2004). If well-designed around evidence-based prescriptions, and properly targeted and

monitored, AESs have been shown to deliver benefits to biodiversity (Evans et al., 2002; Peach et al., 2001). AESs can increase landscape heterogeneity and might bring considerable environmental benefits to habitats other than farmland by restoring the agricultural matrix separating non-productive patches (Donald and Evans, 2006).

The CAP Reform 2014-2020, achieved with the aim to deal more incisively with environmental issues, has provided a new form of direct payments to farmers conditional on compliance with three obligatory "greening measures": the maintenance of permanent grassland, the creation of ecological focus areas and of crop diversification (DG Agriculture and Rural Development, 2013). These measures together with AESs provided in the Rural Developments Programme should improve sustainability of agriculture and significantly contribute to environmental enhancement. Pe'er et al. (2014), however, has highlighted how this new architecture of the CAP is not enough to halt the decline of biodiversity and, among the various proposed recommendations, the emphasis is on the need for studies (e.g. monitoring programs) that allow to evaluate the effectiveness of the agricultural policy.

All issues described above can be found in the Lombardy region (northern Italy) where I developed my research project. Lombardy is one of the regions of Europe where, during the past 30 years, the natural habitats have been strongly destroyed by an unremitting infrastructure and urban sprawl, especially in the foothills, and by the intensification of agricultural practices, in the lowlands. Conversely, the decline of traditional patterns of agriculture on more marginal zones (i.e. mountain areas) leaded to the abandonment of land and to the subsequent expansion of forests (ERSAF, 2014). These processes have triggered widespread conservation problems for many wildlife species that live in increasingly small and isolated populations, due to the destruction and fragmentation of their habitats. In this context, it is crucial to understand how animal populations respond to these processes through studies aimed at identifying the current drivers of the biodiversity decline.

1.1 Objectives and thesis structure

The main aim of my research project is the identification and the application of appropriate modelling methodologies, to case studies concerning species distribution, landscape ecology and habitat quality in areas with a high human impact or land abandonment, in order to contribute to an effective wildlife conservation.

The specific objectives of the project are declared in the single case studies, grouped in three main topics:

Part I - Species distribution

Chapter 3: Species distribution modelling and population trends of breeding birds in agroecosystems: the case of Lombardy (Italy).

Chapter 4: Long- and medium-term changes in the altitudinal distribution of breeding birds in the Italian Alps.

Part II - Landscape ecology

Chapter 5: Land cover drivers at local and landscape scale of butterfly richness and abundance in a human-dominated area.

Part III - Habitat quality

Chapter 6: Habitat and management drivers of butterfly richness and abundance in a human-dominated area.

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Chapter 2

Ecological modelling

Ecosystems, with all their biotic and abiotic components that interact with each other, are extremely complex systems. Therefore, there is the need to build models that give a simplified view of reality and highlight relevant aspects and processes involved in these systems (Soetaert and Herman, 2009). Statistical models are used to make inferences from sample data in many fields of ecology, including conservation biology (Royle and Dorazio, 2008). In this context, the fields of application of the models can be very different, from monitoring programs on large area to understand macro-ecological dynamics, to studies in small areas designed to answer specific scientific hypotheses.

Species Distribution Models (SMDs) are statistical models that predict the distribution and abundance of organisms, by linking census data collected in the field with spatially explicit data (i.e. cartographic digital layers) of some environmental variables (Guisan and Zimmermann, 2000). SDMs assumed an increasing importance in ecology and conservation biology (Guisan and Thuiller, 2005; Pearson, 2010) and they can be used to address different topics, such as assessing the impact of climate, land use and other environmental changes on species distributions (Thomas et al., 2004; Thuiller, 2004). In recent years, ecological modelling has become an important component of conservation planning, and a wide variety of modelling techniques have been developed (Guisan and Thuiller, 2005).

The selection of an appropriate method should not depend only on statistical considerations, but it should fit the aim of the study, the type of data collected and the sampling designs used. Moreover, the trade-off between optimizing accuracy versus optimizing generality should be evaluated (Guisan and Zimmermann, 2000).

One of the most widely adopted statistical approaches in species distribution studies are generalized multiple regressions, that allow to fit a non-Gaussian distribution for the response variable, thus not forcing the data into unnatural scales (Hastie and Tibshirani, 1990). Indeed, this models are more flexible and better suited for analysing ecological relationships, which can be poorly represented by the classical Gaussian distribution (Austin, 1987; Guisan et al., 2002). A generalized model consists of three steps (Zuur et al., 2009). The first one is the definition of the probability distribution for the response variable. Models that use presence-absence data are typically based on the binomial distributions (used in Chapter 4), while for count data the Poisson (used in Chapter 5-6) or negative binomial (used in Chapter 3-5-6) distributions are commonly used. The second step is the definition of the systematic part in terms of covariates (i.e. combination of the explanatory variables) and the last one is the specification of the relationship, called link function, between the expected value of the response variable and the systematic part.

A key step in the analysis process is the definition of an appropriate procedure for model selection, i.e. a process for selecting the most influential predictors in the model (Johnson and Omland, 2004). Several approaches are available using evaluation criteria like the Akaike Information Criterion (AIC, Akaike, 1973; Sakamoto et al., 1988), such as stepwise regression and shrinkage rules (Guisan et al., 2002; Wood, 2006; used in Chapter 3) or multi-model inference (Grueber et al., 2011; used in Chapter 6).

2.1 Generalized additive model (GAM)

In my research project, I used as modelling technique the generalized additive models (GAM; Hastie and Tibshirani, 1990) that link occurrence or abundance of species (field data) to environmental variables (field data and digital maps). The models have allowed studying the population distributions, but also analysing the drivers and processes that act on ecosystems or on habitats at a landscape or a local scale, respectively.

GAMs are data-driven models which can explore the shape of complex relationships between the dependent variable and covariates with much fewer restrictions and assumptions than classic GLMs (Wood, 2006; Yee and Mitchell, 1991). Covariates (x_i) can be described in GAMs by both linear predictors $\sum \beta_i x_i$, as in generalized linear model (GLM; McCullagh and Nelder, 1989; Nelder and Baker, 1972), and non-parametric (i.e. smooth) functions $\sum f_i(x_i)$. Predictors are related to the response variables by means of a link function, whose choice is linked to the probability distribution of the dependent variable (e.g. a logarithm function with a Poisson or a negative binomial distribution; McCullagh and Nelder, 1989; Quinn and Keough, 2002).

In general, the model has the following structure:

$$g\big(E(Y_i)\big) = \sum \beta_{ki} x_{ki} + \ f_1(x_{1i}) + f_2(x_{2i}) + \ f_3(x_{3i}, x_{4i}) + \cdots + \infty$$

where g is the link function, $E(Y_i)$ is the expected value of a response variable Y_i , β_{ki} are the estimated coefficients for parametric model components, f_i are smooth functions of the covariate x_k .

The flexibility and convenience of GAMs comes at the cost of two new theoretical problems. It is necessary both to represent the smooth functions in some way and to choose how smooth they should be (Wood, 2006).

Smooth functions are cubic regression spline constructed from section of cubic polynomial joined together (*mgcv* package, Wood, 2011; Fig. 1.1 and 1.2).

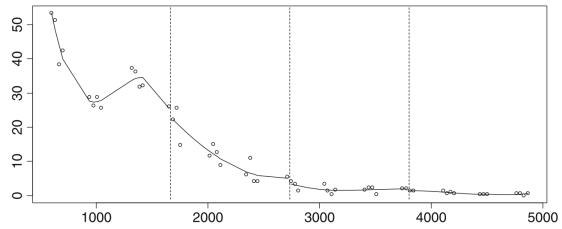


Fig. 1.1 Example of fitting a cubic polynomial on four segment of data (from Zuur et al., 2009). In each segment, the line is the fit from the cubic polynomial model and the dotted lines divided the segments.

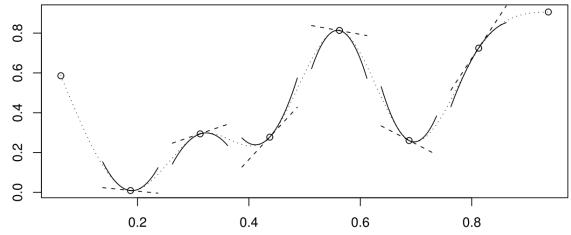


Fig. 1.2 Example of a cubic spline (dotted curve) made up of seven cubic polynomial (from Wood, 2006). The points of union (white dots) are known as the knots of the spline. The curved continuous lines are quadratics matching the first and second derivatives at the knots. Straight dashed lines show the gradient of the spline at the knots.

The level of smoothing, which represents how the function follows the trend of the data, is calibrated by a value known as the effective degrees of freedom (EDF; Harrison et al., 2014) and the choice of this value depends largely on the objectives of the analysis (Fewster et al., 2000). The values of EDFs are estimated by means of a procedure that identifies the best value within a predefined range by cross-validation or by regression splines with fixed degrees of freedom. Subsequently, smooth functions are represented using penalized regression splines (Wood, 2006). This way, the degree of smoothness of model terms is estimated as part of the model fitting procedure.

The choice of the upper limit for the EDF is a key step of the modelling process and should represent the right trade-off between a high goodness-of-fit of the model and the risk of overfitting. When the EDF value is too high, the spline fits the noise of data and decreases the computation efficiency, while when the smoothing parameter is too low the spline fits data poorly (see Fig. 1.3).

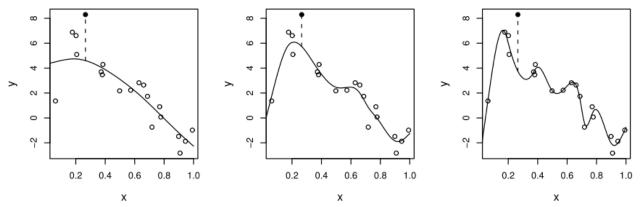


Fig. 1.3 Example of splines with different upper limit for the EDFs fitted on the same data (from Wood, 2006). From left to right: low value, intermediate value, high value.

In addition to the models described up to now, GAMs allow to include a more complex stochastic structure in order to permit a lack of independence of the elements of the response vector. To do this, in the models can be inserted a random effect using a Generalized Additive Mixed Model (GAMM; used in Chapter 5-6). GAMMs can deal with simple independent random effects, by treating a smooths term as random effect (Wood, 2008).

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PART I SPECIES DISTRIBUTION

Part I

Species distribution

The study of distribution and abundance of organisms represents the first step to face conservation problems (Margules and Pressey, 2000). Long-term monitoring programs allow collecting data and assessing population trends. However, these programs are extremely costly in terms of economic, human and time resources and data are often scarce to assess trends for most species (Bart, 2005).

Data on distribution and abundance of bird breeding were collected from 1992 to 2016 as part of different projects in Lombardy. Statistical models permit to pool data collected by different projects and overcome the use of different sampling designs, whose raw data may bias the trend estimation (Massimino et al., 2008). In addition, linking the presence or abundance data with environmental variables, describing the habitat and land use, by means of species distribution models, it is possible to understand the effect of these variables on populations and communities, and build potential distribution maps (Guisan and Zimmermann, 2000; Pearson, 2010).

This georeferenced time series data, coming from the breeding bird monitoring program of Lombardy, can constitute the basis for studies with management or applicative aims (Bani et al., 2009; Dondina et al., 2015), rather than of mainly scientific interest (Ambrosini et al., 2011; Bani et al., 2006, 2002; Dondina et al., 2016; Massimino et al., 2008).

This dataset is the basis of the first part of my PhD thesis where two case studies analysed the species distributions of breeding birds in Lombardy in time and space, focusing on two different species groups.

In Chapter 3, the study described the population trend from 1992 to 2016 and the spatial distribution with maps focusing on agro-ecosystem species. In Chapter 4, the change of altitudinal distribution of alpine species was evaluated.

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Chapter 3

Species distribution modelling and population trends of breeding birds in agro-ecosystems: the case of Lombardy (Italy).

Abstract

We analysed population trends and distributions of breeding birds in Lombardy (Italy), focusing on agro-ecosystem species. We used data derived from a long-term monitoring program and other projects by means of point counts method. Species distribution and abundance were estimated using generalized additive models (GAMs). We assessed the mean annual variation rate for 20 breeding bird species, between 1992 and 2016, applying the discrete population growth model. Moreover, we performed spatial predictions using fitted models in order to build potential distribution maps.

Over the whole period, ten species showed a significant decline, while five species showed a significant increased. As extreme values at regional scale, the Skylark showed a significant population decline, losing about the 90% of starting population, while the Common Wood Pigeon population increased about 2000% from 1992.

3.1 Introduction

The human impact has changed the European landscape causing the appearance of semi-natural habitats that have favoured the spread of many species typical of open environments (Donald et al., 2002).

In recent decades, Europe has undergone an agricultural intensification with a reduction of crop rotations, an increase in the use of pesticides and inorganic fertilizers (Donald et al., 2006; Stoate et al., 2009, 2001; Vickery et al., 2004). This way, many natural and semi-natural habitats, characterizing low-intensity agricultural landscapes (Loos et al., 2014) have disappeared.

In the European Union, the Common Agricultural Policy (CAP) has played an important role in these processes resulting in an increase in agricultural production through price-support policies (Pain and Pienkowski, 1997).

Lowland farmland provides habitat for about 120 birds species of European conservation concern (SPECs; Tucker and Evans, 1997; Tucker and Heath, 1994), but in the last 30 years many bird populations collapsed, including many species considered common (Inger et al., 2015) and in particular agro-ecosystems species (Donald et al., 2006, 2001). This is troubling considering that birds are good indicators of overall farmland biodiversity and of the effects of agricultural intensification on biodiversity (Donald et al., 2002; Wilson et al., 2009).

The availability of time series data, deriving from monitoring program, is the basis for defining the medium and long-term population trend of animal population. In addition, this data is the basis for studies aimed at identifying the factors that influence population dynamics and defining specific actions for the conservation and management of birds.

Lombardy region (northern Italy) launched a Long-Term Monitoring Program Project of breeding birds in 1992 (Fornasari et al., 1998). The project despite some interruptions in the early years is now the longest quantitative monitoring program of breeding birds running at large-scale in Italy. This project, for the environmental diversity of the investigated area (e.g. lowlands, mountains), is able to provide a thorough and comprehensive evaluation of the population dynamics of most of the breeding bird species.

We decided to focus on 20 common bird species breeding in agro-ecosystems. Thus, we used time series data to: (1) perform distribution models depending on the different types of land use; (2) build year-by-year quantitative distribution maps; (3) estimate the annual bird populations; and (4) evaluate and describe the long-term population trends.

3.2 Material and methods

3.2.1 Bird data

All counts were expressed in number of pairs, according to the method described by Blondel et al. (1981).

Point counts were selected according to a stratified sampling design, based on the different landscapes in the region (sub-areas: primary sampling units; Fig. 4). Every year in each primary sampling units a random selection of overall 30 secondary sampling units ("Tavolette IGM": 1:25.000 maps) is performed, distributing them within primary sampling units in proportion to their extension.

In addition, since 2007 surveys were also performed in 23 fixed secondary sampling units, to verify the representativeness of the data collected in the other 30 random secondary sampling units. Point counts were, then, randomly selected within each secondary sampling unit, spacing them at least 500 m, to reduce the probability of double counts. On average were conducted 11.2±6.0 points counts in each secondary sampling unit.

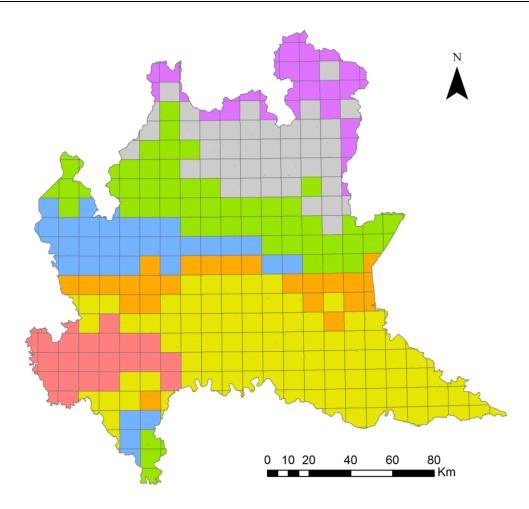


Fig. 3.1 Subdivision of the Lombardy in seven sub-areas (primary sampling units) based on environmental composition (DUSAF, Destinazione d'Uso dei Suoli Agricoli e Forestali [Classification of Agricultural and Forest Lands], ERSAF, 2014) of the "Tavolette IGMI" (1:25.000 maps; secondary sampling units). Sub-areas: Alps (purple, 21 cells); coniferous forests (grey; 41 cells); broadleaf forests (green, 52 cells); foothills (blue, 31 cells); urban lowland (orange, 23 cells); arable lands (mustard, 91 cells); rise fields (red, 23 cells).

We also used data coming from others breeding bird surveys in order to cover period in which the previous project was interrupted. No data were available for 1993, 1994, 1997 and 1998 (Tab. 3.1 and Tab. 3.2).

Tab. 3.1 Number of point counts used for the analyses (1992-2005). Project name: LTP (Log-Term Monitoring Program Pilot Project), LT (Log-Term Monitoring Program Project), OP (Other projects), WRD (Wildlife regional database).

Project name	1992	1995	1996	1999	2000	2001	2002	2003	2004	2005
LTP	373	652	696	-	-	-	-	-	-	-
LT	-	-	-	-	-	-	-	-	-	589
OP	_	-	-	1.101	920	565	251	125	18	-
WRD	-	-	-	-	516	426	340	473	379	497
Total	373	652	696	1.101	1436	991	591	598	397	1.086

Tab. 3.2 Number of point counts used for the analyses (2006-2016). Project name: LT (Long-Term Monitoring Program Project), OP (Other projects), WRD (Wildlife regional database).

Project name	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
LT	439	731	705	759	746	826	769	796	765	808	800
OP	-	-	-	-	-	86	-	-	122	-	-
WRD	609	-	=	-	=	=	=	_	-	_	-
Total	1.04	731	705	759	746	912	769	796	887	808	800

3.2.2 Environmental data

For the species distribution analyses, we used two types of environmental data: field and digital maps. We collected the fractional cover of land use around every sampling point (in a radius of 250 m) evaluated by sight on field, with a resolution of 5%, in 25 categories (Tab. 4).

Moreover, we used the available land cover digital maps and the digital elevation model (20-m resolution), available on Lombardy Geoportal Catalogue

(http://www.cartografia.regione.lombardia.it/geoportale/ptk), to perform models predictions at regional scale and estimate the annual population for each year. We used the land cover maps temporally nearest to the survey year (Tab. 3.3).

Tab. 3.3 Annual matching between land cover digital maps and bird survey data; in brackets land use survey years. CORINE Land Cover 1990. European Environment Agency, EEA; DUSAF, Destinazione d'Uso dei Suoli Agricoli e Forestali (Classification of Agricultural and Forest Lands), ERSAF); SIARL, Sistema Informativo Agricolo della Regione Lombardia (Agricultural Information System of the Lombardy Region), ERSAF.

Land cover digital map	Bird Survey Data
CORINE Land Cover (1990)	1992
DUSAF 1.1 (1998-1999)	1995 - 2002
DUSAF 2.0 (2005-2007)	2003 - 2015
DUSAF 2.1 (2007)	
DUSAF 3 (2009)	
DUSAF 4 (2012)	
SIARL (2003-2015)	

We defined three periods (1992, 1995-2002, 2003-2015) with an increasing level of detail in land cover data within which land use categories remain fixed. This division follows the different detail and resolution of the maps and allows taking advantage of the highest level of information available. CORINE Land Cover 90 is the map with the smallest detail and was used for the estimation of breeding populations in 1992. While for years 1995-2002, we used DUSAF 1.1 map, which has a more detail. For subsequent years, the higher level of detail derives from the integration of the data derived from DUSAF land cover maps and SIARL project data, which annually recorded the crop types. We combined DUSAF and SIARL data, using the detailed information on crops contained in SIARL maps for all areas below 600 m, where farmlands are concentrated. Above 600 m, we used the information provided by DUSAF maps, which discriminate the different types of natural and semi-natural areas, such as woodlands, grasslands and shrublands. Furthermore, in urban areas, we always privileged the DUSAF information, which discriminates between the different forms of urban land use.

We reclassified digital land use categories according with those used in the field (see Tab. 3.4).

Tab. 3.4 Correspondences between the land use variables collected in the field and those derived from digital maps.

Field data category	Description	Period 1 CORINE 1992	Period 2 DUSAF 1995-2002	Period 3 DUSAF and SIARL 2003-2015
100	Continuous urban fabric	111, 120, 130, 140	111, 120, 130, 140	111, 120, 130, 140
112	Discontinuous urban fabric	112	112	112
211A	Uncultivated lands	211, 240	211	250
211B	Plowed fields	211, 240	211	214, 215, 216, 217, 218
211C	Hoed fields	211, 240	211	214, 215, 216, 217, 218
211DE	Maize crops	211, 240	211	212
211F	Other cereals	211, 240	211	211
211G	Vegetables, soybeans, rapeseed	211, 240	211	214, 215, 216, 217, 218
211H	Greenhouses	211, 240	211	214, 215, 216, 217, 218
211I	Plant nursery	211, 240	211	224_{SIARL}
213	Rice fields	213	213	213
221	Vineyards	220	221	221
222	Fruit trees	220	222	222
223	Olive groves	220	223	223
224	Poplar cultivations	311	224	$224_{ m DUSAF}$
231	Meadows	231	231	230
311	Broad-leaved forest	311	311	311
312	Coniferous forest	312	312	312
313	Mixed forest	313	313	313
321	Natural grassland	321	321	321
320	Shrublands	320	320	320
330	Sparsely vegetated areas	330	330	330
410	Inland marshes	410	410	410
511	Water courses	511	511	511
512	Water bodies	512	512	512

For each land use class we built a digital layer performing a neighbourhood analysis (ARCGIS 10.1; ESRI Inc., Redland, CA) in a radius of 250 m, which is the same spatial extent at which land use fractional cover was estimated in the field. These layers with a resolution of 100 meters were the basis of the species distribution maps. We also created a layer of presence/absence of watercourses (including artificial ones) and we used it only in models of those species that lives near rivers, small streams or ditches (*Motacilla flava*, *Motacilla alba*, *Cettia cetti*).

3.2.3 Species distribution models

The estimate of the populations' size of bird species was performed using a modelling approach, in order to overcome the problems arising from the different sampling designs adopted since 1992. Furthermore, this method has the advantage of allowing a direct estimation of regional populations based on digital maps available and provide a model that can be returned cartographically with quantitative distribution maps for each species.

Before applying the model, we filtered the dataset to reduce the uncertainty of the estimates due to the inclusion of true zeros, which we assumed to be those points outside the observed altitudinal distribution of the species. Then, we used only the points inside the elevation range bounded by the maximum and minimum point of presence of each species along the whole time series.

The model used to estimate the number of pairs per point count at the regional scale, was built considering the variables collected in the field (see Tab. 3.4).

For each species, we fitted a generalized additive model (GAM):

$$E[Y_{s,i,t}] = \exp\left(f_s(east_i, north_i, t) + f_s(t) + f_s(elev_i) + \sum_{k=1}^K f_s(cl_{k,i}) + \infty_s\right)$$

where $E[Y_{s,i}]$ gives the expected pairs for species s at point i; elev the elevation; elk the percentage of each of the K land use classes; t represents the year when the point count was performed. The spatial location of sampling points was given by eastings (east) and northings (north).

The space–time smooth $f_s(est_i, nord_i, t)$ incorporate in the models the interactions between space and time (Harrison et al., 2014) and we used a tensor product of a thin-plate regression spline (TPRS) of east and north and a cubic regression spline (CRS) of t (Wood, 2006). The spatial component will capture, along with any spatial autocorrelation, differences in the character of the land cover classes across Lombardy, whereas the temporal component will smooth out fluctuations caused by, for example, an anomalous weather year and it allows to overcome the potential temporal autocorrelation inherent in time series data.

The amount of smoothing required depends on the objectives of the analysis and is controlled by the effective degrees of freedom (EDF). We set an upper limit of 4 for the EDF of the spatial component and of 20 for the temporal component. The actual EDF value is determined by in-built cross-validation (Harrison et al., 2014; Wood, 2006).

To estimate the annual population for each species we included the temporal smooth $f_s(t)$ with a value of EDF of 21, representing the number of years for which data were available (Fewster et al.,

2000). In this case the value of EDF is kept fixed and not estimated as in the other smooths since the purpose is to obtain an annual population estimates that do not result affected by possible long-term trends.

The elevation smooth had 4 as maximum value of EDF, by which we accounted for the altitudinal distribution of species. Finally, even the smooths of the land use variables had a maximum value of 4. We used a CRS with shrinkage (Marra and Wood, 2011) in all smooths (except space—time smooth) that is a method that penalizes the estimated value of EDF by setting it to zero for variables that have not shown an effect on the dependent variable. This helps the selection of variables to be included in the final model allowing in the first instance to eliminate the variables having the value of EDF equal to zero. Subsequently the remaining variables were selected using a backwards stepwise procedure based on significance at the 5% level, starting from the model with the remaining variables and eliminating non-significant ones.

We fitted a model for each periods considered (1992, 1995-2002, 2003-2016) using reclassified land use categories (see Tab. 3.4).

The GAMs were performed with a negative binomial distribution, by means of the *mgcv* package (Wood, 2006) in the statistical software R (R Core Team, 2015).

3.2.4 Spatial prediction of species distribution

We used the fitted models (i.e. one model for period: 1992, 1995-2002 and 2003-2016) and digital raster of each land use category to predict the expected pairs ($\hat{Y}_{c,s,t}$) in each raster cell c, for each species s and year t, using raster package (Hijmans, 2015) in R. Firstly, we created a raster (RasterStack object) with the independent (predictor) variables using the "stack" function that create a collection of raster layer objects with the same spatial extent and resolution. Secondly, we performed a spatial model predictions with the "predict" function using the RasterStack object with the predictors and the model fitted in the previous step. For each species, we used the same elevation range considered to fit the models. We obtained a raster with the expected pairs and another one with their standard error from which we calculated the 95% confidence interval.

Model predictions were saved as raster object using GeoTIFF format and were the basis for the creation of distribution maps. We built a colour scale, adapting it to the values obtained for each species using the "choose palette" function contained within the *colorspace* package (Ihaka et al., 2015). This way, we created an annual map for each species.

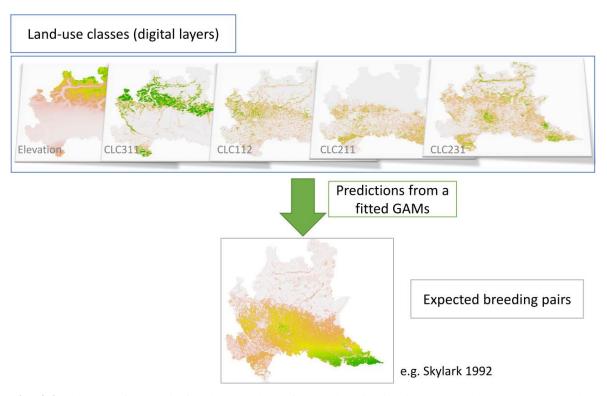


Fig. 3.2 Scheme of analysis for the creation of potential distribution maps (low values: grey, intermediate values: yellow, high values: green).

3.2.5 Long-term population trend

Based on model predictions, we estimated the yearly regional population, by summing all cell values, and dividing the sum by the area defined by the species-specific detection radius (Tab. 3.5):

$$\widehat{N}_{s,t} = \left(\sum_{i=1}^{I} \widehat{Y}_{c,s,t}\right) / (\pi \gamma_s^2)$$

where $\widehat{N}_{s,t}$ is the regional population at time t for species s; $\widehat{Y}_{c,s,t}$ the expected pairs on cell c for species s at time t; γ_s^2 the square of the species-specific detection radius.

Tab. 3.5 Species-specific detection radius *r* used for the calculation of annual populations' estimates.

Species		Radius (m)
Alauda arvensis	Skylark	200
Carduelis carduelis	European Goldfinch	200
Cettia cetti	Cetti's warbler	250
Chloris chloris	European Greenfinch	200
Columba palumbus	Common Wood Pigeon	250
Corvus cornix	Hooded crow	500
Coturnix coturnix	Common Quail	250
Falco tinnunculus	Common Kestrel	400
Hirundo rustica	Barn Swallow	250
Lanius collurio	Red-backed Shrike	100
Luscinia megarhynchos	Common Nightingale	250
Motacilla alba	White Wagtail	200
Motacilla flava	Yellow wagtail	250
Passer italiae	Italian Sparrow	150
Passer montanus	Eurasian Tree Sparrow	150
Phasianus colchicus	Common Pheasant	300
Pica pica	Black-billed Magpie	300
Saxicola torquata	Stonechat	150
Streptopelia turtur	European Turtle Dove	200
Sturnus vulgaris	Common Starling	300

The uncertainty of the estimates was calculated considering the 95% confidence interval provided by the models.

The long-term trend, from 1992 to 2016, was assessed by fitting a discrete population growth model on yearly estimates (see Gotelli, 2001):

$$P_t = P_0(1+R)^t$$

where P_t is the estimated regional population at time t, P_0 is the population at time 0 (year 1992 in our case). R is the geometric rate of increase and t is the year, expressed as the difference from the first year (1992).

The unknown parameters (P_0 and R) were estimated using a weighted least squares regression (Quinn and Keough, 2002), where the weight was the number of annual point counts used to perform species distribution models of each species, in order to account for the different sampling effort. Finally, we tested if the geometric rate of increase was significantly (5%) different from zero by means of a two-tailed t-test.

3.2.6 Assessing change points

The estimates of annual regional populations obtained with the method described above were used to identify the years when a significant change in the trend occurred and to detect the presence of contrasting patterns, by the technique of "change points" (Fewster et al., 2000; Harrison et al., 2014). We created an annual index of abundance (I_t) by dividing each annual regional population (P_t) by the population of 1992 (P_{1992} , the first year of the time series):

$$I_t = \frac{P_t}{P_{1992}}$$

where I_t is the index value of the year t.

The trend was then assessed using a GAM model:

$$E[Y_{s,t}] = f_s(t) + \alpha_s$$

where $E[Y_{s,t}]$ gives the expected index of abundance for species s at time t.

For the temporal component we used a thin plate regression spline (TPRS; Wood, 2006) and we set an upper limit of 8 EDF (Fewster et al., 2000).

The values predicted by the model were the basis for the calculation of the first and second derivative for each year of the time series. This allowed describing the variation of the population trends, identifying change points. Using GAMs, the first and second derivatives are not readily available as mathematical expressions, but can be estimated numerically (Fewster et al., 2000; Harrison et al., 2014):

$$I'_{t} = (I_{t+1} - I_{t-1})/2$$

$$I''_{t} = (I_{t+1} - 2I_{t} + I_{t-1})$$

where I'_t is the first derivative and I''_t is the second derivative at time t.

The significance of the derivatives was assessed using the 95% confidence interval of the estimates based on the standard error derived from GAM models. Combining the significance and direction of first and second derivatives, we obtained different change points (Tab. 3.6).

Tab. 3.6 Change points in trends based on the significance at the 5% of the first and second derivatives of the trend line and their interpretation (classification based on Harrison et al., 2014); pos: positive, neg: negative.

First	Second	Interpretation	Symbol
derivative	derivative		
Sig. pos.	Sig. pos.	Increasing	+++
Sig. pos.	Non sig.	Increasing	+++
Sig. pos.	Sig. neg.	Increasing but rate slowing	++
Non sig.	Sig. pos.	Moving towards increasing	+
Non sig.	Non sig.	No evidence of change	=
Non sig.	Sig. neg.	Moving towards decreasing	-
Sig. neg.	Sig. pos.	Decreasing but rate slowing	
Sig. neg.	Non sig.	Decreasing	
Sig. neg.	Sig. neg.	Decreasing	

Finally, we classified the long-term trend according to the direction of all change points defining five trend types: A ("+"; only positive directions), B ("-"; only negative directions), C ("-/+"; first part of the time series negative, second part of the time series positive), D ("+/-"; first part of the time series positive, second part of the time series negative) and E ("fluctuations"; presence of fluctuations that did not allow to define a precise trend).

3.3 Results

We estimated the regional annual population (see Appendix A), the long-term trend and the change points and we drew the distribution maps for 20 farmland bird species breeding in Lombardy.

In the period 1992-2016, the regional populations of ten species showed a significant decline (R<0; p<0.05; Tab. 1). The species with the largest decline were *Alauda arvensis* (-8.0% of average annual change) and *Chloris chloris* (-6.2%). *Passer italiae* and *Carduelis carduelis* had slightly lower decline rates (-6.1% and -5.9% respectively). While *Saxicola torquata*, *Sturnus vulgaris Luscinia megarhynchos*, *Coturnix coturnix* and *Streptopelia turtur* did not show a significant trend.

Conversely, five species showed a significant increase (R>0; p<0.05). *Columba palumbus*, *Phasianus cholchicus* and *Pica pica* had the highest average annual change (13.5%, 8.2% and 6.0%, respectively).

Tab. 3.7 Trend curve parameters of each species in the period considered (1992-2016). R, geometric growth rate; *P*, *p*-value; Dev, deviance explained percentage by GAMs.

Species	R	P	Dev	Species	R	P	Dev
Alauda arvensis	-0.080	< 0.001	47.8	Columba palumbus	0.135	< 0.001	23.4
Chloris chloris	-0.062	< 0.001	26.0	Phasianus cholchicus	0.082	< 0.001	31.8
Passer italiae	-0.061	< 0.001	55.0	Pica pica	0.060	< 0.001	28.7
Carduelis carduelis	-0.059	< 0.001	19.3	Falco tinnunculus	0.047	< 0.001	10.9
Hirundo rustica	-0.048	< 0.001	36.5	Corvus cornix	0.011	0.033	37.6
Passer montanus	-0.037	< 0.001	33.6	Streptopelia turtur	0.013	0.189	28.4
Lanius collurio	-0.037	< 0.001	20.3	Coturnix coturnix	-0.007	0.795	29.2
Motacilla flava	-0.037	< 0.001	49.5	Luscinia megarhynchos	-0.008	0.219	49.9
Cettia cetti	-0.033	0.044	41.4	Sturnus vulgaris	-0.018	0.091	41.1
Motacilla alba	-0.021	0.010	20.2	Saxicola torquata	-0.029	0.150	24.6

Within the time series, we identified for each species 20 change points (i.e. years in which the curvature of the index curve is statistically significant; see Appendix A.4). GAM models used for the definition of change points can be evaluated by two parameters (Tab. 2.8). First, the significance of the temporal smooth indicates whether the adopted smooth function identifies a trend. Secondly, the deviance explained is a measure of the goodness-of-fit of each model.

Tab. 3.8 Change points: trend type (A: "+", B: "-", C: "-/+", D: "+/-", E: "fluctuations"; see paragraph 3.2.6 for detail) and GAM parameters (df, estimate degree of freedom; *P*, *p*-value of temporal smooth; Dev, deviance explained percentage by GAMs.

G •	Trend	Tempor	Dev	
Species	type	df	P	-
Alauda arvensis	В	6.5	< 0.001	98.1
Cettia cetti	D	2.8	0.034	44.4
Chloris chloris	Е	6.8	< 0.001	94.2
Columba palumbus	С	3.0	< 0.001	95.6
Corvus cornix	A	1.0	0.036	21.1
Coturnix coturnix	D	2.1	0.265	23.2
Falco tinnunculus	Е	6.1	< 0.001	91.7
Hirundo rustica	D	5.8	< 0.001	89.4
Lanius collurio	В	1.0	< 0.001	48.9
Luscinia megarhynchos	Е	6.6	< 0.001	82.4
Motacilla alba	Е	5.8	0.001	77.8
Motacilla flava	Е	5.6	< 0.001	84.0
Passer italiae	D	5.7	< 0.001	89.6
Passer montanus	Е	6.9	< 0.001	96.4
Phasianus cholchicus	A	2.7	< 0.001	89.9
Pica pica	A	1.3	< 0.001	79.7
Saxicola torquata	D	4.0	0.004	64.6
Streptopelia turtur	Е	5.8	0.126	52.5
Sturnus vulgaris	Е	6.7	< 0.001	89.0

Three species (*Phasianus cholchicus*, *Pica pica*, *Corvus cornix*) showed a continuous growth on the long-term trend (A-trend) and had low values of EDF that indicated a nearly linear trend. Nevertheless, the model of *Corvus cornix* had a low value of deviance explained (21.2%), thus the model had a low goodness-of-fit.

Two species (*Alauda arvensis, Lanius collurio*) showed a B-trend, indicating a negative direction of the change points along the time series. We included *Alauda arvensis* in this category although presenting a halt of the decline in the last two change points (2014: "+++"; 2015: "=").

Columba palumbus is the only species with a C-trend with an initial decrease, followed by a steady rise. Five species (Cettia cetti, Coturnix coturnix, Hirundo rustica, Passer italiae, Saxicola torquata) presented a D-trend. The temporal smooth of Coturnix coturnix was non-significant, so there was not a clear trend. Other four species exhibit a similar pattern with a peak at about half of the time series with the last change point with a positive direction located in 1999 (Cettia cetti, Hirundo rustica), 2001 (Passer italiae) or 2003 (Saxicola torquata).

The trend type with the major number of species (eight) was E-trend. These species had the highest number of EDF and showed some fluctuations along the trend with at least two changes of direction. Among these, only *Streptopelia turtur* had a not significant temporal smooth.

In the Appendix A, we reported the regional annual populations (Appendix A.1) and the change points for each species (Appendix A.4). Moreover, we included the population trend plots (Appendix A.2), the change point plots (Appendix A.5) and some distribution maps (Appendix A.3).

3.4 Discussion

Our results highlighted the unfavourable conservation status in Lombardy of many agro-ecosystem species (45%), confirming the general decline of this group across Europe (Eurostat, 2012; Wilson et al., 2009). The decline of farmland species suggests as possible causes the change and intensification in agricultural practices (Frenzel et al., 2015; Wilson et al., 2009), which limit the availability of habitat and resources for the typical avifauna of the croplands.

We observed the major decline in Skylark population with a 86% decrease from 1992 to 2016, although in recent years the decline seems to have stopped. This species has suffered similar reductions in other European populations: between 1970 and 1990 they decreased by more than 50% in the UK, the Netherlands and Germany (Tucker and Heath, 1994). In the 90s, the decline of this species slowed in parts of its range, but the drop continued in most European countries (BirdLife International, 2004). The main causes lie in the changes of its habitat due to the intensification of agricultural practices (Newton, 2004). The Skylark is sensitive to the reduction of crop diversity and rotation, and the loss of meadows (Wilson et al., 2009). In particular, it is sensitive to the reduction of the diversity of crops, the increase of the autumn plowing and sowing practices and the massive use of fertilizers and pesticides (De Carli et al., 1998; Donald et al., 2002). It is likely that these processes play an important role in our region, where intensive agriculture is widespread.

In Lombardy the population of *Chloris chloris* declined of 78% from 1992. Conversely, in other countries (e.g. England) the populations are stable or probably slowly increasing. European Greenfinch feeds on large seeds (e.g. cereal grains), but also uses some invertebrates, especially for nestlings. The decline observed in Lombardy could be linked to a decline in food resources and a lower quality of habitats with a reduction of the marginal areas (e.g. uncultivated land) and of hedgerows where *Chloris chloris* nests using trees or bushes. Another possible potential threat is the spread of diseases. Robinson et al. (2010) reported an emerging protozoal disease (Trichomonosis) on British populations of greenfinch in 2005 that rapidly became epidemic in the following years with a huge increment in mortality.

A similar pattern was observed in the European Goldfinch (77% population decline in Lombardy) for which in England population changes were explained almost entirely by changes in annual survival rates (Baillie et al., 2011). Also in Europe, in the last ten years the populations of this species is moderate decline (BirdLife International 2015). Its diet is based on small seeds (e.g. Asteraceae), but also some invertebrates in summer. The population trend is probably linked to the availability of weed seeds that, due to agricultural intensification, decreased. Indeed, *C. carduelis* nowadays often frequented area near and inside towns and villages, such as gardens or parks, where they can find more food than intensive farming areas.

Unlike other synanthropic species, the House Sparrow had a strong population declines (-78% from 1992). The decline of the *Passer italiae* in Lombardy was confirmed by a study of Brichetti et al. (2008) who estimated a decrease of 50% of the breeding population in northern Italy from 1996 to 2006. In Europe, *Passer domesticus*, a close relative species, presents a similar trend and has mainly suffered from general reduction in food supply in winter, due to the intensification of agriculture practices (Hole et al., 2002). In urban areas, House Sparrows may have disappeared predominantly from the central parts, where changes are more likely to have occurred because of the changes in habitat structure (Shaw et al., 2008). For this reason, the availability of gardens and other green spaces in urban areas is crucial to preventing further decline (Chamberlain et al., 2007).

A typical farmland species is the *Hirundo rustica* and in Lombardy this species is in strong decrease (69% population decline from 1992) and its trend is confirmed at a continental scale (Pazderová and Vorisek, 2007). There is much evidence that the main cause of its decline may be the intensification of agriculture practices. In particular, the *H. rustica* is suffering the loss of meadows (Evans et al., 2007) and the decrease in the number of livestock farms (Ambrosini et al., 2002), with consequent reduction of flying insect populations. Moreover, the Barn Swallow, being a long-range migratory, may also suffer from climate and habitat changes in wintering areas (Sanderson et al., 2006).

Populations of *Passer montanus* has been declining in much of western Europe (BirdLife International, 2004) and also in Lombardy this species has suffered a decline in population from 1992 to 2016, although it has had several fluctuations. This is confirmed in the analysis of the change point where *P. montanus* has the highest value among the 20 species of estimated degree of freedom of the temporal smooth. Like the other species in decline, the decrease of the population is due to the change in farming practices, such as reductions in winter stubble (Baillie et al., 2011).

The Red-backed Shrike suffered a decline of more than 20% between 1970 and 1990, over half of the European population (Tucker and Heath, 1994). This decline continued in the following years although with a lower rate. In Lombardy, the populations declined by 60% from 1992 to 2016.

The Red-backed Shrike suffers from the reduction or removal of hedgerows and shrubs (Lefranc, 1997). Indeed, *L. collurio* is positively associated with grassland grazed by livestock, fence-lines and scattered trees and shrubs, but negatively associated with arable land (Brambilla et al., 2009; Vanhinsbergh and Evans, 2002). The presence of hedgerow is important because Red-backed Shrike hunts from perch (e.g. shrub or tree) carrying prey back to it.

Motacilla flava and Cettia cetti are declining in Lombardy (60% and 55% respectively). They live in farmland, but their presence is linked to the presence of wetlands (e.g. damp meadows, marsh, riverbanks, swamp, reedbed). For both the diet is mainly based on small invertebrates from ground or flycatching. However, they have opposite trends in Europe. Motacilla flava has also been strongly declining trend since 1980 (PECBMS, 2009). Possible causes are farmland drainage, the conversion of pasture to arable land, the change from spring to winter cereals, and the loss of insects associated with cattle (Gibbons et al., 1993; Nelson et al., 2003). Conversely, the population of Cettia cetti have risen widely in Europe (PECBMS, 2009). This species is resident and sensible to cold winters, thus a warming climate may enhance the populations through a reduction in winter mortality and expanding its range northwards (Robinson et al., 2007; C.D. Thomas and Lennon, 1999). On the contrary, in Lombardy the decline of the population could also be linked to habitat drivers similar to those of Yellow Wagtail.

The long-term trend of *Motacilla alba* (40% population decline from 1992) is confirmed at the European level where populations are in moderate decline (BirdLife International, 2015). *M. alba* is a species that frequents open country, often near water and feeds on small invertebrates, and its decline is probably link to a general reduction of habitats quality in farmland.

Among the 20 farmland species considered, five species have a positive trend with an increase of the populations from 1992 to 2016. Four of these (*Columba palumbus*, *Pica pica*, *Phasianus cholchicus*, *Corvus cornix*) are generalist species. The increase of these species in the community can be

considered an indicator of the reduction of habitat quality in croplands due to an increasingly urbanization and a reduction of natural and semi-natural habitat.

The species that had the highest population growth from 1992 to 2016 (1989%) is *Columba palumbus*. This species may have been favoured by the spread of intensive arable cultivation, especially of oilseed rape and winter-sown cereal (Gibbons et al., 1993; Inglis et al., 1990; O'Connor and Shrubb, 1986; Wilson et al., 2009). Common Woodpigeon also lives in urban areas and this has led to changes in the ecology of its synurbic populations, which took advantage of a higher population density, a prolonged breeding season and a greater longevity as consequence to a lower predator pressure and a higher winter survival due to favourable food and climatic conditions (Tomialojc, 1980; Tomiałojć, 1976).

Another synanthropic species is the Black-billed Magpie, whose population in Lombardy has increased by 305% from 1992, thanks to a generalist ecology and to the capacity to prosper in suburban and intensively farmed landscapes (Baillie et al., 2011). Jerzak (2001) found in Poland that *Pica pica* abundance increased three times faster in urban than rural settings, where birds found a warmer climate and more food resources.

The Hooded crow, a farmland generalist, have increased populations, but with a lower growth rate than the previously described species (30% from 1992). This is confirmed at the European level where there is evidence of a population increase (Snow and Perrins, 1998). This increase is probably supported by the urban populations that increased due to the presence of suitable habitats and a lack of predators (Vuorisalo et al., 2003).

The species with the second highest increase in Lombardy from 1992 is the Pheasant, a gamebird whose population dynamics is principally determined by releases of reared birds for shooting (Baillie et al., 2011). Some studies found that high Pheasant densities potentially have negative effects on other birds due to the spread of disease and parasites, and competition for food (Fuller et al., 2005). Falco tinnunculus in Europe is the most urbanized raptor species and occur in different habitats, such as urban parks, open grassland and farmland. In Lombardy Common Kestrels presented a strong increase of the population from 6885 breeding pairs in 1992 to 18982 breeding pairs in 2016. Analysing in more detail the population trend, the pattern presented a fluctuation with a decline from 2007 to 2009, which was followed by a recovery. In Europe, the species has undergone a strong decline between 1970 and 1990, due to the lethal and sub lethal effects of organochlorine pesticides. The recovery of populations in subsequent years was probably reduced due to the effects of agricultural intensification on farmland habitats and small mammals populations (Gibbons et al., 1993). Since the start of 90s, the population in some European countries have recovered but with

fluctuations without an evident long-term trend (e.g. England; Baillie et al., 2011). Nowadays the species is considered in moderate decline in Europe (BirdLife International, 2016).

3.5 Conclusion

The use of GAM models has allowed exploiting to use data from several projects and to overcome the possible biases of spatial and temporal autocorrelation using smooth functions. Furthermore, the GAM models through the "change points" technique have allowed to study the long-term trend of the populations removing the noise due to annual fluctuations which in some cases may mask the population dynamics.

The long-term trends of breeding bird populations in Lombardy highlighted the unfavourable conservation status of many agro-ecosystem species. The decline of farmland species suggests as possible causes the change and intensification in agricultural practices in northern Italy.

The conservation of the most demanding species require an agricultural environment with diversified crops and grassland, often used for foraging (e.g. *Hirundo rustica*) and/or nesting (e.g. *Alauda arvensis*). Farmland should be managed with low intensive agricultural practices (e.g. low mowing intensity in meadows) and farm management should include the maintenance and creation of seminatural habitats (e.g. hedgerows, small wetlands). In Europe, a boost in this direction could come from the agri-environmental scheme and greening measures provided by the new agricultural policy of the European Union (i.e. CAP Reform 2014-2020).

Further researches may analyse in more detail population dynamics using the generalized additive mixed models (GAMM) that allow to decompose the trends by separating short-term fluctuations from long-term population change (Knape, 2016). This will make it possible to obtain more robust inference and deeply analyse the relationships between observed population dynamics with changes in agricultural practices and crop surfaces at the regional and sub-regional scale, or the effects of meteo-climatic variables in breeding and wintering grounds.

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Appendix A

A.1 Regional populations

We reported the annual regional populations estimate by the GAMs for each species.

Tab.3.9 Estimate of annual regional populations express as breeding pairs for agro-ecosystem species based on GAMs.

	1992	1995	1996	1999	2000	2001	2002	2003	2004	2005	2006
A. arvensis	152938	75484	55241	58353	56912	48009	45088	50647	40883	52016	39964
C. carduelis	61241	38605	53388	60120	65410	56286	42067	50822	37974	39918	26121
C. cetti	4067	5200	5203	10013	7919	12210	4231	4298	9413	8410	3657
C. chloris	53992	39659	35664	58353	66390	42918	39089	28320	23098	25184	22382
C. palumbus	9271	8989	3472	6023	8277	5538	4712	5026	4951	6972	14561
C. cornix	33981	19827	20029	34374	30399	29519	32448	24608	28899	31272	35724
C. coturnix	4147	4550	893	3028	6329	6932	3725	4755	5012	20603	8236
F. tinnunculus	533	395	339	625	1049	1483	1079	1605	2128	1894	2769
H. rustica	216853	126030	153994	173461	170811	142387	159568	125388	107453	105022	126063
L. collurio	18718	15910	10067	11149	10414	14192	9140	4252	9411	11588	8719
L. megarhynchos	81386	44233	44529	51540	46019	41890	34688	42677	41411	48839	41795
M. alba	14456	7815	9272	9786	12459	14258	13924	10954	9911	8530	9510
M. flava	60062	34538	26813	32820	40264	33007	32280	37163	25860	30350	26830
P. italiae	641704	483984	276787	676544	593581	513069	819475	662369	440887	335921	348057
P. montanus	240434	127895	86775	195288	201478	167692	122703	112209	92376	109971	137580
P. colchicus	6885	2178	3959	5060	7122	6520	5231	7544	4532	5669	9567
P. pica	2348	6037	3027	4736	6091	5276	6781	7706	5859	10227	11146
S. torquata	13954	7237	21222	21777	21763	31428	24826	24520	41572	45729	12614
S. turtur	19484	23867	7132	25794	24832	16679	22584	9913	14302	17509	17925
S. vulgaris	125479	65971	29341	105948	109671	100341	110707	107467	96352	102247	121071

Tab.3.10 Estimate of annual regional populations express as breeding pairs for agro-ecosystem species based on GAMs.

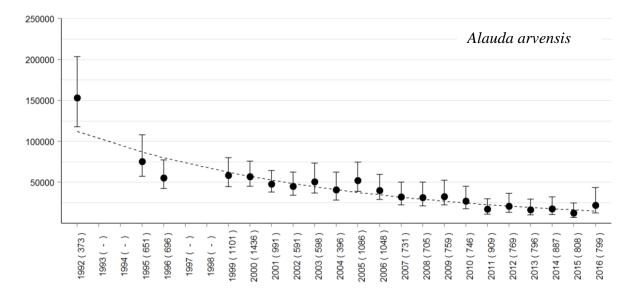
	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
A. arvensis	32203	31360	32667	27028	17149	20772	16281	17391	12525	21819
C. carduelis	24855	22283	17637	15686	12925	21005	20637	16565	16663	14646
C. cetti	5658	8929	4458	2647	4510	2148	1850	2052	3557	4971
C. chloris	18645	23832	13549	13018	17876	22592	14197	12201	15273	12558
C. palumbus	12069	14075	14805	20459	28914	22816	29222	32790	35002	44625
C. cornix	29419	31708	26892	32007	36457	33566	35511	37774	30358	30467
C. coturnix	5329	4847	4990	8264	4389	3877	3488	2526	3131	2369
F. tinnunculus	2104	2219	1408	1727	1476	1632	1861	2254	2366	2537
H. rustica	90464	81240	72004	109506	74763	51962	80981	62484	50823	77277
L. collurio	14551	10823	8261	8638	4703	3867	8709	7152	5844	7150
L. megarhynchos	63641	55867	51043	50046	41349	38951	50053	43950	37303	42829
M. alba	8419	7791	6624	6133	9616	5882	9587	8007	7238	9443
M. flava	23109	25071	30801	24043	21960	17404	32133	13388	16675	13896
P. italiae	218947	232760	179764	172504	143164	137484	123105	103844	118474	106039
P. montanus	131544	140100	128093	91912	79120	77686	69206	83997	86155	84101
P. colchicus	11957	9308	14590	14785	12683	16405	17953	15222	20914	18982
P. pica	6944	7875	9442	10549	9443	13545	15244	10453	12967	16450
S. torquata	25406	22492	8089	13009	6857	4949	12450	8665	9564	7430
S. turtur	29047	28366	32820	30395	18491	25336	20567	28100	20984	22091
S. vulgaris	98479	115851	75206	60150	57711	60370	51009	64564	54774	63175

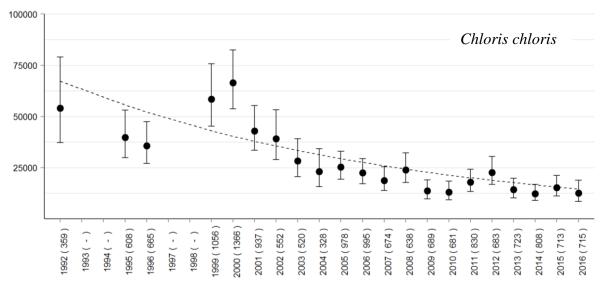
A.2 Trend plots

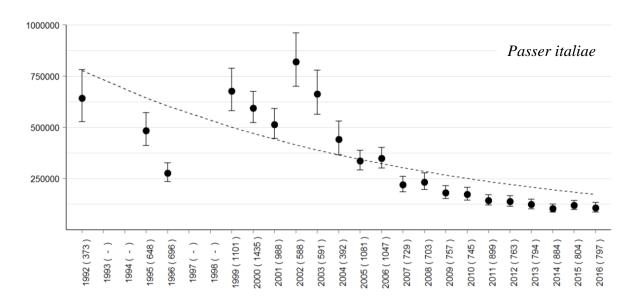
We reported the trend plots of the four species with the highest decline and of the four species with the highest increase.

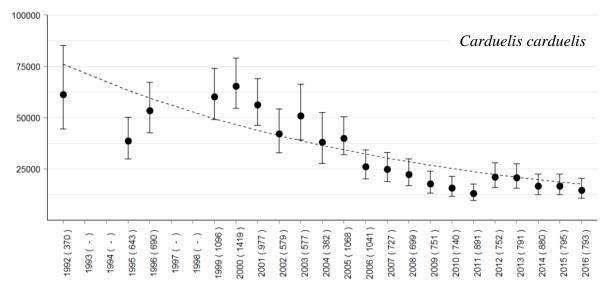
Figures caption

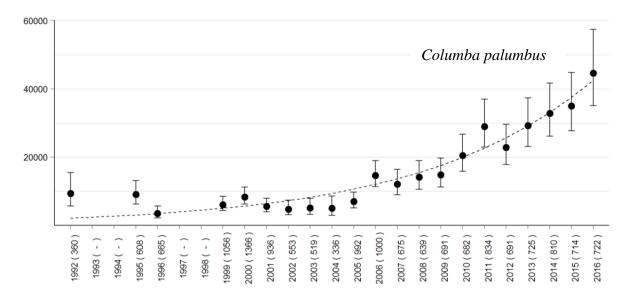
Population trend plot. Black dots: estimate of annual population with 95% confidence interval; dashed line: trend estimate by the discrete population growth model; x-axis: the year and in brackets number of points used in the analysis; y-axes: breeding pairs.

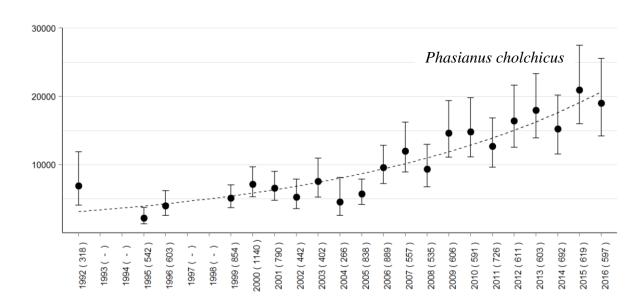


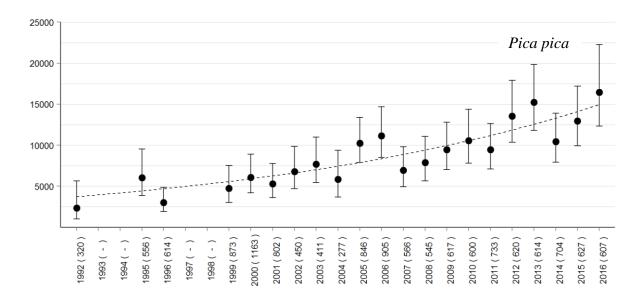


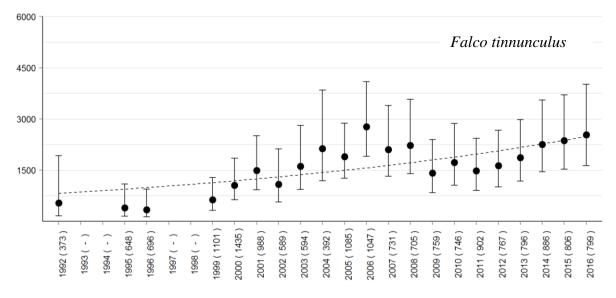








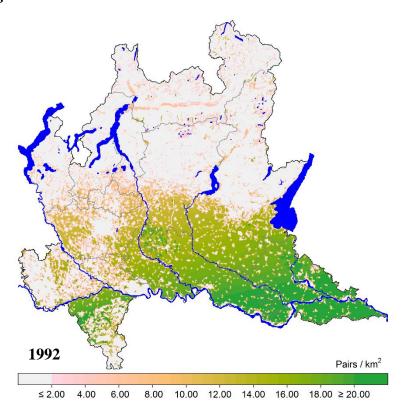


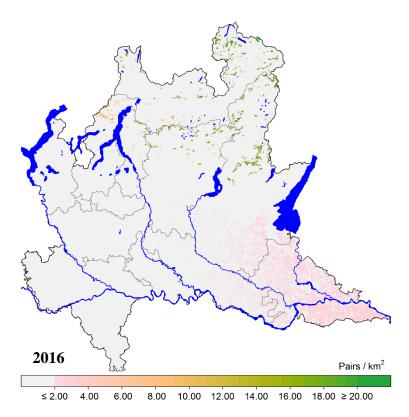


A.3 Distribution maps

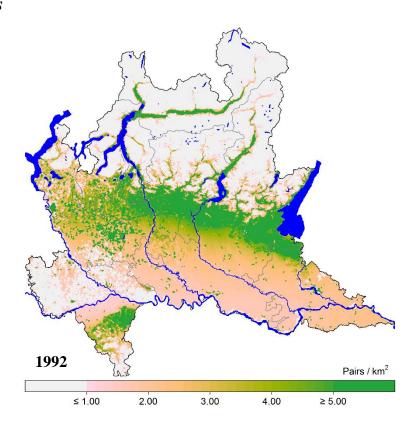
We reported two distribution maps (1992 and 2016) of the two species with the highest increase.

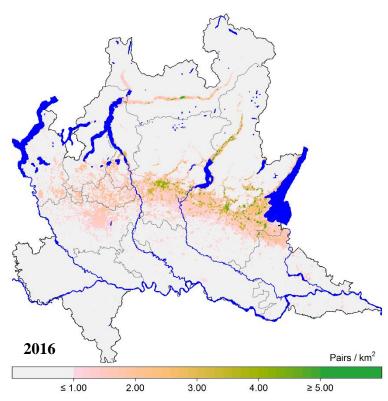
Alauda arvensis





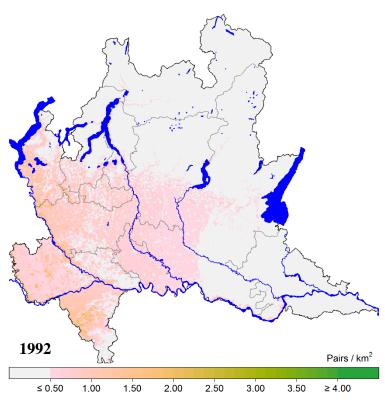
Chloris chloris

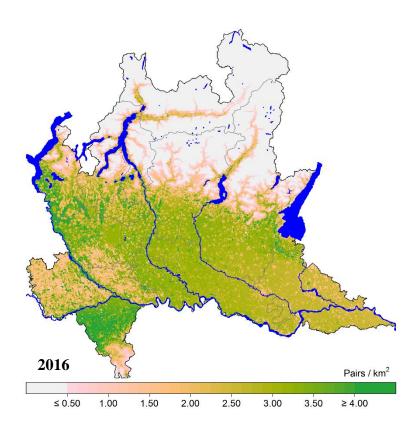




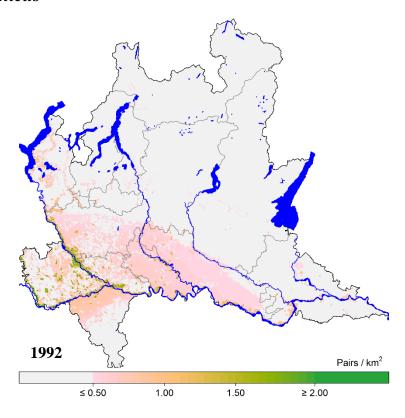
We reported two distribution maps (1992 and 2016) of the two species with the highest decline.

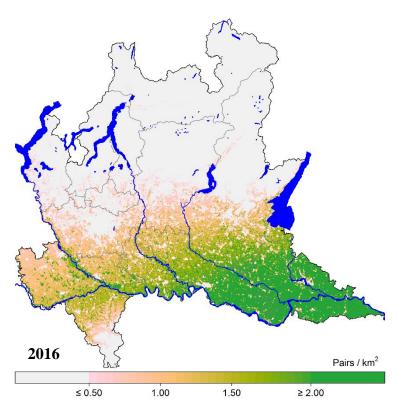
Columba palumbus





Phasianus colchicus





A.4 Change points

We reported the change points for each species with their interpretation.

Tab. 3.11 Change points for each species (1995-2006). Types of change points: +++ increasing; ++ increasing but rate slowing; + moving towards increasing; = no evidence of change; - moving towards decreasing; -- decreasing but rate slowing; --- decreasing.

Year	1995	1996	1999	2000	2001	2002	2003	2004	2005	2006
Period of	1992	1995	1996	1999	2000	2001	2002	2003	2004	2005
assessment	1996	1999	2000	2001	2002	2003	2004	2005	2006	2007
A. arvensis				-						
C. carduelis		+++	++							
C. cetti	+++	+++	++	-						
C. chloris		+++	++							
C. palumbus				+	+++	+++	+++	+++	+++	+++
C. cornix	++	+++	++	+++	+++	+++	+++	+++	+++	+++
C. coturnix	=	+++	++	++	++	++	++	++	++	
F. tinnunculus	+	+++	++	+++	+++	+++	+++	++	++	++
H. rustica		+++	++							
L. collurio										
L. megarhynchos		+	++				+++	+++	+++	++
M. alba		+++	++	++	++					
M. flava			++	++	-					
P. italiae		+++	++	++	++					
P. montanus		+++	++					+++	+++	++
P. colchicus	=	+++	++	+++	+++	+++	+++	+++	+++	+++
P. pica	++	+++	++	+++	+++	+++	+++	+++	+++	+++
S. torquata	+++	+++	++	++	++	++	++			
S. turtur	+	+++	++					+++	+++	+++
S. vulgaris		+++	++	++				+++	++	-

Tab. 3.12 Change points for each species (2007-2015). Types of change points: +++ increasing; ++ increasing but rate slowing; + moving towards increasing; = no evidence of change; - moving towards decreasing; -- decreasing but rate slowing; --- decreasing.

Year	2007	2008	2009	2010	2011	2012	2013	2014	2015
Period of assessment	2006 2008	2007 2009	2008 2010	2009 2011	2010 2012	2011 2013	2012 2014	2013 2015	2014 2016
A. arvensis								+++	=
C. carduelis					+++	+++	++		
C. cetti								=	=
C. chloris					+++	+++	++		
C. palumbus	+++	+++	+++	+++	+++	+++	+++	+++	+++
C. cornix	+++	+++	+++	+++	+++	+++	+++	+++	+++
C. coturnix									=
F. tinnunculus					+++	+++	+++	+++	+++
H. rustica									=
L. collurio									
L. megarhynchos	++								=
M. alba				+++	+++	+++	+++	+++	=
M. flava									
P. italiae									=
P. montanus	++						+++	++	=
P. colchicus	+++	+++	+++	+++	+++	+++	+++	+++	+++
P. pica	+++	+++	+++	+++	+++	+++	+++	+++	+++
S. torquata								=	=
S. turtur	++	++	-						=
S. vulgaris							+++	+++	=

A.5 Change point plots

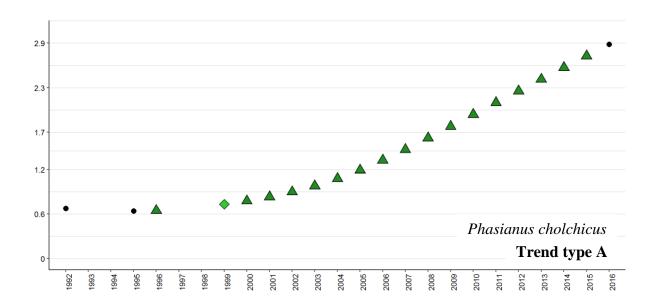
We reported a change point plots for each trend types. For detail in change points interpretation see Tab. 3.6.

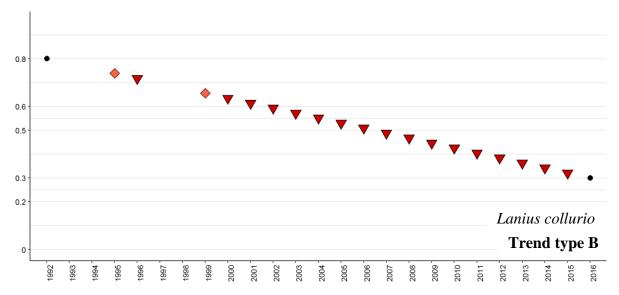
Figure caption

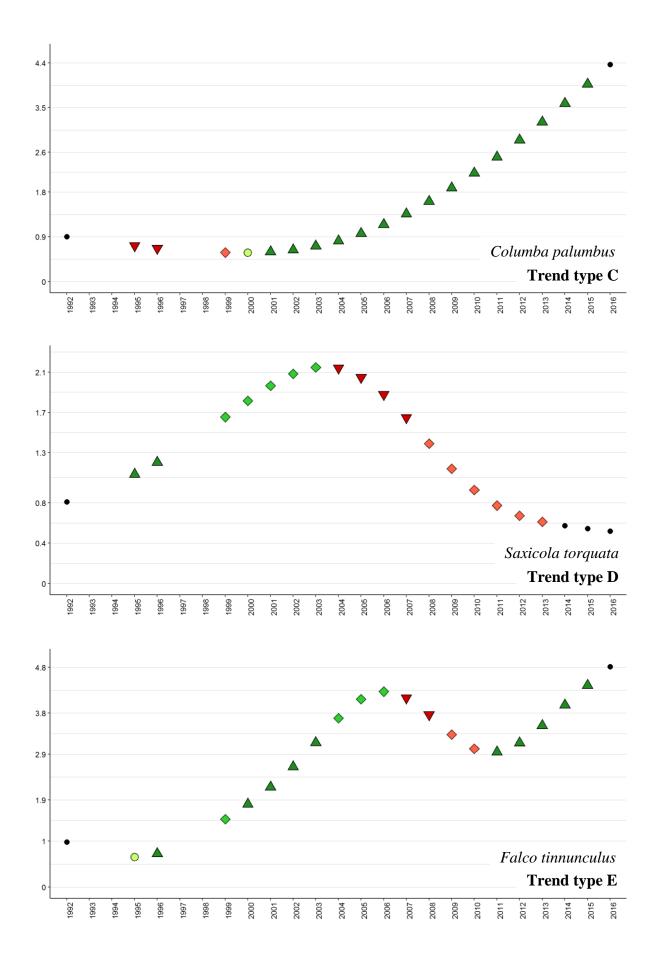
Change point plot. Trend types: A ("+"; only positive directions), B ("-"; only negative directions), C ("-/+"; first part of the time series negative, second part of the time series positive), D ("+/-"; first part of the time series positive, second part of the time series negative) and E ("fluctuations"; presence of fluctuations that did not allow to define a precise trend). x-axis: the year; y-axes: index of abundance.

Symbol legend









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Chapter 4

Long- and medium-term changes in the altitudinal distribution of breeding birds in the Italian Alps

Abstract

The altitudinal distribution of several organism has recently changed following different patterns across the species' range. This highlights the importance of comparing altitudinal distributions between different species and geographical areas, in order to understand the potential drivers of these changes. We used the response curve shape method to investigate changes in altitudinal distributions of breeding birds over a long-term period (form 1982 to 2015) in the central Alps, and over a mediumterm period (from 2006 to 2015) to compare the dynamics occurred in the central and western Alps. To understand if the ecological traits of species could play an important role in shaping their altitudinal distribution, we classified birds according to their breeding habitat and migration strategy. During the long-term period, all species exhibited changes in at least one part of their altitudinal distribution. Most woodland species expanded towards higher and lower altitudes, probably stimulated by forest regrowth and/or temperature increase. Almost all alpine grassland species retracted the lower portion of their altitudinal range, moving towards the summit. Particularly, we observed a contraction of the altitudinal distribution of long-distance migrants. During the mediumterm period, both areas showed an increase in species moving downwards, which confirms the relevance of this apparently contrasting pattern. However, the species and ecological groups of the two areas revealed some differences in altitudinal changes, probably due to the interaction between local and wide-scale processes. The latter include climate change and forest expansion, which are probably the main drivers of the general patterns of change.

4.1 Introduction

Several studies have demonstrated that species ranges have changed in recent decades (Parmesan et al. 1999; Hickling et al. 2006; Zuckerberg et al. 2009; Gillings et al. 2015). In many cases, the ranges have shifted upwards or polewards, and it was documented that they were probably driven by the recent raise of temperatures (Chen et al., 2011; Parmesan and Yohe, 2003; Chris D. Thomas and Lennon, 1999). Generally, changes on biota are more evident with increasing latitude or elevation (Deutsch et al., 2008; Loarie et al., 2009). Nevertheless, species inhabiting medium-latitude mountains, such as the Alps, have been shown to suffer not only the effects of global warming, but also changes in agro-forestry and pastoral practices, which have played an important role in shaping their distribution in those areas for a long time (Ausden, 2007). Indeed, even though species are theoretically expected to move upwards with the increase of temperatures, both physical (Sun et al., 2013) and ecological limiting factors (Newton 1998, 2013) can prevent the establishment of suitable habitats at high elevations. This process may lead to the extinction of a species at the lower boundary of its distributional range, but not necessarily to a colonization at the upper parts. This can result in a range restriction instead of a range shift. However, not all species respond in the same way to the drivers of altitudinal range change (Maggini et al. 2011; Reif & Flousek 2012), probably because of differences in ecological traits (Reif & Flousek 2012; Auer et al. 2014; Hovick et al. 2016). Moreover, species responses may vary within different geographic contexts due to the local specificity and variability in climatic and ecological features (Archaux 2004; Popy et al. 2010; Chamberlain et al. 2013; Flousek et al. 2015). For this reason, in order to obtain a more comprehensive picture of the heterogeneity in altitudinal changes, it is fundamental to compare different species in different geographic areas. Moreover, long-term series of data on distribution are needed in order to depict and quantify the actual changes in a species' range. This requirement is also crucial to counteract the intrinsic and often wide sources of noise contained in biological data, which could make it difficult to detect significant and strong long-term trends (Hovick et al. 2016).

In our study, we explored the changes occurred in the altitudinal ranges of breeding birds in two areas located in the central and western Italian Alps. Birds are a conspicuous taxon for which long-time series of data are often available, and are particularly sensitive to climate and land-use changes (Laiolo et al., 2004; Lehikoinen et al., 2014; Lemoine et al., 2007). They are also relatively easy to study (Hovick et al. 2016). Indeed, several recent studies on climate change impact have focused on the range shift of bird species (Auer et al. 2014; Massimino et al. 2015; Tayleur et al. 2015).

In our study areas, long-term series of breeding bird data have been available since 1982 and 2006 in the central and western Alps, respectively. This gave us the opportunity to investigate changes occurred in the altitudinal ranges of 44 species in the central Alps, and of 27 species in the western Alps. In order to detect any possible pattern of change, we analysed the whole distribution of the species within the altitudinal range considered instead of its average or centroid, according to the conceptual framework first proposed by Maggini et al. (2011), which allows assessing range changes along altitudinal gradients and classifying the patterns of change. Different authors successfully applied this concept to bird species to detect upward and northward shifts (Massimino et al., 2015; Tayleur et al., 2015).

We compared the altitudinal shift patterns of species between the two mountain areas (central and western Alps), considering the overlapping period of 10 years (2006-2015) within the two time series, in order to identify differences or similarities in changes of bird ranges between different alpine contexts.

Finally, assuming that ecological traits could play a crucial role in shaping the pattern of range shifts in birds, we classified species based on their breeding habitat and migration strategy, and we searched for differences in ecological group responses.

The aim of this study can be summarized by three main questions:

- (1) Has the altitudinal range of mountain breeding birds shifted during the last 34 years?
- (2) Are the shifting patterns consistent in the western and central Alps?
- (3) Are there any differences in changes of elevation distribution between ecological groups?

4.2 Material and methods

4.2.1 Study area

The study area is divided in two parts: Central Alps (C-Alps) and Western Alps (W-Alps).

Central Alps

The study area located in the central Italian Alps (C-Alps) encloses the whole mountain area of the Lombardy region (northern Italy, 45°N, 9°E) (Fig. 4.1). Northern Lombardy is a mainly mountainous area, which covers almost half of the whole region, whereas lowland areas prevail in the South. A small portion of the northern Apennines is also present in the south-western corner of the Region (not investigated in the present study).

Lombardy mountains can be divided into two main sub-regions: the Prealps in the South, and the Alps. The Prealps have a mean altitude of 840 m and cover 27% of the Lombardy territory, while the Alps covers 17% of the regional surface and has a mean altitude of 1860 m.

The two mountainous sub-regions show some differences in land cover patterns. About one half (52%) of the prealpine area is covered by forests, mainly composed of deciduous species. Grasslands cover 15% of this sub-region, waterbodies 8%, and both rocks and shrubs 6%.

By contrast, the Alps are mostly occupied by rocks (35%) and forests (35%), with a large amount of coniferous species, while both grasslands and shrubs percentages are similar to those of the Prealps. The two sub-regions are subjected to a different degree of continentality, which leads to a variation in climate regimes. Indeed, climatic conditions gradually change from the Prealps to the inner Alps, ranging from a suboceanic regime to a strictly continental one (Caccianiga et al., 2008).

Western Alps

The study area in the western Italian Alps (W-Alps) was split into three sampling sites located in different protected areas: the Gran Paradiso National Park (GPNP; 44°25'N - 7°34'E), the Orsiera Rocciavrè Natural Park (ORNP; 44°75'N - 6°90'E) and the Veglia Devero Natural Park (VDNP; 46°18' N - 8°13' E) (Fig. 4.1).

The GPNP covers an area of 720 km^2 and has a mean altitude of 2400 m. ORNP has a surface of 110 km^2 and is the site with the lowest mean altitude, equal to 1970 m, while the VDNP has an area of 86 km^2 and a mean altitude of 2230 m.

The GPNP is dominated by rocks and grasslands, which cover 31% and 27% of the protected area, respectively, while forests and shrubs cover 24% and 6%, respectively. The ORNP is mainly characterized by grasslands (39%) and forests (35%), and, secondly, by rocks (18%) and shrubs (7%). Grasslands and rocks are the predominant land cover classes in the VDNP, showing the same cover

percentages as in the GPNP. Forests cover 22% of this study site, while shrubs occupy 6% of the area.

All protected areas are characterized by a continental climate showing modest differences in terms of climatic regimes (highest monthly precipitation and lowest annual mean temperature in the VDNP). The overall environmental variability of the three parks can be considered a representative sub-sample of the western Italian Alps (Viterbi et al. 2013).

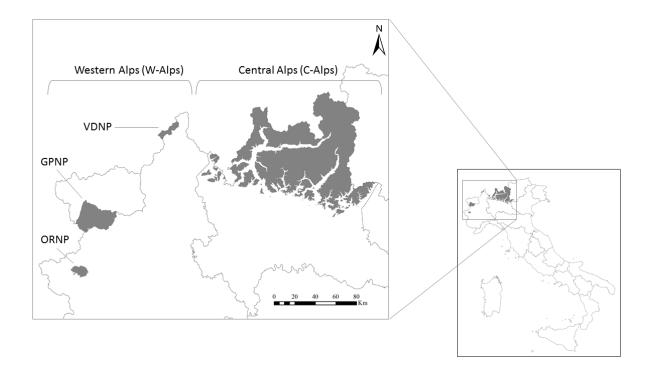


Fig. 4.1 Location of the study areas: central Alps (C-Alps): the zones above 600 m are highlighted in grey; western Alps (W-Alps) with the protected areas (Gran Paradiso National Park – GPNP; Orsiera Rocciavrè Natural Park – ORNP; Veglia Devero Natural Park – VDNP).

4.2.2 Bird data

Central Alps

Bird data for the C-Alps were taken from the long-term series (1992-2015) of the monitoring program of breeding birds in Lombardy (Bani et al., 2009). The project started in 1992 with the aim of monitoring the population status of breeding birds in the whole region. Due to the discontinuity in the availability of resources, data are not available for the years 1993, 1994, 1997 and 1998.

Data collection followed a stratified sampling design, according to the landscape and habitat variability of the study area (for details see Massimino et al. 2008; Bani et al. 2009).

Bird data were collected using the unlimited distance point count technique, performed during the breeding season (10 May-20 June) from sunrise to 11.00 am, only in good weather conditions (sunny to cloudy, without rain or strong winds) (Blondel et al. 1981; Fornasari et al. 1998; Bibby et al. 2000; Massimino et al. 2008). From the regional database, we selected the 4680 point counts performed above 600 m in order to compare them with historical data collected only above this threshold.

Indeed, the time series was extended backwards with data covering a timespan of 7 years (1982-1988), collected and published by Realini (1988). These data were georeferenced and collected using the same sampling technique adopted for the monitoring program of breeding birds in Lombardy. Because the author performed yearly sampling activities even outside the breeding season, we only considered the data collected from the last week of April until the second week of July.

The two sources of data were joined, and a 34-year bird data time series (1982-2015) was obtained, which included 6617 sampling points distributed across the whole mountain areas of Lombardy.

Western Alps

For the W-Alps, we used bird data collected during the Alpine Biodiversity Monitoring program, a multi-taxa project started in 2006 (Viterbi et al. 2013). The 69 sampling units were located between 1150 m and 2700 m at 200 m intervals (for details see Viterbi et al. 2013).

As in the C-Alps, birds were recorded by means of point counts with the unlimited distance method (Blondel et al. 1981, Bibby et al. 2000), performed twice during the breeding season (from the last week of April to the first week of July). Because of logistical constraints, the number of performed points differed between years and study areas.

For this study, we focused on a time series of 451 point counts performed in the three protected areas from 2006 to 2015.

4.2.3 Statistical analyses

We investigated the altitudinal species' range changes calibrating separate models for three distinct periods of assessment (t₀=1982-1986, t₁=2006-2010 and t₂=2011-2015). Data analysis was performed in two main steps. The first step focused on C-Alps study area, where we aimed to detect changes in altitudinal distribution over the longest time interval (t₀ vs t₂, long-term changes), considering the widest altitudinal range (from 600 m to 2700 m). In the second step of the analysis, in order to compare range shift patterns in the two mountain areas, we selected a C-Alps bird data subset according to the lower altitudinal range (from 1150 m to 2700 m) and the shorter time interval (t₁ vs t₂, medium-term changes) covered by W-Alps bird data. We considered bird data collected up to 2700

m because few bird occurrence data were available for higher altitudes in our study areas.

The sampling units showed some differences between years in terms of quantity and altitudinal distribution. The use of 5-years time-windows allowed us to obtain a more balanced and robust sample to model species altitudinal distribution in each period of assessment (t₀, t₁ and t₂) and for both study areas (Supporting information, Table S1, S2, S3). Furthermore, by combining data sampled over several years in one single period we were able to counteract the possible environmental and demographic yearly stochasticity (Maggini et al. 2011). Because W-Alps point counts were performed twice a year, we considered a species as present when it was detected at least in one of the two sampling sessions.

In order to assess bird altitudinal ranges, we modelled the presence of each species as a smooth function (thin plate regression spline; Wood 2006) of the elevation and of the interaction between northing and easting, using generalized additive models (Wood 2006, Maggini et al. 2011).

The structure of the models was:

$$g(E(Y_{s,i})) = f_s(east_i, north_i) + f_s(elev) + \propto_s$$

where g is the binomial link function, $E[Y_{s,i}]$ gives the probability of occurrence of species s on point i; elev the elevation. The spatial location of sampling points was given by eastings (east) and northings (north).

We set the maximum degrees of freedom to 15 for the space smooth (geographic coordinates) and to three for elevation. The latter setting allowed us to avoid overfitting and obtain unimodal curves, which are more easily comparable between periods of assessment (Maggini et al. 2011, Massimino et al. 2015).

The response curve that defines the species' elevation distribution was calculated keeping the spatial coordinates at their average over the whole sample (Massimino et al. 2015). Three types of curves can describe the altitudinal distribution of birds. Bell-shaped curves represented the entire altitudinal distribution of species, while truncated curves at lower or upper ends were typical of partially captured distributions (Fig. 4.2). Indeed, working within a predefined altitudinal range could lead to truncated distributions, thus preventing the detection of changes at the non assessable boundary and the unequivocal identification of the change pattern.

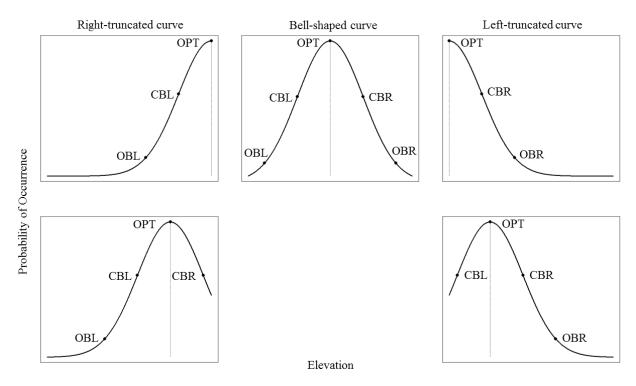


Fig. 4.2 Three types of curves describe the altitudinal distribution of birds and the reference points (OBL: outer border left; CBL: central border left; OPT: optimum; CBR: central border right; OBR: outer border right). Bell-shaped curves represent the entire altitudinal distribution of a species, while truncated curves are typical of partially captured distributions.

The curves were described using up to five reference points: OBL (outer border left); CBL (central border left); OPT (optimum); CBR (central border right); OBR (outer border right) (Heegaard 2002, Maggini et al. 2011, Massimino et al. 2015, Tayleur et al. 2015). The optimum represents the maximum occurrence probability, while the central and the outer borders result from a fraction of the maximum response (Heegaard, 2002). The outer border points were defined as the OPT * exp(-2), while the central border points were defined as the OPT * exp(-0.5).

Bird occurrence data were bootstrapped (n=200) and one curve for each bootstrapped sample was fitted in order to assess the estimates variability within each period of assessment.

For each species, the difference between reference point values of two periods of assessment was tested using the Mann-Whitney U test in order to detect the statistical significance of changes in altitudinal distribution. When the number of bootstrapped reference point values for each period of assessment was lower than or equal to 20, the Mann-Whitney U test was considered unreliable and the changes non-significant. The change of each reference point within each time interval (e.g. t_0 vs t_2) was coded according to Maggini et al. (2011): + for a significant upward shift; – for a significant downward shift; 0 for a non-significant shift; n meaning "no data available", usually for truncated curves or for models not fitting the data.

By combining the codes of the five reference points, we classified the changes in altitudinal distribution between two periods of assessment according to the theoretical framework proposed by Maggini et al. (2011). We integrated the classification method reported by the authors with patterns of change that included their directionality. Thus, we defined 12 theoretical patterns of change: trailing edge retraction, trailing edge expansion, optimum downward shift, optimum upward shift, downward shift, upward shift, leading edge retraction, leading edge expansion, retraction, expansion, range expansion, range retraction. When the combination of codes of the reference points was not interpretable, we classified it as an unclear pattern. In the case of truncated curves, changes in altitudinal distribution can be classified according to one or two potential patterns. We observed these conditions for some species and we reported both patterns in the results. To summarize the results, we also classified the patterns into three general categories: retraction, expansion and shift (Tab. 4.1).

Tab. 4.1 Combination of the reference point codes obtained from our analysis and their pattern classifications. Pattern of change: 12 theoretical patterns, 6 combination of two potential patterns and unclear pattern. General pattern: - unclear pattern. Reference points codes: + for a significant upward shift; - for a significant downward shift; 0 for a non-significant shift; n meaning "no data available"; () unique pattern defined for grassland species due to the physical limitations of upper altitudinal distribution.

Patterns of change	General pattern			Referen	ce points co	odes		
retraction	retraction	(+++nn)	++++0	+++00	(+++0n)	00		
expansion	expansion	0++++	0					
leading edge expansion	expansion							
leading edge retraction	retraction							
trailing edge expansion	expansion	(0nn)						
trailing edge retraction	retraction	(++0nn)						
range expansion	expansion	nn-++	+	0+	++	n++	n0-0+	0++
		nn-0+	n0+	00+	0++			
range retraction	retraction	+	n0++-	++n	+0-0-	+0	n+++-	+0
		++0	n0+0-	n++	+++-0	++++-	00+	
optimum upward shift	shift	00++0						
optimum downward shift	shift	00						
downward shift	shift							
upward shift	shift	+++++						
leading edge retraction -	retraction	nn0	nn0	nn00-				
range retraction								
trailing edge retraction -	retraction	+-0nn	++-nn	+nn				
range retraction								
upward shift - expansion	-	n++++	nn+++					
leading edge expansion -	expansion	nn0++	n00++					
range expansion								
downward shift - retraction	-	nn	n-0	n				
expansion - range expansion	expansion	n0+++						
unclear pattern		nn0-0	nn0	n00	n0++n			

In order to detect differences in altitudinal range changes between ecological groups, we classified each bird species according to its breeding habitat and migration strategy. We defined three habitat groups (woodland, edge, and grassland species) and three migration groups (long-distance migrant, short-distance migrant, and resident species). Since habitat and migration features were defined according to the mountainous geographical context where birds were surveyed, the ecological traits of some species may differ from the traditional classification of European birds (Pan-European Common Bird Monitoring Scheme, http://www.ebcc.info/index.php?ID=592#Explantions, accessed on August 16, 2016). We considered bird seasonal movements occurring between mountains and plains as narrow-area displacements, and we thus classified altitudinal migrants as resident species. We defined the bird species that complete the migration within the Mediterranean area as short-distance migrants, whereas bird species moving beyond the Sahara desert were considered as long-distance migrants.

We assessed long-term (t_0 vs t_2) changes in the altitudinal distribution range of 44 bird species in the C-Alps, and we also compared the medium-term (t_1 vs t_2) changes for 39 and 27 species in the C-Alps and in the W-Alps, respectively. In this study, we analysed species belonging to *Passeriformes* and *Piciformes* only, as they are typically more linked to the site where they were surveyed.

All analyses were performed using R (R Core Team 2015), with the package mgcv (Wood, 2006).

4.3 Results

4.3.1 Long-term changes (C-Alps)

In the C-Alps, in the t₀-t₂ time period, six of the 44 species (14%) shifted upwards. Eleven bird species (25%) showed an expansion pattern, while 17 species (39%) experienced a retraction of their altitudinal distribution (Tab. 4.2).

Tab. 4.2 Changes of the altitudinal distribution for 44 species in the central Alps during the long-term period (t₀, 1982-1986 and t₂, 2011-2015). We reported for each species: ecological group (H: breeding habitat [w: wood; e: edge; g: grassland] and M: migration strategy [r: resident, sd: short-distance, ld: long-distance]); mean shift (m) between the periods of assessment (t₀ vs t₂); the significance of the change (+ for significant upward shift; – for significant downward shift; 0 for non-significant shift; n for no data available) and the general pattern GP (S: shift; E: expansion; R: retraction; - unclear pattern). Reference points: OBL (outer border left); CBL (central border left); OPT (optimum); CBR (central border right); OBR (outer border right).

			Ref	ference	points 1	mean sh	ifts		Referer	ice poin	ts codes	5	
Species	H	M	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	GP
Anthus trivialis	e	ld	355	238	221	257	280	+	+	+	+	+	S
Carduelis cannabina	e	sd	208	189	241	367	324	+	+	+	+	+	S
Carduelis spinus	W	sd	420	402	257	155	78	+	+	+	+	+	S
Loxia curvirostra	W	r	178	180	229	315	384	+	+	+	+	+	S
Poecile montanus	W	r	440	320	280	294	298	+	+	+	+	+	S
Prunella modularis	e	sd	385	242	176	145	70	+	+	+	+	+	S
Certhia familiaris	W	r	-203	-173	-86	2	91	-	-	=	0	+	Е
Emberiza citrinella	e	r	0	508	371	289	265	0	+	+	+	+	Е
Lophophanes cristatus	W	r	-54	-41	-22	4	18	-	-	-	0	+	Е
Parus major	W	r			0	250	269	n	n	0	+	+	Е
Pyrrhula pyrrhula	w	sd	0	233	149	121	119	0	+	+	+	+	Е
Regulus ignicapillus	W	sd	-33	-43	-8	32	56	-	-	-	+	+	Е
Regulus regulus	W	sd	-34	-46	-20	13	13	-	-	-	+	+	Е
Sylvia atricapilla	W	sd			-13	272	225	n	n	-	+	+	Е
Turdus merula	W	sd			0	274	136	n	n	0	+	+	Е
Turdus philomelos	W	sd		-295	-129	118	296	n	-	-	+	+	Е
Turdus pilaris	e	sd	-159	-123	-75	-20	49	-	-	-	-	+	Е
Parus major	W	r			0	250	269	n	n	0	+	+	Е
Aegithalos caudatus	W	r			-3	-58	-105	n	n	0	-	-	R
Alauda arvensis	g	sd	1027	1084	930			+	+	+	n	n	R
Anthus spinoletta	g	sd	395	102	0			+	+	0	n	n	R
Carduelis flammea	e	r	250	173	118	75	1	+	+	+	+	0	R
Chloris chloris	e	sd			-2	-205	-401	n	n	0	-	-	R
Dendrocopos major	W	r			-2	-35	-67	n	n	0	0	-	R
Montifringilla nivalis	g	r	344	69	-17			+	+	-	n	n	R
Nucifraga caryocatactes	W	r	151	165	224	351	0	+	+	+	+	0	R

Tab. 5.2 (cont.)

			Ref	ference	points	mean sh	ifts		Referer	ice poin	ts codes	6	
Species	H	M	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	GP
Oenanthe oenanthe	g	ld	319	-30	4			+	-	0	n	n	R
Phoenicurus ochruros	g	sd	223	151	0			+	+	0	n	n	R
Phylloscopus bonelli	e	ld		0	329	29	-148	n	0	+	+	-	R
Picus viridis	W	r			1	-13	-83	n	n	0	-	-	R
Prunella collaris	g	r	116	-55	-41			+	-	-	n	n	R
Sylvia borin	e	ld	62	-152	-268	-378	-490	+	-	-	-	-	R
Sylvia curruca	e	ld	294	197	129	68	-3	+	+	+	+	0	R
Turdus torquatus	e	r	283	51	-263	-370		+	+	-	-	n	R
Turdus viscivorus	W	r	34	-7	-12	-8	-16	+	0	-	0	-	R
Carduelis carduelis	e	sd			-358	-469	-300	n	n	-	-	-	S/R
Cyanistes caeruleus	w	r			35	267	213	n	n	+	+	+	S/E
Erithacus rubecula	w	sd		107	112	158	170	n	+	+	+	+	S/E
Fringilla coelebs	w	sd			21	224	176	n	n	+	+	+	S/E
Garrulus glandarius	w	r			174	293	29	n	n	+	+	+	S/E
Periparus ater	w	r		56	61	114	65	n	+	+	+	+	S/E
Phoenicurus phoenicurus	w	ld			134	640	581	n	n	+	+	+	S/E
Phylloscopus collybita	W	sd		229	222	326	441	n	+	+	+	+	S/E
Troglodytes troglodytes	W	sd		15	147	393		n	0	+	+	n	S/E
Saxicola rubetra	g	ld	56	-49	-22	20	50	+	-	-	0	+	-

For bird species classified according to two patterns of change, we observed a shift or expansion pattern in eight species (seven with an upward shift and one with an optimum upward shift), while one species showed a downward shift or retraction. Only one species did not show any clear pattern. Considering the 24 species for which the reference points moved upwards, with a significant variation in the long-term, we observed conspicuous mean altitudinal shifts: 309 ± 67 m for OBL, 255 ± 56 m for CBL, 176 ± 39 m for OPT, 256 ± 28 m for CBR, 195 ± 36 m for OBR.

Among the woodland species, expansion was the predominant pattern of change. Nine of the 25 species showed an expansion pattern, whereas three species shifted upwards. Eight species showed a truncated distribution and were classified according to two potential patterns of change (seven with an upward shift or expansion, one with an optimum upward shift or expansion; Tab. 4.2, Fig. 4.3a). The state of the edge species appeared less clear. Six of the 12 edge species (50%) experienced a retraction, three showed an upward, two expanded their altitudinal range, and one displayed a downward shift or retraction pattern (Tab. 4.2, Fig. 4.3b).

For grassland species, in case of curves truncated at the upper end, we considered retraction as the only potential pattern because of the physical limitations of their upper altitudinal distribution. Consequently, species living at the highest altitudes highlighted a dramatically noticeable framework,

as they suffered a remarkable retraction of the lower altitudinal boundary (six out of 7 species; 86%; Tab. 4.2, Fig. 4.3c).

Considering the migration group, we detected a clear predominant pattern of change for long-distance migrants. Indeed, four of the seven trans-Saharan migrants (57%) retracted their altitudinal distribution. Conversely, most short-distance migrants (74%) colonized high altitudes with an expansion or an upward shift. Resident species did not show any clear altitudinal pattern of change (Tab. 4.2).

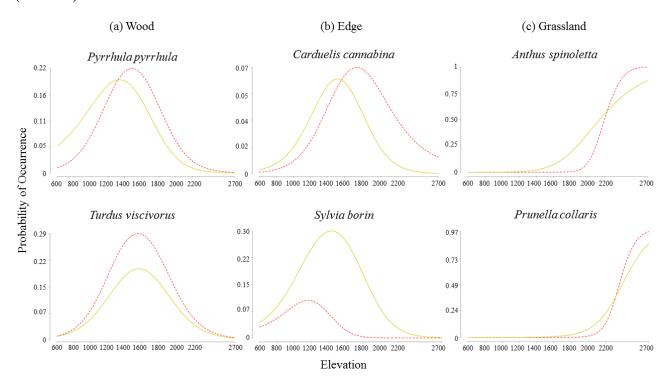


Fig. 4.3 Response curves of six bird species in the central Alps for the period t_0 =1982-1986 (solid line) and t_2 =2011-2015 (dashed line). We reported two examples per habitat group. From left to right, we represented (a) two predominant patterns of change for woodland species (upward shift, expansion), (b) the contrasting patterns showed by edge species (upward shift, range retraction), and (c) the retraction pattern of grassland species.

4.3.2 Medium-term changes (C-Alps vs W-Alps)

Considering all species together, we did not observe any reliable variation between the two alpine areas for the altitudinal patterns of change in the medium-term period.

In the C-Alps, 10 species (26%) expanded their range, 11 species (28%) showed a retraction, whilst three species (8%) displayed a shift (one completely upwards, one completely downwards and one shifted its optimum downward) in the medium-term period (t_1 - t_2). Considering the bird species classified according to two patterns of change, we observed four species (10%) shifting downwards or retracting, and four (10%) shifting upwards or expanding their altitudinal range. Seven species showed an unclear pattern (Tab. 4.3).

Tab. 4.3 Changes of the altitudinal distribution for 39 species in the central Alps during the medium-term period (t₁, 2006-2010 and t₂, 2011-2015). We reported for each species: ecological group (H: breeding habitat [w: wood; e: edge; g: grassland] and M: migration strategy [r: resident, sd: short-distance, ld: long-distance]); mean shift (m) between the periods of assessment (t₀ vs t₂); the significance of the change (+ for significant upward shift; – for significant downward shift; 0 for non-significant shift; n for no data available) and the general pattern GP (S: shift; E: expansion; R: retraction; - unclear pattern). Reference points: OBL (outer border left); CBL (central border left); OPT (optimum); CBR (central border right); OBR (outer border right).

			Re	ference	points 1	mean sh	ifts		Referer	ice poin	ts code	S	G.D.
Species	H	M	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	GP
Nucifraga caryocatactes	W	r	56	167	141	108	83	+	+	+	+	+	S
Prunella modularis	e	sd	-14	-17	-19	-71	-114	-	-	-	-	-	S
Turdus pilaris	e	sd	-12	-89	-127	-95	-57	0	-	-	-	0	S
Carduelis carduelis	e	sd		-209	-24	70	148	n	0	0	+	+	E
Carduelis spinus	W	sd	-70	-192	-238	-65	30	-	-	-	-	0	E
Cyanistes caeruleus	W	r	0	53	40	31	54	0	+	+	+	+	E
Fringilla coelebs	W	sd			-41	-7	22	n	n	-	0	+	E
Garrulus glandarius	W	r		0	-154	-78	8	n	0	-	-	+	E
Loxia curvirostra	W	r	0	-332	-162	247	397	0	-	-	+	+	E
Oenanthe oenanthe	g	ld	-138	-275	0			-	-	0	n	n	E
Phoenicurus ochruros	g	sd	-36	-34	-4			-	-	0	n	n	Е
Poecile montanus	W	r	0	187	140	66	52	0	+	+	+	+	E
Pyrrhula pyrrhula	W	sd		0	-118	-13	114	n	0	-	0	+	E
Alauda arvensis	g	sd	672	683	482			+	+	+	n	n	R
Anthus spinoletta	g	r	142	143	0			+	+	0	n	n	R
Anthus trivialis	e	ld	77	86	75	62	9	+	+	+	+	0	R
Carduelis flammea	e	r	70	7	-81	-86	-16	+	+	-	-	0	R
Muscicapa striata	e	ld		-32	41	31	-115	n	0	+	0	-	R
Periparus ater	W	r			12	-105	-125	n	n	0	-	-	R
Regulus ignicapillus	W	sd		17	58	28	-19	n	+	+	+	-	R
Regulus regulus	W	sd		-4	-10	-76	-88	n	n	0	-	-	R
Sylvia curruca	e	ld	16	-2	-39	-102	-82	+	0	-	-	-	R
Troglodytes troglodytes	w	sd		38	53	-103	-33	n	+	+	-	-	R
Turdus torquatus	e	r	127	-62	-258	-214	-218	+	0	-	-	-	R
Certhia familiaris	W	r		1	185	278	135	n	n	+	+	+	S/E
Lophophanes cristatus	W	r			-264	-284	-104	n	n	-	-	-	S/R
Phoenicurus phoenicurus	w	ld			-35	-96	-157	n	n	-	-	-	S/R
Phylloscopus bonelli	e	ld		-24	11	-12	-107	n	-	0	-	-	S/R
Phylloscopus collybita	W	sd		59	52	36	19	n	+	+	+	+	S/E
Saxicola rubetra	g	ld		-191	-393	-298	-181	n	-	-	-	-	S/R
Serinus serinus	e	sd			74	160	150	n	n	+	+	+	S/E
Turdus philomelos	W	sd			88	251	53	n	n	+	+	+	S/E

In bold species occurred in both study areas (C-Alps and W-Alps).

Tab. 4.3 (cont.)

~ .			Re	ference	points 1	mean sh	ifts		6				
Species	H	M	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	GP
Dendrocopos major	W	r			-318	-203	-58	n	n	-	-	0	-
Erithacus rubecula	W	sd			11	-21	20	n	n	+	-	+	-
Monticola saxatilis	g	ld	-61	31	-29			0	+	-	n	n	-
Parus major	W	r			-9	46	-11	n	n	0	+	0	-
Sylvia atricapilla	W	sd			44	37	-73	n	n	+	+	-	-
Turdus merula	W	r			0	-38	0	n	n	0	-	0	-
Turdus viscivorus	W	r		-130	-53	-8	-13	n	-	-	0	0	-

In bold species occurred in both study areas (C-Alps and W-Alps).

During the medium-term period, in the W-Alps, two the 27 bird species (7%) showed a shift (one shifted its optimum upwards while the other shifted downwards), 12 (44%) expanded their altitudinal range, and 10 (37%) suffered a retraction pattern. Two of the 27 species (7%) displayed a downward shift or a retraction pattern. Only one species did not show a clear pattern (Tab. 4.4).

Overall, the analysis of the medium-term period surprisingly showed that some species had moved towards lower altitudes. Indeed, for 14 species out of the 39 (36%) in the C-Alps, and for six species out of the 27 (22%) in the W-Alps, all the significant reference points had negative values (Tab. 4.3, Tab. 4.4). For instance, in the C-Alps we found a noticeable average shift at all the five reference points for these species: -54±23 m for the OBL, -106±32 m for the CBL, -103±37 m for the OPT, -113±28 m for the CBR, -81±18 m for the OBR.

Conversely, focusing on ecological groups, the differences between the two alpine areas became more evident. In the C-Alps, the most represented pattern of change for woodland species was expansion, but with a smaller number of species than in the W-Alps. Indeed, in the C-Alps, 7 of the 23 species (30%) expanded their altitudinal range and three species (13%) showed either an upward shift or an expansion pattern, while in the W-Alps almost all woodland species (83%) expanded their altitudinal range (Tab. 4.3, Tab. 4.4, Fig. 4.4a).

The edge species group revealed some slight similarities between the central and western Alps. Retraction was the predominant pattern in both areas (50% of the species in the C-Alps; 38% in the W-Alps). In the C-Alps, both expansion and downward shift patterns were observed in one species out of 10, while one species showed a downward shift or retraction. In the W-Alps, two out of the 8 species showed an expansion, one species displayed a downward shift, and one species exhibited either a downward shift or a retraction pattern (Tab. 4.3, Tab. 4.4, Fig. 4.4b).

Almost all grassland species (86%) showed a remarkable retraction at the trailing edge of their altitudinal range in the W-Alps. In the C-Alps we observed a more heterogeneous framework. Two

of the six species suffered a retraction of their altitudinal range, two species expanded their distribution towards lower altitudes in clear contrast with the W-Alps, one showed a downward shift or retraction, while the last one showed an unclear pattern (Tab. 4.3, Tab. 4.4, Fig. 4.4c).

Tab. 4.4 Changes of the altitudinal distribution for 27 species in the western Alps during the medium-term period (t₁, 2006-2010 and t₂, 2011-2015). We reported for each species: ecological group (H: breeding habitat [w: wood; e: edge; g: grassland] and M: migration strategy [r: resident, sd: short-distance, ld: long-distance]); mean shift (m) between the periods of assessment (t₀ vs t₂); the significance of the change (+ for significant upward shift; – for significant downward shift; 0 for non-significant shift; n for no data available) and the general pattern GP (S: shift; E: expansion; R: retraction; - unclear pattern). Reference points: OBL (outer border left); CBL (central border left); OPT (optimum); CBR (central border right); OBR (outer border right).

			Rei	ference	points 1	mean sh	ifts		Referer	ce poin	ts codes	S	
Species	H	M	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	GP
Sylvia borin	e	ld	63	37	82	23	1	0	0	+	+	0	S
Sylvia curruca	e	ld	-256	-131	-140	-178	-170	-	-	-	-	-	S
Carduelis cannabina	e	r	-19	-141	-219	-123	-14	-	-	-	-	0	Е
Erithacus rubecula	w	sd			0	32	32	n	n	0	+	+	Е
Fringilla coelebs	w	r			-42	122	85	n	n	0	+	+	Е
Garrulus glandarius	W	r			-5	147	213	n	n	0	+	+	Е
Lophophanes cristatus	w	r	-175	-129	-73	-10	39	-	-	-	0	+	Е
Nucifraga caryocatactes	W	r	-335	-346	-266	-130	16	-	-	-	-	0	Е
Periparus ater	w	r		47	48	115	121	n	0	+	+	+	Е
Phylloscopus bonelli	e	ld	-42	-62	-100	-4	98	0	-	-	0	+	Е
Poecile montanus	W	r	11	70	88	85	66	0	+	+	+	+	Е
Turdus merula	W	r			-3	49	77	n	n	0	+	+	Е
Turdus philomelos	W	sd			-10	215	189	n	n	0	+	+	Е
Turdus viscivorus	W	r	-67	-174	-37	102	101	0	-	-	+	+	Е
Alauda arvensis	g	sd	251	376	342	15	119	+	+	+	0	0	R
Anthus spinoletta	g	sd	82	136	113			+	+	+	n	n	R
Anthus trivialis	e	ld	24	-22	-58	-41	-70	0	0	-	-	-	R
Emberiza cia	e	sd	-132	18	138	-71	-179	0	0	+	-	-	R
Loxia curvirostra	w	r	111	80	45	-62	-15	+	+	+	-	0	R
Montifringilla nivalis	g	r	70	74	-42			+	+	-	n	n	R
Oenanthe oenanthe	g	ld	87	186	78			+	+	+	0	n	R
Prunella collaris	g	r	60	61	6			+	+	0	n	n	R
Prunella modularis	e	sd	267	248	176	41	-89	+	+	+	+	-	R
Saxicola rubetra	g	ld	55	28	137	103	50	+	+	+	+	0	R
Parus major	W	r			-158	-158	-98	n	n	-	-	-	S/R
Phylloscopus collybita	e	sd		-76	-214	-148	-70	n				-	S/R
Phoenicurus ochruros In hold species occurr	g	sd	98	46	-15			0	+	-	n	n	-

In bold species occurred in both study areas (C-Alps and W-Alps).

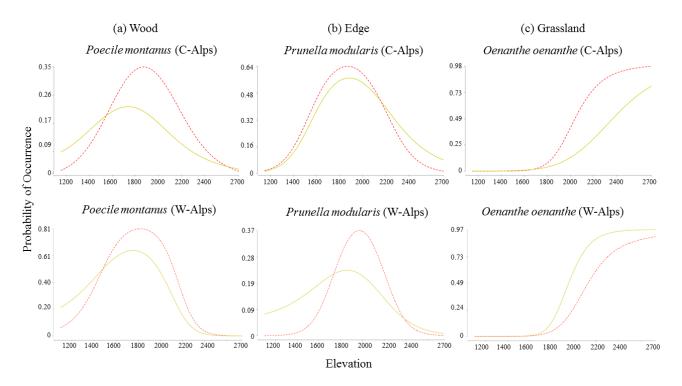


Fig. 4.4 Comparison between the response curves of three bird species occurring both in the central and the western Alps for the period t_1 =2006-2010 (solid line) and t_2 =2011-2015 (dashed line). We reported one example per habitat group in order to highlight analogies and differences between the two areas. (a) For the woodland group the predominant pattern is consistent in both areas (e.g. *Poeciloe montanus*, expansion), while edge and grassland species showed some differences in change patterns, i.e. (b) *Prunella modularis* experienced a range retraction in the W-Alps and a downward shift in the C-Alps, while *Oenanthe oenanthe* suffered a range retraction in the W-Alps and a trailing edge expansion in the C-Alps (c).

As regards the migration group, long-distance migrants in the C-Alps showed a clear pattern of overall retraction. In particular, three of the 8 species suffered an altitudinal range retraction, whereas three species showed a retraction or downward shift. On the contrary, most resident species experienced clear expansion patterns (69%).

We did not find any clear predominant pattern for the other migration group (Tab. 4.3, Tab. 4.4).

Twenty-two bird species occurred in both study areas during the medium-term period (t₁ vs t₂). Of these, only six species showed the same general patterns of change, while 11 species displayed different altitudinal range changes. Six of the 11 species were even characterized by opposite patterns. Five species were not comparable because they showed an unclear pattern in at least one area (Tab. 4.3, Tab. 4.4).

4.4 Discussion

4.4.1 Long-term changes (C-Alps)

All 44 studied breeding bird species exhibited long-term changes (1982-2015) in their altitudinal distribution in the C-Alps. To our knowledge, no previous researches on bird altitudinal shifts reported similar results. For instance, in two areas of French Alps, Archaux (2004) observed significant altitudinal changes for 33% and 8% of the bird species, respectively, over a 30-years study period (1973-2002). In Switzerland, 64% of the bird species experienced altitudinal changes during 9 years (1999-2007; Maggini et al., 2011). For the Italian Alps (Val Sessera, Piedmont), Popy et al. (2010) did not find any significant shift at the community level, although most species showed an increment in altitude between 1992 and 2005. More recent studies, carried out in other geographic contexts, demonstrated that bird altitudinal ranges had changed over time, but to a much lower extent compared to our findings (Auer et al. 2014, Massimino et al. 2015).

Overall, bird altitudinal ranges have changed over the last 34 years in the C-Alps, following different patterns. Considering only the species with unequivocal patterns of change, we observed that 14% of the bird species have shifted upwards, 25% have expanded their altitudinal distribution, and 39% have experienced a retraction pattern. Even though the study performed by Maggini et al. (2011) covered a shorter period of time, the authors reported percentage values per category similar to our findings. On the other hand, we found a much more evident altitudinal displacement for our bird species compared to those studied by Maggini et al. (2011). This difference between mean reference points values may be due to the different time period considered. During our long-term study period (34 years), several drivers, such as habitat modifications (Lemoine et al., 2007), competition (Lenoir et al., 2010) and climate change (Reif and Flousek, 2012; Tayleur et al., 2015) may have affected bird distribution on a long time scale, thus causing much clearer altitudinal changes. Indeed, if we compare our results with the study carried out by Archaux (2004) during 30 years, the variation in altitudinal shift for some species is highly consistent (e.g. *Erithacus rubecula*, upward shift of 114 m and 112 in the French Alps and in the central Italian Alps, respectively).

Some recent studies have demonstrated the important role of species ecological traits in shaping the altitudinal changes of birds (Reif & Flousek 2012; Auer et al. 2014; Hovick et al. 2016), and our results confirm the relevance of this aspect, as demonstrated by the different responses between ecological groups. For the woodland species group, we observed that 80% of the species have extended their range to either higher or lower altitudinal areas during the last 34 years. One of the possible drivers enhancing this trend is forest expansion, which may act together with temperature warming. Indeed, there is a growing evidence that the abandonment of traditional agricultural

practices has favoured forest regrowth, thus reducing the availability of open areas (Gehrig-Fasel et al., 2007; Gellrich et al., 2007; Pellissier et al., 2013). This phenomenon has been occurring across all Europe (Hatna and Bakker, 2011), in the European mountains (Beguería, 2006; Gehrig-Fasel et al., 2007) and particularly in the Alpine regions (Hunziker, 1995; Pellissier et al., 2013; Tasser et al., 2007). Moreover, the altitude of the treeline has been increasing, probably enhanced by the documented increase of temperature, which may have spurred the development of forest vegetation at higher altitudes (Dirnböck et al., 2003; Gehrig-Fasel et al., 2007; Švajda, 2008). In the Alps of Lombardy, huge portions of pastures and meadows have been abandoned, leading to forest regrowth (ERSAF 2012, Appendix B, Table 4.7). Our findings suggest that woodland birds have likely expanded and shifted their altitudinal ranges upwards following forest recolonization at lower and higher altitudes. Tree encroachment resulting from the abandonment of open areas has made the invasion by woodland bird species easier (Laiolo et al., 2004; Rolando et al., 2006), and this trend might continue in the future (Chamberlain et al., 2013). In contrast with our results, Reif and Flousek (2012) and Popy et al. (2011) did not find any altitudinal changes for woodland bird species, which showed that the upper limit of forests was probably acting as a barrier against their shifts. However, the two above-mentioned researches focused on shorter time periods than those analysed in our study, and forest cover changes were thus less detectable. Moreover, the study sites were located in different mountain contexts, which were likely subjected to different local land use dynamics. A methodological perspective might explain the different reactions of woodland birds, too. The response curve technique is sensitive to changes at different portions of the altitudinal distribution, which allows to detect even an initial shifting process, and thus more detailed patterns of change (Maggini et al. 2011). By using only the central part of the distribution (optimum), we would have not probably detected the altitudinal shift of woodland birds, because most changes occurred at the trailing and/or the leading edge of the species distribution. It should be acknowledged that climate warming might have acted as an important driver of upward expansion, too. It is widely known that the Alps have suffered a temperature increase in the last century (Acquaotta et al., 2014; Beniston, 2006, 2003; Brunetti et al., 2009). Even if wide-scale, fixed-station and long-term instrumental meteorological measures are not available, there are many robust clues indicating that temperatures have increased in the Alps of Lombardy, too, during the 34-years study period. Milder climatic conditions may have favoured the upward colonization of woodland bird species inhabiting lower altitude forest areas.

We did not identify a common pattern of change for the edge species group, probably due to the structural and climatic complexity of the treeline habitat (Alftine and Malanson, 2004; MacDonald et

al., 1998; Rai et al., 2012) or lower altitude edge habitats, where each bird species may react differently.

Conversely, almost all grassland species retracted their altitudinal range. Because of logistical constraints, the trends and distribution of this ecological group are poorly known (EEA 2010; Chamberlain et al. 2012), and only few researches have focused on alpine birds altitudinal changes. In the Alps, high altitude birds did not show any significant altitudinal range shifts (Archaux 2004; Popy et al. 2010; Maggini et al. 2011), whilst some evidence was reported for the Giant Mountains in the Czech Republic (Flousek et al., 2015; Reif and Flousek, 2012). High altitude birds are among the most threatened species (Chamberlain et al. 2016), but the lack of knowledge complicates the assessment of the main threats (habitat loss or climate change) affecting them (EEA 2010; Chamberlain et al. 2013). The upward shift of the treeline, with the consequent loss of open habitats, is one of the main threats for alpine birds (Chamberlain et al. 2013, 2016). Our results suggest that grassland species have retracted the trailing edge of their altitudinal range, thus losing the lower altitude open habitats, because of the considerable forest cover expansion at lower altitudes (ERSAF 2012, Supporting information, Table S6) and the upward shift of the treeline that has occurred in Lombardy. This habitat loss has led to the concentration of alpine species at higher altitudes, where the availability of suitable habitat is increasingly limited. The scenario could be exacerbated by the impossibility of the grassland habitats to colonize new upper areas. The reduction of the snow cover at high altitudes causes inadequate soil insulation and colder soils temperatures, which prevent the formation of grassland habitats (Edwards et al. 2007; Freppaz et al. 2010). Simultaneously, at lower altitudes, a further adverse factor like the edge effect may negatively affect high altitude birds (Chamberlain et al., 2012). Besides physically limiting the occurrence of grassland bird species, treeline habitats may act as a functional barrier. As reported by Donald (2004) for lowland areas, the proximity of the forest negatively affects the nesting behaviour of Alauda arvensis. Similar results were recently obtained by Masoero et al. (2016), who demonstrated that nesting close to the treeline in alpine environment increases predation pressure. Thus, a potential edge effect may amplify the treeline advancement impact on high altitude species, further reducing the availability of suitable areas. Habitat loss is likely the major threat for alpine birds, but climate change may play an additional negative role (Sekercioglu et al., 2008), interacting with the habitat loss process (Mantyka-pringle et al., 2012; Oliver and Morecroft, 2014) and favouring other adverse factors such as a decreasing food supply (Pearce-Higgins et al., 2010), increasing competition (Jankowski et al., 2010), predation rate (Melendez and Laiolo, 2014; Prop et al., 2015) or physiological stress (Barbosa et al., 2007; Gifford and Kozak, 2012).

As for migratory birds, we observed that most long-distance migrants (about 60%) contracted their altitudinal distribution. Several studies have demonstrated that long-distance migrant birds are particularly vulnerable and show noticeable populations declines (Bani et al., 2009; Both et al., 2010; Møller et al., 2008; Vickery et al., 2014). On the contrary, few researches have focused on the range contraction or shift of migratory birds (Auer et al. 2014; Hovick et al. 2016), and, to our knowledge, no specific studies have ever reported altitudinal range changes for this ecological group. It is quite hard to identify the main cause of the retraction pattern showed by our results, because long-distance migrants could be affected by processes acting at breeding sites, like the phenological mismatch (Both and te Marvelde, 2007; Jenni and Kéry, 2003), or by threats acting on the often unknown wintering areas (Vickery et al., 2014). Anyway, our findings confirmed a negative assessment for this group of birds, which, due to its globally threatened status, should be better investigated in mountain areas, too. We also observed an expansion for most short-distance migrants, but almost all these species breed in forests, and their patterns are thus probably linked to the expansion of this habitat.

4.4.2 Medium-term changes (C-Alps vs W-Alps)

In both areas, during the medium-term period, the number of bird species showing downward movements was remarkable. This trend is in contrast with the expectations and results of several studies showing and predicting upward shifts as a response of mountain birds to climate warming (Maggini et al. 2011; Reif & Flousek 2012; Auer et al. 2014) and habitat loss (Chamberlain et al., 2013). However, downward shifts are not so unusual. A review made by Lenoir et al. (2010) reported that, in a warming climate, many species pertaining to different taxa, had moved downwards, while other species had moved upwards. About 25% of the species involved had moved their mid-range positions towards lower altitudes. Among the studies involved, the one considering mountain bird species (Archaux 2004) outlined that five out of 8 species had shifted downwards. In a more recent study, Maggini et al. (2011) reported that 30% (28 out of 95) of birds had shifted downwards.

According to our findings, 36% and 22% of the species have shifted downwards in the C-Alps and the W-Alps respectively, which confirms that downward displacements are important patterns of altitudinal change.

Stochastic population fluctuations, associated with measurement errors, may potentially lead to this unexpected pattern (Lenoir et al., 2010). By using 5-years time windows, we tried to avoid the effect of yearly random population fluctuations (Maggini et al. 2011), and to obtain a more reliable altitudinal range assessment. Indeed, the unexpected downward shifts reported by our findings were likely caused by other factors. Lenoir et al. (2010) pointed out that climate warming alone, or in concert with habitat alterations, might reduce interspecific competition at lower altitudes. As the

lower boundaries of the altitudinal range are mainly controlled by biotic interactions (Brown and Lomolino, 1998; Connell, 1978; MacArthur, 1972), when environmental stressors, such as temperature warming and habitat modifications, become more severe, some species are forced to move upwards, with a consequent decrease of competitive pressure that likely allows other species to move towards lower altitudes. Actually, the downward movements of birds might be affected only by habitat alterations, without any biotic influence, as reported for the French Alps, where some forest species shifted downwards probably thanks to coniferous regrowth at lower altitudes (Archaux, 2004). However, analysing the available digital cartography, DUSAF 1.1 (ERSAF 2000) and DUSAF 4.0 (ERSAF 2014), it appears that no significant forest expansion occurred in the C-Alps between 1999 and 2012 along the whole altitudinal range considered (Supporting information, Table S6). This suggests that changes in species interactions may have played an important role in driving bird species downwards during the short-term period. However, further *ad hoc* studies on bird interspecific competition in mountain habitats are required to confirm this hypothesis.

The comparison between the C-Alps and the W-Alps confirmed that the altitudinal range changes of mountain birds are not universal, as reported by several studies (Archaux 2004; Popy et al. 2010; Maggini et al. 2011; Reif & Flousek 2012). The two alpine areas showed important dissimilarities both at the species and at the ecological group level. For all ecological groups, the birds of W-Alps revealed change patterns more similar to those found for the C-Alps long-term period, rather than for the medium-term period.

As mentioned above, the Alps of Lombardy experienced forest recolonization in the past, but no significant forest changes during the recent period (1999-2012). Consequently, woodland birds of the C-Alps have expanded their altitudinal ranges in the long-term period, but not evident patterns were detected during the more recent medium-term period. By contrast, in the W-Alps, most woodland birds showed an expansion pattern as in the C-Alps during the long-term period. Taking into account this relationship, we might suppose that during the medium-term interval, the C-Alps and W-Alps may have experienced different land use dynamics. Even though all Europe has undergone a well-documented and widespread dynamic of land abandonment (Lasanta et al., 2016; Pellissier et al., 2013), this process may have occurred at different times and with a different intensity across the continent. Thus, land abandonment was probably delayed and slower in the W-Alps compared to the C-Alps, which instead has suffered a faster depopulation of the mountain rural areas due to the huge urban development in the southern urban district of the Greater Milan area and in the Po Valley during the last 50 years (ERSAF 2012). Hinojosa et al. (2016) reported different patterns of land abandonment across mountain areas, depending on the attractive power of urban centres and on the land use regulation of national or regional Parks. In the W-Alps, all bird data were collected in

protected areas. Therefore, a protected area effect may be present, which may have mitigated the land abandonment process. Indeed, in the W-Alps protected areas, forest expansion is probably still occurring, while in the C-Alps this process is now more stationary.

As showed by the C-Alps long-term analysis, even in the W-Alps almost all grassland species lost the lower portion of their altitudinal range, likely as a consequence of the advancement of forest cover (Chamberlain et al., 2012, 2013) and climate warming (Flousek et al., 2015; Reif and Flousek, 2012), or due to the interaction of the two factors (Lenoir et al. 2010; Mantyka-Pringle et al. 2012; Oliver and Morecroft 2014).

In the medium-term comparison, the C-Alps showed unexpected patterns, providing evidence of the downward expansion of two grassland birds, while one species retracted its distribution and moved towards lower altitudes.

Several processes and factors, like changes in population size (Flousek et al., 2015; Lehikoinen et al., 2014), biotic interactions (Melendez and Laiolo, 2014), new habitats availability (Archaux, 2004) or the degree of plasticity (Lenoir et al., 2010), may have acted simultaneously leading to contrasting responses by alpine birds in different areas. Furthermore, species responses might change between areas due to sensitivity to the local environmental (Randin et al. 2009) and climatic variability (Lenoir and Svenning, 2015). Species traits and local-scale processes and factors might explain the results provided by the comparison between the species occurring in both areas, too. Most of the 22 bird species occurring in both study areas showed different or even opposite altitudinal changes, likely because they were affected by environmental and climatic pressures at different spatial and time scales.

4.5 Conclusions

We observed that *all* the investigated mountain bird species have changed at least a part of their altitudinal distribution during the last decades. However, the patterns of change differ between species, both in entity and directionality. This variability can be partially due to processes acting at a local-scale (e.g. habitat transformations or biotic interactions), as suggested by the observed differences in altitudinal ranges between the two investigated geographic areas. However, when grouping species according to homogeneous ecological traits (breeding habitat or migratory strategy), we observed consistent responses. This suggests that the general patterns of change may be shaped mainly by the effect of two processes acting at a wide scale, climate change and forest expansion. Therefore, in order to obtain a more detailed picture on the drivers affecting the entity and directionality of range changes, it is crucial to isolate the effects of these two wide-scale processes.

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Appendix B

Tab. 4.5 Numbers of sampling points per 300-m altitudinal belt for the long-term comparison (t₀: 1982-1986, t₂: 2011-2015) in the central Alps.

C-Alps	600-900	900-1200	1200-1500	1500-1800	1800-2100	2100-2400	2400-2700	Total
1982-1986	215	349	407	388	288	143	60	1850
2011-2015	220	230	143	172	316	68	27	1176
Total	435	579	550	560	604	211	87	3026

Tab. 4.6 Numbers of sampling points per altitudinal belt for the medium-term comparison (t_1 : 2006-2010, t_2 : 2011-2015) in the central and western Alps.

	1150-1400	1400-1600	1600-1800	1800-2000	2000-2200	2200-2400	2400-2700	Total
C-Alps								
2006-2010	132	97	83	188	108	18	10	636
2011-2015	135	106	112	242	113	29	27	764
Total	267	203	195	430	221	47	37	1400
W-Alps								
2006-2010	11	22	42	33	42	34	43	227
2011-2015	14	23	40	33	41	33	40	224
Total	25	45	82	66	83	67	83	451

Tab. 4.7 Changes in woodland cover between altitudinal belts for the central Alps area from 600 m to 2700 m during two time periods (1980-2012, 1999-2012). We considered as woodland the combination of three different land cover classes (coniferous, mixed and deciduous forests). Sources: digital cartography, Land Use Map 1980 (ERSAF 2011), DUSAF 1.1 (ERSAF, 2000) and DUSAF 4.0 (ERSAF, 2014).

Altitudinal belts		600-800	800-1000	1000-1200	1200-1400	1400-1600	1600-1800	1800-2000	2000-2200	2200-2700
Woodland	(%)	5.9	7.1	8.9	6.2	4.2	2.3	1.7	2.5	0
increase 1980-2012	(ha)	5704	6744	7576	4584	2676	1456	1148	1528	16
Woodland	(%)	0.5	0.8	1.0	0.6	0.4	-0.1	0	-0.1	0
1999-2012	(ha)	492	776	828	404	280	-84	-20	-56	-16

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PART II LANDSCAPE ECOLOGY

Part II

Landscape ecology

After the Part I, where I analysed the distribution of species in space and time, in the next step I investigated the role of environment in determining the spatial distribution of species.

Many studies highlighted the importance of adopting a multi-scale approach to perform a detailed analysis of species-environment relationship (Bani et al., 2006; Dover and Settele, 2009; Olivier et al., 2016). Indeed, the relationship between spatial pattern and ecological processes is not restricted to a particular scale, but ecological processes vary in their effects or importance at different scales (Risser et al., 1984).

The analysis at a landscape scale has an important role in understanding the processes and drivers involved in very dynamic environments due to human impact (Kaiser et al., 2016; Lizée et al., 2012). The landscape is defined by Forman (1995) as a mix of local ecosystem or land use type repeated over the land. While Wu and Hobbs (2007) considered landscapes as spatially heterogeneous geographic areas characterized by diverse interacting patches or ecosystems, ranging from relatively natural systems (e.g. forests, grasslands) to human-dominated environments (e.g. croplands and urban areas).

"Landscape" is a central concept in landscape ecology, the science of studying and improving relationships between ecological processes in the environment and particular ecosystems. Moreover, it is a highly interdisciplinary science focuses explicitly upon spatial pattern and its heterogeneity (i.e. multiscaled structure composed of patchiness and gradients in space and time; Wu, 2013, 2006).

One of the key topic in landscape ecology is the study of the causes, processes, and consequences of land cover change, mainly due to human activities, that determine the structure, functioning, and dynamics of most landscapes (Wu and Hobbs, 2002).

I developed this topic in a study that used as indicator group the butterflies (Rhopalocera), which are one of the most studied taxa, due to their sensitivity to environmental changes and their relative easiness of census. Moreover, butterflies are an important flagship taxon for invertebrate conservation and in general for biodiversity (New, 1995; Thomas, 2005; van Swaay et al., 2006).

In Chapter 5, I present the first part of the study aimed to identify the land cover drivers of butterflies richness and abundance in an area characterized by a high human impact, with wide urban areas, infrastructure and intensive agriculture.

The second part of the study, which focused on habitat and management drivers, is described in Chapter 6 (Part III).

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Chapter 5

Land cover drivers at local and landscape scale of butterfly richness and abundance in a human-dominated area.

Abstract

Butterflies (Rhopalocera) declined over the last decades, mainly as a consequence of agricultural intensification and land-use changes. Therefore, it is crucial to quantify the specific effects of anthropogenic disturbances on butterfly communities in order to counteract this negative trend. This research was performed in northern Italy, in a human-dominated area of about 170 km². Overall, from April to September 2014 and 2015, we surveyed butterflies in 494 50-m sections, grouped into 44 line transects. As the effects of environmental variables on butterfly richness and abundance are strictly linked to species-specific ecological traits, we performed the analyses at functional group level, in order to account for differences in the degree of mobility and habitat preferences. By means of GAMMs, we analysed the effects of different types of land cover (both at the local and at the landscape scale) on butterfly richness and abundance in each 50-m section. Transect was included as a random effect.

Land cover models showed that butterfly communities are positively affected by meadows at the local scale, although this effect decreases when the artificial surface increases at the landscape scale. Conversely, arable lands at the local scale had a positive effect when associated with a high level of urbanization. This pattern was probably due to an increase of landscape heterogeneity and an increased presence of semi-natural habitats in peri-urban areas, compared to intensive farmlands.

5.1 Introduction

Human activities are by far the most important causes of landscape changes. However, not all human-induced changes have had the same effect on habitats and wild animals. Natural environments have been progressively reduced and fragmented leading to agriculture landscapes, characterized by mosaics of human and natural elements. In these landscapes, some taxa, such as many invertebrates, have taken advantage of the diversification generated by human exploitation of natural resources (Bignal and McCracken, 2000; Loos et al., 2014). However, the pressure whereby humans have modified the original landscapes cannot be considered constant. In Europe, during the last century, and especially in the last decades, the anthropogenic impact has drastically exacerbated. Particularly, in lowland areas the urban sprawl and the intensification of agricultural practices have generated a new kind of landscape, increasingly poor in natural elements, and dominated by the human footprint (Stoate et al., 2009, 2001). In these contexts, built-up areas and infrastructures prevail on agroecosystems, which, in turn, lose the natural and semi-natural elements that act as a refuge for fauna (Bubová et al., 2015; Öckinger et al., 2009; Olivier et al., 2016; Wood and Pullin, 2002). Therefore, even those taxa that formerly benefitted from human modifications of the original forest landscapes are now under threat (Van Dyck et al., 2009).

The degree of suitability for fauna of human-dominated landscapes depends on the amount of the residual or semi-natural habitats, such as urban green spaces in built-up areas or meadows and hedgerows in agricultural contexts. However, the suitability of these refuges for animal species is strongly affected by local and landscape features. At the local scale, inadequate management practices of meadows (e.g. frequent mowing and trampling) often lead to the loss of the role of refuge of this potentially suitable habitat for several species (Bubová et al., 2015). Even the use of insecticides and herbicides can be detrimental as they affect not only the target species within the crop field, but also the other species living in herbaceous margins (Davis et al., 1991; Longley and Sotherton, 1997). At the landscape scale, the composition and the spatial configuration of the elements of the matrix (i.e. areas between habitat patches) could play a critical role in determining the isolation of habitat patches (Dover and Settele, 2009; Öckinger et al., 2012; Sweaney et al., 2014). Thus, even in the case of good habitat management practices, too isolated habitat refuges can remain vacant of species, particularly of those characterized by a low dispersal capability (Schtickzelle et al., 2006).

Urban sprawl and agricultural intensification have deeply shaped most of the European lowlands, and, among them, the Po Plain is not an exception. The Po Plain represents the widest lowland area in Italy, and one of the most populated region in Europe, where urban and intensive agricultural areas largely prevail over natural residual habitats.

In many European lowlands, butterflies are currently one of the fastest declining invertebrate taxa (Bonelli et al., 2011; Van Dyck et al., 2009; Van Swaay et al., 2013). During the last 20 years, populations of grassland butterflies have declined by almost 50% in Europe, and one of the main drivers was the intensification of agricultural practices in floodplains (Van Swaay et al., 2013). Butterflies are good indicators of the effect of human impact on ecosystems, because of their complex ecology and their ability to quickly react to environmental changes (Thomas, 2005; Van Swaay et al., 2013). Moreover, in order to counteract the poor conservation status of this taxon, it is crucial to provide qualitative and quantitative knowledge about the effects that anthropogenic disturbances and management practices have both on butterfly species, and on their habitat. Many studies showed how butterflies are linked to specific local conditions, such as nectar resources and host plants (Clausen et al., 2001; Curtis et al., 2015; Dover et al., 2000; Pywell et al., 2004; Sparks and Parish, 1995). However, the composition of butterfly communities can be also strongly affected by other variables characterizing the landscape, such as the amount and the degree of fragmentation of residual habitats (Bergerot et al., 2011; Dover and Settele, 2009; Öckinger et al., 2012, 2009).

To obtain a comprehensive knowledge of the role of each environmental variable in shaping butterfly communities, either at a local or at a landscape scale, it is crucial to adopt a multiscale approach (Olivier et al., 2016). Moreover, the effects of environmental variables on butterflies are strictly linked to specific ecological traits (Curtis et al., 2015; Kuussaari et al., 2007; Melero et al., 2016; Olivier et al., 2016). Therefore, community-level studies should be performed considering homogeneous functional groups based on species-specific ecological traits (e.g. Dondina et al., 2016a).

In this research, we analysed the overall butterfly richness and abundance, and those of functional groups, in a human-dominated landscape located in the Po Plain, with the purpose of identifying their local and landscape drivers. Specifically, we investigated the effects of local land covers in different landscape contexts.

5.2 Material and methods

5.2.1 Study Area

Our research was performed in a human-dominated area (about 170 km²), North of Milan (Lombardy Region; 45°37'N 9°19'E – northern Italy; Fig. 5.1), located between 118 and 305 m altitude.

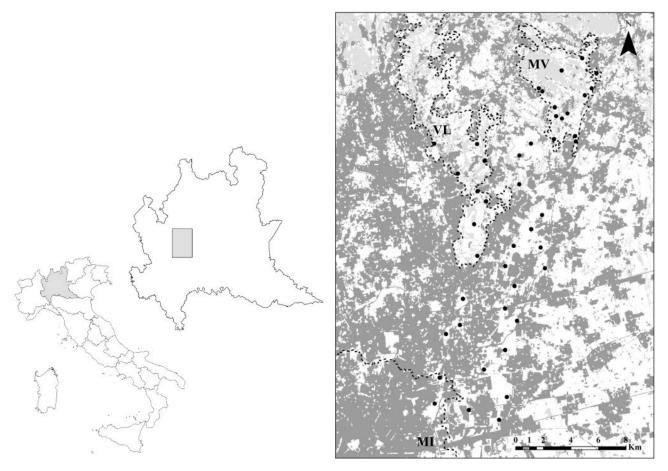


Fig. 5.1 Study area. From left to right: the location of the study area in northern Italy and in the Lombardy region (45°37'N 9°19'E). Black dots: location of the survey transects. Background: land cover map (dark grey: artificial surfaces; light grey: forest areas). Black dashed lines: boundaries of the municipality of Milan (MI) and of the protected areas (VL: Valle del Lambro Regional Park; MV: Montevecchia e Valle del Curone Regional Park).

Data collection was carried out during a two-year sampling period. In 2014, we surveyed a sample area extending from the North-East outskirts of Milan, northwards to the nearest moraine hills. The southern part of this sample area is characterized by infrastructures and buildings, with urban green spaces and few residual croplands. The central and northern part is partially included in the Valle del Lambro Regional Park, characterized by the presence of the Lambro River, a great amount of broadleaved forests, and an anthropogenic matrix with small urban areas and croplands. Permanent

meadows, maize and winter cereals are the main crops, while soybean, rapeseed and alfalfa represent a smaller portion of the cultivable surface. In the southern part of the Valle del Lambro Regional Park is the Monza Park, a large walled park extending over an area of 688 hectares, characterized by a wide extension of meadows and deciduous forests.

In 2015, data were collected in the neighbouring Montevecchia e Valle del Curone Regional Park, located north-east of the previous sample area. The butterfly survey was carried out in the southern part of the protected area, which is characterized by small crop fields with maize, winter cereals, soybean and permanent meadows, and by a wide network of streams flowing from North to South, bordered by broadleaved riparian vegetation.

5.2.2 Butterfly data

Butterfly data were collected using the line transects method, following the Pollard and Yates (1993) protocol. Transects were walked in both directions, but on the way back we considered new species only. We counted and identified each butterfly observed within 2.5 m of each side of the transect, and 5 m in front of the observer. Each transect was divided in 50-m sections, which represented the sampling units to which fauna and environmental data were associated. The length of 50-m can be considered adequate for restraining the environmental variability within each sampling unit, and finding a more accurate relationship between fauna data and environmental variables.

We used a butterfly net to catch individuals that required a closer observation for species identification, and we released them in the trapping site.

In both sample areas, line transects were randomly selected in order to collect a representative sample of the butterfly communities inhabiting the study area. All habitats were covered, from woodland edges to open croplands and built-up zones, and only areas characterized by a continuous urban or forest cover were excluded.

Overall, from April to September 2014 and 2015, we surveyed 494 50-m sections, grouped into 44 line transects, the length of which varied between 8 and 26 sections.

In the south-western sample area, we collected data on 300 50-m sections, belonging to 30 transects that were surveyed once a month, while in the north-eastern sample area we considered 194 50-m sections belonging to 14 transects, which were surveyed twice a month. A total of 6 and 12 survey rounds were performed in the south-western and north-eastern sample area, respectively. The choice to perform a once-a-month survey in the south-western sample area was due to the poor resource availability in 2014.

5.2.3 Environmental data

We created a map with a 20 m resolution combining two 1:10,000 digital maps (SIARL [Agricultural land use digital map of Lombardy; ERSAF, 2015] and DUSAF 4.0 [Classification of Agricultural and Forest Lands of Lombardy; ERSAF, 2014]). In particular, we used the SIARL map as base reference, as this map shows a more detailed crop categorization. Subsequently, we overlaid the more detailed layers of the DUSAF 4.0 map representing forest areas and artificial surfaces on the reference map.

We obtained land cover variables from digital maps at the two scales, measuring land-use fractional cover in a 50-m (local scale) and 500-m (landscape scale) buffer centred on the middle point of each section. We considered four land cover categories: artificial surfaces, arable lands, meadows and forest areas. We considered as meadows both the permanent meadows in croplands, and the meadows inside urban green areas, because the difference between these two land cover categories is not always clear in our study area.

The creation of the land cover map and the calculation of all the land cover variables were performed using ARCGIS 10.1 (ESRI Inc., Redland, CA).

5.2.4 Statistical analyses

We performed analyses considering all butterfly species together and clustering them according to functional groups, based on ecological traits (see Appendix C, Tab. 5.2), such as habitat preferences (open herbaceous, subnemoral, nemoral) and mobility (less mobility, score [1-2]; high mobility, score [3 to 5]) according to Balletto and Kudrna (1985) revised by Balletto & Bonelli (personal communication).

Within each sampling unit (i.e. each 50-m section), butterflies belonging to the genus *Pieris*, but not identified at a species level, were considered as a single taxon in the definition of species richness. Conversely, if other *Pieris* were recognized at a species level, those classified at the genus level only were disregarded. In addition, as the genus *Pieris* includes open herbaceous and subnemoral species, the individuals of this genus not identified at a species level were considered in the abundance of both functional groups.

For each sampling unit, we pooled data collected in every survey round performed from April to September in both sample areas. For the butterfly abundance, we considered the maximum value recorded among all survey rounds.

We performed Generalized Additive Mixed Models (GAMMs; Wood, 2006) to assess the effects of land cover, using a Poisson or Negative binomial distribution assessed *a posteriori* based on the models' AICs.

First, we checked for the collinearity of the explanatory variables (maximum threshold r = 0.7; Dormann et al., 2013).

Then, we fitted models including a space smooth (TPRS) of East and North coordinates of the middle point of each section, setting 15 as the upper limit for the EDF (Wood, 2006), and we included transects as a random effect to deal with the absence of independence among sampling units due to spatial auto-correlation. We used *a posteriori* Moran's I test in order to check for the possible presence of residual spatial correlation (Gittleman and Kot, 1990).

Within the models, we used the land cover variables as parametric components and we included the logarithm of the number of survey rounds as offset term to account for differences in sampling effort (Kotze et al., 2012).

We performed all statistical analyses in R (R Core Team, 2015), using the packages mgcv, ape and MuMIn.

5.2.4.1 Land cover models

We performed land cover models to investigate the effects on butterfly richness and abundance of three local land covers considering the potential habitat for butterflies (arable lands, meadows and forests, measured in a 50-m radius) within different landscape contexts (urban, arable lands, meadows and forests, measured in a 500-m radius). We evaluated land cover effects on richness and abundance of species and functional habitat groups. Particularly, we tested the local effects of arable lands and meadows on abundance and richness of open herbaceous species, the local effects of all the local land covers on subnemoral species, and the local effects of forest cover only on nemoral species. Finally, we tested the effect of all local land covers on the overall species richness and abundance.

The structure of the land cover models was:

$$E[Y_s] = \exp(\propto + f(east_s, north_s) + (vcov50_s * vcov500_s) + 1 \mid transect + offset(ln(nsur_s))$$

where $E[Y_s]$ is the expected butterfly richness or abundance within each section s; nsur is the number of survey rounds; vcov50 is the land cover variable within the 50-m buffer; and vcov500 is the land cover variable within the 500-m buffer. The spatial location of sections is given by eastings (east) and northings (north), while transect is the random effect.

When two continuous variables and their interaction are considered in a model, the main effect of each variable corresponds to the value that we would obtain if the other variable is equal to zero.

As we were interested in evaluating the effects of local land cover variables for different amount of landscape land cover, we centred all the latter variables using three different values, i.e. the 10th, 50th and 90th percentile of the distribution of their observed values (see Tab. 5.3 for centred values used). This way, we shifted the distributions of the values of the landscape land cover variables so that the zero of the new distributions corresponds to the 10th, 50th and 90th percentile of the original distributions. Thus, we created three different datasets called "low", "median" and "high" to evaluate the influence of low, median and high landscape land cover on the effect of the local variables, respectively. The variables at the local scale were only centred using the 50th percentile.

As a first step, we performed 8 sets of models using the median-datasets. The sets of models correspond to the local land cover variables related to the four landscape variables calculated for the entire set of species (3 local land cover variables), open herbaceous species (2 local land cover variables), subnemoral species (3 local land cover variables) and nemoral species (1 local land cover variable). These sets of models were performed for both richness (4 sets of models) and abundance (4 sets of models) of every group of species considered, making a total of 8 sets. Subsequently, we ordered the models pertaining to the same set according to their AIC value corrected for small samples (AICc). For each set, we defined a top model set with a cut-off of 2 AICc (Grueber et al., 2011). As a second step, we re-fitted all the models pertaining to the 8 top model sets, using the low and high-datasets.

5.3 Results

Overall, during 64 field surveys, we detected 8304 individuals pertaining to 51 species (see Appendix C, Tab. 5.2). Most common species belonged to the genus *Pieris* (25.6%, with a dominance of *Pieris napi* and *Pieris rapae*), *Maniola jurtina* (13.6%) and *Polyommatus icarus* (12.8%).

Tab. 5.1 List of most abundant species with their corresponding ecological traits according to Balletto and Kudrna (1985) revised by Balletto and Bonelli (personal communication); O (open herbaceous), S (subnemoral), N (nemoral); L (less mobile, 1-2 scores), H: (high mobility, 3-5 scores). For the whole set of surveyed species see Tab. 5.2 in Appendix C.

Species/Group species	Abundance	Frequency (%)	Habitat	Mobility
Pieris spp.*	2129	25.6	S/O	Н
Maniola jurtina	1130	13.6	S	L
Polyommatus icarus	1066	12.8	S	Н
Coenonympha pamphilus	701	8.4	O	L
Ochlodes sylvanus	613	7.4	S	L
Cupido argiades	341	4.1	S	L
Pararge aegeria	338	4.1	N	L
Celastrina argiolus	247	3.0	N	L
Colias crocea	193	2.3	S	Н
Lycaena phlaeas	190	2.3	S	Н

^{*}The most common species in *Pieris* spp. group are *P. napi* and *P. rapae*.

5.3.1 Land cover variables

In most of the models, the effect of local scale variables on richness and abundance of the different functional habitat groups, changed according to the values used for centering the landscape scale variables (Appendix C, Tab. 5.3).

As regards open herbaceous species, the effect of the amount of meadows at the local scale on species abundance was positive, with low and median value of meadows amount at the landscape scale, but in a landscape dominated by meadows this effect disappears (Fig. 5.2a). Considering artificial surfaces as landscape variables, we found a positive effect of meadows on richness of open herbaceous species only when associated with a low value of urban surfaces (Fig. 5.2b). Conversely, the presence of meadows showed a growing positive effect on richness with the increase of forest cover at the landscape scale (Fig. 5.2c).

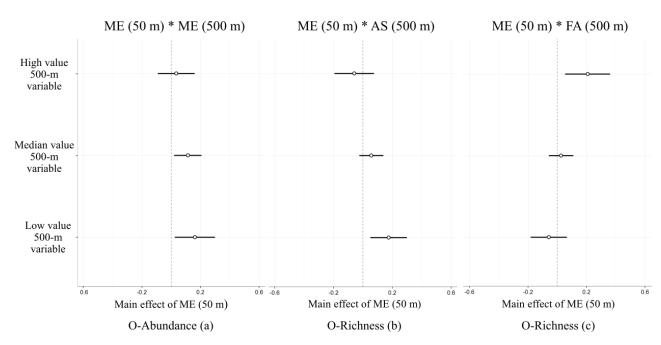


Fig. 5.2 Results of the land cover models containing an interaction between a local scale variable (50-m buffer) and a landscape scale variable (500-m buffer). The main effects of the 50-m variables are shown for each of the three models with a different centred value (i.e. low-10th, median-50th, high-90th percent coverage) of the 500-m variables. Functional groups: O (open herbaceous). Land cover categories: AS (artificial surfaces), ME (meadows), FA (forest areas). See Table S3 for the complete summary of the land cover models.

Focusing on the subnemoral species group, the results showed similar positive effects of meadows on richness and abundance with medium and high values of arable land at the landscape scale (see Fig. 5.3a for the effect on species richness).

Moreover, the same pattern was obtained considering the croplands at the local scale, which had similar positive effects on overall and subnemoral species richness and abundance when associated with a high value of artificial surfaces (see Fig. 5.3b for the effect on subnemoral species abundance). Conversely, in landscapes mainly characterized by arable lands, the richness of overall and subnemoral species was found to be negatively affected by the presence of arable lands at the local scale (see Fig. 5.3c for the effect on subnemoral species richness).

Nemoral species were manly affected by habitat at the local scale, as the effect of forest cover within a 50-m radius was consistent in landscape contexts with a different woodland cover.

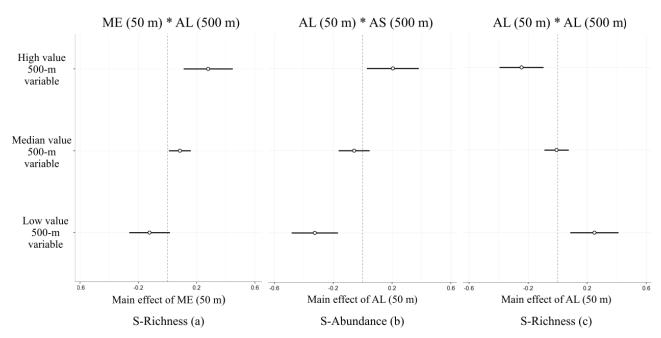


Fig. 5.3 Results of the land cover models containing an interaction between a local scale variable (50-m buffer) and a landscape scale variable (500-m buffer). The main effects of the 50-m variables are shown for each of the three models with a different centred value (i.e. low-10th, median-50th, high-90th percent coverage) of the 500-m variables. Functional group: S (subnemoral). Land cover categories: AS (artificial surfaces), AL (arable lands), ME (meadows). See Table S3 for the complete summary of the land cover models.

5.4 Discussion

Considering the high level of anthropization in the investigated areas, we found a quite high butterfly richness. This result highlights the important role of semi-natural areas in maintaining biodiversity in a human-dominated landscape. However, habitat management and land cover play a crucial role in affecting the habitat suitability for butterflies.

5.4.1 Land cover

Exploring the landscape context is fundamental because it can influence the distribution of species over large areas, affecting the suitability of the local habitat and the effectiveness of management practices undertaken for butterfly conservation (Dover and Settele, 2009). Indeed, different studies showed that both habitat and landscape variables have a significant impact on butterfly assemblages (Öckinger and Smith, 2006; Olivier et al., 2016; Schneider and Fry, 2001).

For open herbaceous species, we found a positive effect of meadows on species abundance, although this effect disappeared when a high cover of meadows was present at the landscape scale (38%; i.e. the highest value used to centre this variable). This pattern is in contrast with the results of some studies, which found a positive effect of the proportion of overall grasslands area on butterfly

communities (Botham et al., 2015; Loos et al., 2014; Öckinger and Smith, 2006). However, this apparent contradiction can be explained considering the characteristics of our study area. The most extended meadows are located within urban green areas, where urbanization and management practices can reduce the suitability of these areas for butterflies.

The urban sprawl causes a reduction of semi-natural habitats with a consequent decrease of nectar and host plants availability, and many studies showed that species richness and abundance are generally low in urban contexts (Di Mauro et al., 2007; Fontaine et al., 2016; Lizée et al., 2012; Öckinger et al., 2009; Olivier et al., 2016). In our study, we found a positive effect of meadows on open herbaceous species richness only in landscape contexts characterized by low covers of urban surfaces (13%). Conversely, with a small increase of urban coverage (25%), the significant effect of meadows disappeared. The negative effect of urbanization may also be exacerbated by the presence of intensive farming, in the surrounding landscape, which is unlikely to be a source area for butterflies (Öckinger et al., 2009; Snep et al., 2006).

Similarly to Olivier et al. (2016), we found that urbanization negatively affects open herbaceous species, usually characterized by a lower mobility and a high level of specialization, although in our functional group we had a similar number of less mobile (e.g. *Coenonympha pamphilus*) and highly mobile (e.g. *Pieris rapae*) species. This pattern was probably due to the presence of an impoverished fauna, with a low proportion of specialized species that are mainly present in less urbanized areas (Öckinger et al., 2009).

Our results also showed a positive effect of meadows on open herbaceous species richness when the landscape is characterized by a high cover of woodland, which in our area corresponds to 36%. Other studies highlighted that the suitability of meadows is affected by the presence of woodlands at a landscape level. Indeed, woodlands enhance species richness by increasing the amount of shelter and the overall landscape heterogeneity (Marini et al., 2009; Perović et al., 2015; Villemey et al., 2015). Furthermore, woodland patches can provide additional microhabitats, which offer complementary resources (Tscharntke et al., 2012) and supplementary refuges, especially during management practices, such as mowing (Marini et al., 2009).

We found that meadows have a growing positive effect on the richness and abundance of subnemoral species with increasing coverage of agricultural areas at the landscape scale. This relationship could be due to the reduction of urbanization and the increase of semi-natural habitats (e.g. hedgerows, herbaceous margins) in agricultural areas. These habitats are surrogates of suitable habitats for many subnemoral species, and could reduce the possible isolation of grassland patches in human-dominated areas (Lizée et al., 2012).

Focusing on the effects of arable lands at the local scale, we found a significant influence of landscape context on the suitability of croplands for butterfly communities.

Urbanization selectively affected butterfly assemblages, favouring generalist species (Bergerot et al., 2011; Deguines et al., 2016), which are more prone to use temporary resources and to face the isolation of habitat patches, thanks to their greater mobility. In our analysis, the group of subnemoral species was positively affected by the increase of artificial surfaces surrounding local arable lands, since it contains many generalist species, such as Pieris napi. We hypothesized that the great heterogeneity characterizing urban landscapes (Hardy and Dennis, 1999), also due to the high accessibility of potential refuges (e.g. gardens; Fontaine et al., 2016), may enhance habitat availability for already poor faunal communities. Moreover, in our study area, farmlands embedded into urban areas are usually not managed with intensive practices, because they are residual areas of low economic interest. In addition, Öckinger et al. (2009) found that a mosaic of urban and intensive farmland areas could support relatively rich communities, compared to more homogeneous farmlanddominated areas. This is confirmed by our results, which showed that crops within landscapes dominated by intensive farmlands (54% of arable lands) were particularly poor in butterflies. Conversely, when farmlands strongly decreased at the landscape level (16%), the richness of subnemoral species increased. These conditions may be related to the lack of source populations in intensive croplands (Öckinger et al., 2009), while more extensive and heterogeneous farmland landscapes, characterized by the presence of semi-natural habitats (e.g. hedgerows, field margins), could host more species and individuals (Dover and Sparks, 2000; Loos et al., 2014).

Unlike other functional groups, nemoral species seemed to be less affected by landscape context compared to the amount of woodland at the local scale. The positive effect of the local scale coverage of woodlands, which represent the ideal habitat for nemoral species, was indeed similar at different levels of woodland coverage at the landscape scale.

This pattern can be linked to the presence of *Pararge aegeria* in the nemoral species group, which has a high level of ecological plasticity (Merckx and Van Dyck, 2006). Indeed, besides having a woodland ecotype, *P. aegeria also* has an agricultural ecotype inhabiting hedgerows along croplands where adequate levels of shelter are available (Kaiser et al., 2016; Merckx et al., 2003).

5.5 Conclusion

The use of a multi-scale approach allowed us to highlight the most important land cover drivers shaping butterfly communities in a human-dominated landscape.

Our results confirmed the effect of landscape context on local variables. The distribution of functional groups within the study area varies according to local land covers (i.e. meadows, arable lands), although the suitability for butterflies is also affected by the degree of urbanization at the landscape level. Urban areas generally have low levels of biodiversity, but if surrounded by intensive farmland, they may play a more complex role, which is not always negative. Overall, a higher level of environmental heterogeneity can favour biodiversity in human-dominated areas. However, butterfly communities inhabiting such context still remain poor compared to those of low-intensity agricultural landscapes (e.g. eastern Europe).

Further studies may analyse in more detail the effect of urbanization on butterfly assemblages comparing along a gradient communities present at different levels of urbanization and identifying indicator species applying the IndVal method (Dufrêne and Legendre, 1997). Another important issue in a human-dominate landscape is the ecological connectivity that may be analysed applying the circuit theory to the study of the landscape (Bani et al., 2015), using the CIRCUITSCAPE software (Shah and McRae, 2008).

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Appendix C

Tab. 5.2 List of surveyed species with their corresponding ecological traits according to Balletto & Kudrna (1985) revised by Balletto & Bonelli (personal communication); Hab (habitat), Mob (mobility); O (open herbaceous), S (subnemoral), N (nemoral); L (less mobile, 1-2 scores), H (high mobile, 3-5 scores). Naming of butterfly species according to Balletto et al. (2014).

Species	Abundance	Hab	Mob	Species	Abundance	Hab	Mob
Maniola jurtina	1130	S	L	Cacyreus marshalli	26	S	L
Polyommatus icarus	1066	S	Н	Gonepteryx rhamni	26	S	L
Pieris spp.*	1059	S/O	Н	Aricia agestis	22	S	L
Pieris napi	740	S	Н	Carcharodus alceae	22	O	L
Coenonympha pamphilus	701	O	L	Coenonympha arcania	21	S	L
Ochlodes sylvanus	613	S	L	Papilio machaon	16	S	Н
Cupido argiades	341	S	L	Aglais urticae	14	O	H
Pararge aegeria	338	N	L	Satyrium w-album	12	S	L
Pieris rapae	312	O	Н	Pieris mannii	11	S	L
Celastrina argiolus	247	N	L	Pyrgus armoricanus	11	S	L
Colias crocea	193	S	Н	Apatura ilia	9	N	Н
Lycaena phlaeas	190	S	Н	Erynnis tages	9	S	L
Melitaea athalia	155	S	L	Melanargia galatea	9	S	L
Lasiommata megera	123	O	L	Pieris brassicae	7	O	Н
Melitaea phoebe	121	S	L	Favonious quercus	5	N	L
Issoria lathonia	115	O	Н	Hamearis lucina	4	S	L
Argynnis paphia	95	N	Н	Colias alfacariesis	2	O	Н
Leptidea sinapis	89	S	L	Cupido alcetas	2	N	L
Polygonia c-album	83	S	Н	Nymphalis polychloros	2	S	Н
Pyrgus malvoides	71	S	L	Lycaeides argyrognomon	2	O	L
Vanessa atalanta	66	S	Н	Glaucopsyche alexis	1	S	L
Iphiclides podalirius	63	S	Н	Lampides boeticus	1	S	Н
Vanessa cardui	62	O	Н	Libythea celtis	1	S	L
Inachis io	35	S	Н	Minois dryas	1	S	L
Anthocharis cardamines	29	S	L	Pyronia tithonus	1	S	L
Melitaea didyma	29	O	L	Thymelicus sylvestris	1	S	L

^{*}Butterflies belonging to the genus *Pieris*, but not identified at the species level.

Table 5.3 Summary results of the land cover models (within a cut-off of 2 AICc) containing an interaction between a local scale variable (50-m buffer) and a landscape scale variable (500-m buffer). The main effects of the 50-m variables are shown for each of the three models with a different centred value (i.e. low- 10^{th} , median- 50^{th} , high- 90^{th} percent coverage) of the 500-m variables. R_{adj} ²: adjusted R-squared of the model. Dependent variable: ric (richness), abu (abundance). Functional groups: O (open herbaceous), S (subnemoral), N (nemoral), - (overall species). Land cover categories: AS (artificial surfaces), AL (arable lands), ME (meadows), FA (forest areas).

	E 4' 1				50-m v	500-m variable				
	Functional groups	R_{adj}^{2}	50*500	Land cover category	Main effect	SE	Confi interva	dence al 95%	Centred value	Land cover category
				8 1	-0.058	0.064	-0.182	0.067	2.55	
ric	O	0.289	ME*FA	ME	0.026	0.043	-0.058	0.110	11.77	FA
					0.208	0.078	0.054	0.362	36.41	
					0.175	0.063	0.051	0.299	12.94	
ric	O	0.291	ME*AS	ME	0.057	0.042	-0.025	0.139	25.34	AS
					-0.059	0.069	-0.193	0.076	43.91	
					0.162	0.070	0.024	0.299	12.40	
abu	O	0.317	ME*ME	ME	0.114	0.048	0.020	0.207	19.74	ME
					0.035	0.064	-0.091	0.160	38.42	
					0.114	0.072	-0.027	0.254	2.55	
abu	O	0.319	AL*FA	AL	0.037	0.050	-0.061	0.134	11.77	FA
					-0.131	0.091	-0.309	0.047	36.41	
					0.249	0.083	0.086	0.412	16.29	
ric	S	0.619	AL*AL	AL	-0.007	0.042	-0.089	0.076	31.51	AL
					-0.244	0.076	-0.393	-0.095	54.47	
					-0.126	0.055	-0.235	-0.018	12.94	
ric	S	0.623	AL*AS	AL	0.019	0.038	-0.056	0.095	25.34	AS
					0.163	0.070	0.025	0.300	43.91	
					-0.096	0.063	-0.220	0.028	12.94	
ric	S	0.622	FA*AS	FA	-0.107	0.047	-0.199	-0.015	25.34	AS
					-0.118	0.087	-0.289	0.053	43.91	
					-0.123	0.071	-0.262	0.017	16.29	_
ric	S	0.613	ME*AL	ME	0.086	0.038	0.010	0.161	31.51	AL
					0.279	0.086	0.111	0.448	54.47	
					-0.325	0.081	-0.483	-0.167	12.94	
abu	S	0.444	AL*AS	AL	-0.058	0.054	-0.163	0.048	25.34	AS
					0.206	0.090	0.029	0.382	43.91	
					-0.084	0.087	-0.255	0.087	16.29	
abu	S	0.425	ME*AL	ME	0.183	0.051	0.084	0.283	31.51	AL
					0.432	0.108	0.221	0.643	54.47	
					0.346	0.141	0.069	0.624	2.55	
ric	N	0.397	FA*FA	FA	0.321	0.104	0.118	0.524	11.77	FA
					0.267	0.086	0.098	0.437	36.41	
					0.591	0.162	0.274	0.909	2.55	
abu	N	0.475	FA*FA	FA	0.474	0.119	0.240	0.709	11.77	FA
					0.220	0.096	0.032	0.408	36.41	

Tab. 5.3 (cont).

	Functional				50-m v	500-m variable				
	$\frac{\mathbf{runctional}}{\mathbf{groups}}$ $\mathbf{R_{adj}}^2$ 5		50*500	Land cover category	Main effect	SE		dence al 95%	Centred value	Land cover category
					0.183	0.068	0.050	0.317	16.29	
ric	-	0.575	AL*AL	AL	0.019	0.037	-0.053	0.091	31.51	AL
					-0.134	0.058	-0.247	-0.021	54.47	
					-0.129	0.049	-0.226	-0.032	12.94	
ric	-	0.572	AL*AS	AL	0.018	0.033	-0.047	0.084	25.34	AS
					0.163	0.056	0.053	0.274	43.91	
					-0.239	0.060	-0.357	-0.120	12.94	
abu	-	0.454	AL*AS	AL	-0.018	0.041	-0.098	0.062	25.34	AS
					0.199	0.067	0.067	0.331	43.91	

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PART III HABITAT QUALITY

Part III

Habitat quality

After dealing with the study of the species distribution (Part I) and the landscape analysis, through the effect that land cover can have at different scales on butterfly assemblages (Part II), the last part of my research project focused on habitat use and management.

At this point, the question arises on how to get to an effective conservation. One way is to investigate in more detail the species-environment relationship analysing the habitat quality, which includes features such as the availability of food resources and vegetation structure (Clausen et al., 2001; Curtis et al., 2015; Öckinger et al., 2006; Pöyry et al., 2006; Pywell et al., 2004). Furthermore, management practices can positively or negatively affect the habitats quality (Bubová et al., 2015).

The study focused on butterflies using a multiscale approach, from a landscape scale (see Chapter 5) to a local scale (habitat, Chapter 6). Indeed, both landscape composition and habitat quality can affect the species richness and communities composition of butterflies in semi-natural habitats (Öckinger and Smith, 2006).

Therefore, the habitat quality is a key topic to be evaluated in order to understand what are the factors producing the observed decline of Europe butterfly communities (Van Swaay et al., 2013).

The human impact often has the effect of reducing the habitat quality. The negative effect can be related to land-use intensity in farmland as a result of management practices, such as high fertilizer inputs and mowing intensity (Bubová et al., 2015; Wallisdevries et al., 2012), or to urbanization causing habitat destruction, air pollutants input and invasion of alien flora (Bergerot et al., 2011).

In this context, the residual semi-natural habitats in human-dominated areas is crucial, if properly managed, can have an important role in the conservation of biodiversity. In fact, farmland, if managed less intensively, can host high levels of biodiversity (Loos et al., 2014). While, urban areas, in regions dominated by intensive human land use, can host semi-natural habitats with relatively high conservation value (Öckinger et al., 2009).

In Chapter 6, I present the second part of the study on butterflies, focusing on habitat, to identify drivers that can influence butterflies in an area with a high human impact.

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Chapter 6

Habitat and management drivers of butterfly richness and abundance in a human-dominated area.

Abstract

Butterflies (Rhopalocera) declined over the last decades, mainly as a consequence of agricultural intensification and land-use changes. Therefore, it is crucial to quantify the specific effects of anthropogenic disturbances on butterfly communities in order to counteract this negative trend. This research was performed in northern Italy, in a human-dominated area of about 170 km². Overall, from April to September 2014 and 2015, we surveyed butterflies in 494 50-m sections, grouped into 44 line transects. As the effects of environmental variables on butterfly richness and abundance are strictly linked to species-specific ecological traits, we performed the analyses at functional group level, in order to account for differences in the degree of mobility and habitat preferences. By means of GAMMs, we analysed the effects of habitat characteristics, and management actions on butterfly richness and abundance in each 50-m section. Transect was included as a random effect.

Among habitat variables, the abundance of flowers is the most important driver of both species richness and abundance. In addition, the negative effect of the number of meadow cuts, and the positive effect of the width and height of herbaceous margins along crop fields, highlighted the importance to adopt correct management measures for the conservation of this taxon.

6.1 Introduction

In the second part of the study of butterflies (the first part is described in chapter 5), we analysed the overall butterfly richness and abundance, and those of functional groups, in a human-dominated landscape located in the Po Plain, with the purpose of identifying their habitat and management drivers. Specifically, we investigated the effects of: (1) habitat characteristics (i.e. crop type, nectar abundance, shelter availability and hedgerows occurrence); and (2) management practices of seminatural habitats (i.e. meadows, herbaceous margins and hedgerows).

6.2 Material and methods

For a detailed description of the study area and how the butterfly data was collected, see the previous chapter (sections 5.2.1 and 5.2.2, respectively) where the first part of the study was described.

6.2.1 Environmental data

We collected habitat and management variables (see Tab. 6.1 and 6.2, respectively) in the field along each section and in the adjoining areas.

6.2.1.1 Habitat variables

Within a 5-m buffer surrounding each section, we recorded detailed habitat variables during each survey round (Tab. 6.1). We detected the presence/absence of each crop type, meadows (including meadows located both in croplands and inside urban green areas and fallow meadows), herbaceous margins along crop fields and hedgerows. Moreover, we considered as uncultivated areas crop fields temporarily not used for production and small not managed areas.

For each section, we also defined the amount of shelter, i.e. the number of directions by which wind is halted, with a score (0-8) based on the eight principal compass points, following the method described by Dover (1996). We recorded flower abundance, considering all potential nectar plants belonging to 39 families (Appendix D, Tab. 6.3), along each section within the 5-m buffer. We defined a scale to classify the quantitative cover estimates: 0.25 (occasional <5%), 1 (frequent 5-25%), 2 (abundant 25-50%), 3 (dominant > 50%) using a modified version of the DAFOR scale (Hill, 2005). We identified species/groups of species in the field or subsequently by photographs taken during the survey. We considered only open flowers and we did not measure abundance of flowers from grasses (*Poaceae*; Halbritter et al., 2015). Abundance scores were visually evaluated by the same person (ML) to avoid differences in the estimates. Finally, we defined a nectar index equal to

the sum of the flower abundance scores of all nectar species considered in each section. From the analyses, we excluded flowers with an overall abundance less than one, over the study period.

As we chose to focus on the community-level analysis, we did not consider the abundance of the host plants among the selected covariates, although this driver has been recognized to have a strong positive effect on the abundance of some species (Curtis et al., 2015).

Tab. 6.1 Description of habitat variables and their scores collected in each section of transects.

Variable description	name	scores
Meadows in cropland and inside urban green areas	meadows	1 = present; $0 = $ absent
Hedgerows along crop fields	hedgerow	1 = present; $0 = $ absent
Herbaceous margins along crop fields	herb_margin	1 = present; 0 = absent
Amount of shelter estimated with method described by Dover (1996) and subsequently grouped	shelter	A: 0-1; B: 2-3; C: 4-5; D: 6-7-8
Cultivations of <i>Medicago sativa</i>	alfalfa	1 = present; 0 = absent
Maize crops	maize	1 = present; 0 = absent
Wheat and barley crops	w-cereals	1 = present; 0 = absent
Soybean crops	soybean	1 = present; 0 = absent
Uncultivated arable lands	uncult	1 = present; 0 = absent
Abundance of flowers as sum of the abundance- score based on cover	nectar	0.25 < 5%; 1 < 5-25%; 2 < 25-50%; 3 > 50%

6.2.1.2 Management variables

As management variables, we considered the characteristics of three semi-natural habitats (i.e. meadows, hedgerows and herbaceous margins; Tab. 6.2).

For sections crossing meadows, we recorded the number of cuts during the survey season. For those crossing crop fields with herbaceous margins, we registered three categories of margin width (< 1 m; 1-3 m; > 3 m) and three categories of dicots cover (< 10%; 10-40%; > 40%). In both cases, we recorded the height of the herbaceous layer classifying it in three categories (< 15 cm; 15-50 cm; > 50 cm).

Finally, when sections were associated to hedgerows, we scored their height (< 1 m; 1-2 m; 2-3 m; > 3 m), the occurrence of hedgerow gaps (none; <20% of hedgerow length; 20-40% of hedgerow length; > 40% of hedgerow length) and the abundance of bramble bushes (*Rubus ulmifolius*, *Rubus caesius*) using the same scale used for flower abundance.

Tab. 6.2 Description of management variables and their scores collected in sections with semi-natural habitats (i.e. meadows, herbaceous margins and hedgerows).

Variable description	name	scores	Semi-natural habitat
Number of cuts of meadows	mowing	A: 0-1; B: 2; C > 2	
Average height of herbaceous layer	height_me	1 =< 15 cm; 2 = 15-50 cm; 3 > 50 cm	Meadows
Width of herbaceous margin	width_ma	1 = < 1 m; 2 = 1-3 m; 3 = > 3 m	
Percentage cover of dicotyledons in field margin	perc_dic	1 =< 10%; 2 = 10-40%; 3 => 40%	Herbaceous margins
Average height of herbaceous layer	height_ma	1 = < 15 cm; 2 = 15-50 cm; 3 > 50 cm	
Hedgerow height	height_he	1 =< 1 m; 2 = 1-2 m; 3 = 2-3 m; 4 => 3 m	
Hedgerow gaps described as by Pywell et al. (2004)	gap	1 = none; 2 <= 20% of length; 3 = 20-40% of length; 4 => 40% of length	Hedgerows
Percentage cover of bramble bushes	brambles	0 no brambles; 1 < 5%; 2 < 5-25%; 3 < 25-50%; 4 > 50%	

6.2.4 Statistical analyses

We performed analyses considering all butterfly species together and clustering them according to functional groups, based on ecological traits (see Appendix C, Tab. 5.2), such as habitat preferences (open herbaceous, subnemoral, nemoral) and mobility (less mobility, score [1-2]; high mobility, score [3 to 5]) according to Balletto and Kudrna (1985) revised by Balletto & Bonelli (personal communication).

Within each sampling unit (i.e. each 50-m section), butterflies belonging to the genus *Pieris*, but not identified at a species level, were considered as a single taxon in the definition of species richness. Conversely, if other *Pieris* were recognized at a species level, those classified at the genus level only were disregarded. In addition, as the genus *Pieris* includes open herbaceous and subnemoral species, the individuals of this genus not identified at a species level were considered in the abundance of both functional groups.

For each sampling unit, we pooled data collected in every survey round performed from April to September in both sample areas.

For the butterfly abundance and the nectar index, we considered the maximum value recorded among all survey rounds. For grass height and shelter scores, we calculated the median of the scores registered in each survey round, to obtain a unique value characterizing each section for the whole survey period.

We assorted the median score of shelter in four groups (A: 0-1; B: 2-3; C: 4-5; D: 6-7-8) and the number of meadow cuts in three groups (A: 0-1; B: 2; C: > 2) to obtain larger and more balanced groups among sampling units.

We performed Generalized Additive Mixed Models (GAMMs; Wood, 2006) to assess the effects of habitat and management variables separately, using a Poisson or Negative binomial distribution assessed *a posteriori* based on the models' AICs.

First, we checked for the collinearity of the explanatory variables (maximum threshold r = 0.7; Dormann et al., 2013).

Then, we fitted models including a space smooth (TPRS) of East and North coordinates of the middle point of each section, setting 15 as the upper limit for the EDF (Wood, 2006), and we included transects as a random effect to deal with the absence of independence among sampling units due to spatial auto-correlation. We used *a posteriori* Moran's I test in order to check for the possible presence of residual spatial correlation (Gittleman and Kot, 1990).

Within the models, we used the habitat or management variables as parametric components and we included the logarithm of the number of survey rounds as offset term to account for differences in sampling effort (Kotze et al., 2012).

We performed all statistical analyses in R (R Core Team, 2015), using the packages *mgcv*, *ape* and *MuMIn*.

6.2.4.1 Habitat and management models

We performed 12 habitat models (GAMMs) to investigate the effects of crop type, nectar abundance, hedgerows and shelter on richness and abundance of all species and of all the five functional groups. We excluded herbaceous margins as an independent variable due to its collinearity with the "meadows" variable.

Moreover, we performed management models in order to investigate the effect of management variables in three semi-natural habitats: meadows (number of mowing and grass height); herbaceous margins (margin width, grass height and cover of dicots); hedgerows (hedgerow height, gaps and brambles).

The structure of habitat and management models is:

$$E[Y_S] = \exp\left(\propto + f(east_S, north_S) + \sum_{k=1}^{K} var_{k,S} + 1 \mid transect + offset(\ln(nsur_S)) \right)$$

where $E[Y_s]$ is the expected butterfly richness or abundance within each section s; nsur is the number of survey rounds; var is the value of each k habitat or management variable. The spatial location of sections is given by eastings (east) and northings (north) and transect is the random effect.

Both for habitat and management, we performed an automated model selection using the dredge approach (Barton, 2015), by which we first generated a set of models considering all possible combinations of the variables, always including the random effect, the space smooth and the offset term. Then we performed a model averaging, considering a 2 AIC_C cut-off (Grueber et al., 2011). We used the zero method to calculate the model-averaged parameters focusing on the effect of the covariates on the response variable (Burnham and Anderson, 2002; Nakagawa and Freckleton, 2011). Before performing models, in order to compare the effects of independent variables, we centred the binomial variables (Schielzeth, 2010) and we scaled continuous variables by dividing by two standard deviations (Gelman, 2008). For the categorical covariates, we created dummy variables, and we subsequently centred them (Grueber et al., 2011; Schielzeth, 2010).

6.3 Results

6.3.1 Habitat variables

The habitat models showed consistent results between richness and abundance of species and functional groups (Tab. 6.4).

The nectar index showed a strong positive effect on the overall butterfly richness (b = 0.469, SE = 0.054) and abundance (b = 0.623, SE = 0.083) and on the richness and abundance of the functional groups, except for nemoral species. Other variables with a positive effect were the presence of meadows, hedgerows and alfalfa. We found a positive effect of uncultivated arable land only on overall richness (b = 0.155, SE = 0.078), and a positive effect of soybean on the abundance of less mobile species. However, the latter relationship showed a 95% confidence interval that included zero (b = 0.450, SE = 0.235).

The increase in the degree of shelter promoted greater richness and abundance of nemoral species, while intermediate and high levels of shelter (B-C-D) had a similar positive effect on abundance of highly mobile species (b = 0.399, SE = 0.173, b = 0.608, SE = 0.194, b = 0.436, SE = 0.227, respectively). On the contrary, high degrees of shelter (D) showed a strong negative effect on the richness and abundance of species pertaining to the less mobile group (b = -1.439, SE = 0.437, b = -1.454, SE = 0.347, respectively), on the richness and abundance of open herbaceous species and on subnemoral species richness.

Finally, the presence of winter cereal crops showed a negative effect on overall species richness (b = -0.183, SE = 0.080), highly mobile species richness, subnemoral species richness and nemoral species abundance.

6.3.2 Management variables

Considering only the sections with meadows, the number of cuts per season did not affect butterfly richness. Conversely, an increasing number of cuts (2 and >2) showed a negative effect on the overall abundance (b = -0.282, SE = 0.123, b = -0.523, SE = 0.158, respectively; Fig. 6.1a) and on the abundance of less mobile, highly mobile and subnemoral species (Appendix D, Tab. 6.5).

Considering the herbaceous margins along crop fields, an increase of width showed a positive effect on the overall and subnemoral species richness, as well as a strong effect on abundance of the less mobile species (width > 3 m: b = 0.975, SE = 0.298; Fig. 6.1b).

Moreover, we found a positive effect of an increase of grass height (15-50 cm and > 50 cm) on richness and abundance of species in general, as well as of open herbaceous and subnemoral species

(Fig. 6.1c). A high cover of dicots (10-40 % and > 40 %) in margins showed a general positive effect on butterfly abundance (Fig. 6.1d), and positively affected the richness of nemoral species (b = 0.753, SE = 0.335, b = 0.904, SE = 0.300, respectively; Appendix D, Tab. 6.5).

Hedgerows with a height between 1 m and 2 m showed a positive effect on overall species richness (b = 0.211, SE = 0.077) and of subnemoral species richness. Conversely, higher hedgerows showed a negative effect on overall species abundance (2-3 m: b = -0.333, SE = 0.137, >3 m: b = -0.501, SE = 0.186), as well as on the abundance of most functional groups (less mobile species; Fig. 6.1e). Furthermore, hedgerows with a high cover of bramble bushes (>50%) showed a positive effect on richness, especially for the highly mobile (b = 0.405, SE = 0.193) and subnemoral group (Fig. 6.1f; Appendix D, Tab. 6.5).

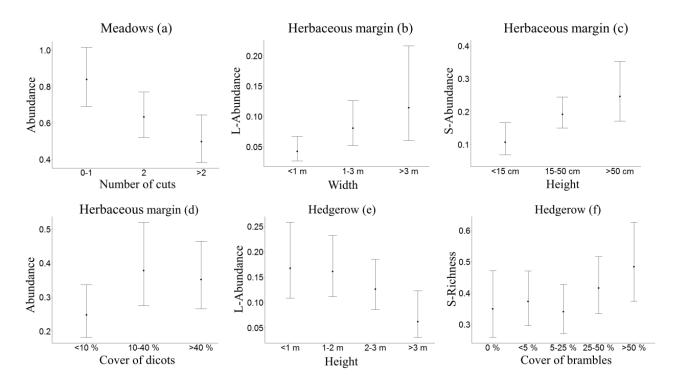


Fig. 6.1 Effect plots for abundance and richness per survey round, for the most important independent variables resulted from management models. Functional groups: L (less mobile), S (subnemoral). See Tab. 6.2 for a description of the independent variables. See Appendix D, Tab. 6.5 for a complete summary of the management models.

6.4 Discussion

6.4.1 Habitat

Our results showed that the abundance of nectar sources was the most important driver of species richness and abundance in our study area, and this relationship was consistent among groups (except for nemoral species). The same positive effect was found by other studies (Clausen et al., 2001; Curtis et al., 2015; Feber et al., 1996; Milberg et al., 2016; Öckinger and Smith, 2006; Pywell et al., 2004) and confirms the need to maintain an adequate source of nectar in urban and intensive farmland areas to sustain a good level of butterfly diversity. This result is in agreement with some studies, which claim that the butterfly decline observed in Europe can be linked to a decrease in flower abundance, due to nitrogen pollution and landscape changes (Van Dyck et al., 2009; Wallisdevries et al., 2012). Conversely, a meta-analysis on 30 butterfly species, focusing on drivers of long-term population trends, found a weak correlation between food availability and adult abundance (Thomas et al., 2011). This apparent contradiction with our results could be explained by the different level of analysis adopted. Furthermore, most of previous studies were performed in northern Europe, under different environmental conditions (i.e. climate, land use, human impact). In dissimilar geographical areas, species may occupy different successional stages (Thomas et al., 1999, 1998), characterized by different amount of flowers (Erhardt, 1985).

Agricultural landscapes are characterized by a wide heterogeneity, due to the presence of different types of crops subjected to different cultural techniques (e.g. amount of water, pesticides, and fertilizers). In addition, further components of heterogeneity are marginal zones (e.g. uncultivated areas, hedgerows and grassy strips), which, when properly managed, are important reservoirs of biodiversity (Ernoult et al., 2013).

In our study area, agricultural landscapes are dominated by maize and our results did not show any significant effect of this crop type. Cornfields cannot be considered a suitable habitat for butterflies, since corn plants do not represent nectar sources for this taxon. Therefore, butterfly communities inhabiting these areas probably depend on the mosaic of marginal habitats surrounding cornfields (e.g. herbaceous margins, hedgerows). Some studies (Lang et al., 2015, 2013) highlighted the negative impact of some genetically modified (GM) maize (i.e. BT maize) on non-target lepidopteran species. However, in Italy, the use of GM crops is currently prohibited. For this reason, we did not observe this potential negative effect on butterfly richness or abundance.

Conversely, we found a negative effect of winter cereals on butterfly richness. This result is confirmed by another study (Pywell et al., 2004), which suggested a possible link with the scarcity of weed species within these crops.

Moreover, the different effect on butterfly richness produced by maize and winter cereals may be due to the different production cycle of these crops. Indeed, the harvest of winter cereals mainly occurs in June or July, which correspond to the period of flight for most of the butterfly species present in our study area. Conversely, the harvest of maize crops usually starts at the end of the summer, allowing maize plants to reach a sufficient height to provide a shelter for butterflies. Moreover, the permanence of uncut herbaceous margins along crops until the end of the production cycle (Ernoult et al., 2013) provides a marginal but suitable habitat during summer.

We found a weak positive effect of soybean fields on the abundance of less mobile species. This result contrasts with a study carried out on the monarch butterfly in the Midwestern United States (Pleasants and Oberhauser, 2013). However, this study refers to GM soybean, which is not present in our study area.

The detection of several individuals pertaining to less mobile species (e.g. *Cupido argiades*) on soybean flowers during July and August surveys, suggests that the positive effect of this crop could be related to the nectar provided by soybean plants in this period, available for adult individuals. Furthermore, as for maize crops, the harvest of soybean occurs in late summer, which reduces the disturbance during the summer months.

Moreover, in our study area soybean crops were rather localized and located in different environmental contexts. Almost all butterflies observed foraging on soybean flowers were detected in the northern part of the study area, which is characterized by small fields within a mosaic of different crops, with meadows and hedgerows. Therefore, in this context, we can hypothesize that soybean fields can contribute to supporting butterfly communities by providing supplementary nectar sources.

Another crop type showing a positive effect on both butterfly richness and abundance is alfalfa. This crop is usually a part of crop rotation, and represents a forage source for livestock. Alfalfa provides nectar for adults and can be the host plant for some butterfly species (Loos et al., 2014). Despite its scarce occurrence within the study area, the positive effect of alfalfa was significant on overall butterfly richness, and even more strongly for subnemoral species. Alfalfa is a mass-flowering crop and may provide a huge nectar source for different species of pollinators (Holzschuh et al., 2013; Westphal et al., 2003). However, recent studies showed that the effect of mass-flowering agricultural habitats varies among species and landscape contexts (Holzschuh et al., 2016; Montero-Castaño et al., 2016), and that their importance seems to be less significant for butterflies than for other pollinators (Stanley and Stout, 2013).

Uncultivated lands showed a positive effect on the overall butterfly richness only, and this relationship is confirmed by literature information (Loos et al., 2014; Skórka et al., 2007; Toivonen

et al., 2016). These areas can benefit butterfly communities thanks to the occurrence of shrubs and high vegetation (Bubová et al., 2015), even if the continuation of succession can lead to a reduction in habitat quality (Skórka et al., 2007). Uncultivated areas, where production activities have ceased recently, are often characterized by early vegetation stages with short periods of mass flowering, followed by phases of scarcity of nectar sources. Moreover, this pattern could be strongly affected by management practices that often includes mowing and/or herbicides application prior to autumn sowing. In our study, this latter aspect could explain the lack of positive effect of uncultivated areas on overall butterfly abundance and on the abundance of the functional groups.

Many studies highlighted that in arable lands, shelter is an important variable with a positive effect on butterflies richness and abundance (Clausen et al., 2001; Dover, 1996; Pywell et al., 2004). The presence of a shelter (e.g. hedgerows) modifies the local microclimate and can increase habitat quality (Dover et al., 1997). We found different effects of shelter among functional groups, and this evidence is consistent with other studies (Clausen et al., 2001; Pywell et al., 2004). The increase of shelter favours nemoral species that usually live near hedgerows and forest edges. Instead, the abundance of highly mobile species seemed to be similarly favoured by different amounts of shelter, and this can be explained by a potential advantage provided by shelter for the species included in this functional group, which have different habitat preferences. Moreover, shelter can influence the propensity of butterflies to fly, thus enhancing dispersal capability (Thomas et al., 2011).

On the other hand, the highest shelter scores (i.e. 6, 7 and 8), provided by the presence of elements such as woodlands, continuous hedgerows or maize crops, have a significant negative impact especially on less mobile species. This result shows the potential barrier effect that these features can exert on butterfly with reduced dispersal ability (Kallioniemi et al., 2014).

6.4.2 Management

Besides the abundance of nectar sources, meadows were found to be one of the strongest positive drivers of butterfly richness and abundance. Indeed, grasslands represent the breeding habitat for many species of this taxon (Brereton, 2004; WallisdeVries and Van Swaay, 2009). However, meadow quality is strongly affected by microclimate conditions and management practices.

Focusing on the latter, the number of cuts during the flying season is a key factor that heavily affects butterfly communities (Bruppacher et al., 2016). High mowing rates produce a reduction in the availability of larval host plants, as well as a drastic decrease of nectar source availability (Bubová et al., 2015; Halbritter et al., 2015). A direct effect on mortality of adult butterflies is unlikely due to their escape ability (Halbritter et al., 2015), but some techniques, such as flail or rotary cutting, usually kill the larvae during mowing operations (Humbert et al., 2009). Our results confirmed the negative effect of an increasing number of cuts on butterfly abundance, although not on richness. This is consistent with the results of a recent experimental study carried out by Bruppacher et al. (2016), who did not find a significant difference in overall species richness between different mowing regimes. In our study area, the number of cuts ranges from 0 in fallow meadows, generally located in marginal suburban areas, to a maximum of 5 in non-productive grasslands, typically linked to recreational

suburban areas, to a maximum of 5 in non-productive grasslands, typically linked to recreational green spaces within urban areas. In farmland areas, the usual management of hay meadows includes two or three cuts during the butterfly flying season.

The intensity of meadow management, and particularly the moving rate, affects grass height. Some

The intensity of meadow management, and particularly the mowing rate, affects grass height. Some studies showed that tall vegetation positively affects many butterfly species (Öckinger et al., 2006), while other studies highlighted how this effect changes depending on the species considered (Milberg et al., 2016; Sjödin et al., 2008). Furthermore, Pöyry et al. (2006) found a unimodal trend between vegetation height and butterflies, with a higher richness for intermediate vegetation heights (about 30 cm). Nevertheless, in our study, we did not observe a significant effect of grass height in meadows, because of possible contrasting responses of different species in a community level analysis.

Overall, several studies performed by means of an experimental approach, affecting grass height during the flying season, showed that the optimal management of meadows for butterflies should include at least one of the following management types: rotational mowing, delaying of the first cut, and maintenance of uncut grass strips (e.g. Bruppacher et al., 2016; Bubová et al., 2015).

Besides the presence of meadows, farmlands can support butterfly communities, when field crops are bordered by semi-natural marginal habitats (Ouin and Burel, 2002). For instance, herbaceous borders along fields, when adequately managed, can become an additional suitable habitat for many butterfly species (Field et al., 2005; Marshall and Moonen, 2002; Pywell et al., 2011). Moreover, some studies

(Delattre et al., 2013, 2010) showed that these borders can also serve as a corridor between habitat patches (i.e. meadows).

Our results highlighted the importance of border width, cover of dicots in the border area and grass height in affecting butterfly communities.

Considering border width, larger margins showed a significant positive effect compared to those less one meter wide. This confirms that tiny margins are not sufficient to restore butterfly communities (Delattre et al., 2013; Kovács-Hostyánszki et al., 2016; Reeder et al., 2005). Nevertheless, we did not find any significant difference between the edges ranging from 1 to 3 m and those over 3 m. Thus, even medium margins (1-3 m wide) could be effective in supporting and enhancing our butterfly communities, characterized by a general low diversity. Conversely, in order to support a high butterfly diversity, such as that of traditional agricultural landscapes, it is necessary to focus on the overall landscape mosaic, which results from the use of low-intensity farming practices (Loos et al., 2014). Furthermore, we found a significant and strong effect of medium (1-3 m) and wide (>3 m) margins on the abundance of less mobile species. For this functional group, narrow margins fail to provide sufficient additional habitat to support populations, or to serve as corridors. Indeed, some studies using *Maniola jurtina* as a model species (less mobile species of agricultural landscapes) showed that the margins may become potential corridors only if they have a width of at least 5 m, and the higher the distance between fragments is, the wider the margin should be (Delattre et al., 2013, 2010).

As Pywell et al. (2004), we found a positive effect of dicots on butterfly abundance, and this can be linked to a great amount of flowers in margins with high cover of these plants. This result underlines the importance of increasing the quality of habitats along the margins of field crops, using wildflower seed mixtures that supply nectar resources and larval host plants (Feber et al., 1996; Meek et al., 2002; Thomas and Marshall, 1999).

The grass height of field margins showed a positive effect on butterfly richness abundance. This result is in apparent contrast with that obtained for meadows, for which the height of vegetation was never significant in affecting butterfly communities. However, meadows and herbaceous borders have very different characteristics. Herbaceous borders are small marginal habitats hosting low-diversity butterfly communities compared to those found in meadows (Villemey et al., 2015). Thus, the herbaceous margins may be more vulnerable and susceptible to disturbance related to agricultural practices. Furthermore, field borders have a different species composition (Villemey et al., 2015), with a greater presence of more mobile species, which can exploit the temporary nectar sources available when the grass layer is well developed (i.e. with high grass) and hosts a great diversity of flowers.

Hedgerows play an important role in supporting butterfly communities in intensive agricultural landscapes (Dover and Sparks, 2000; Pywell et al., 2004). This was confirmed by our results, as the presence of hedgerows significantly increased butterfly richness. More specifically, while hedgerow continuity did not seem to affect butterfly communities, thus confirming the results of other studies (Clausen et al., 2001; Pywell et al., 2004), the height of hedgerows was found to be a key factor. Medium height hedgerows (1-2 m) showed a positive effect on overall butterfly richness, compared to low hedgerows (<1 m). Conversely, highest hedgerows (> 3 m) negatively affected species abundance, particularly that of less mobile species, probably because of the possible barrier-effect that these habitat features may have on species with low dispersal capability (Thomas, 1983). Hedgerows improve habitat quality by guaranteeing shelter and, depending on the floristic composition, also by providing nectar and host plants. In our study area, brambles are among the most abundant species within hedgerows, and we found a positive effect of high cover of these plants on butterfly richness. Brambles produce many flowers rich in nectar and for a long period. Some studies showed how their flowers are usually used as nectar sources by many species (Dover, 1996; Tudor et al., 2004), although the dominant presence of brambles in farmland can be linked to an increase of nitrogen pollution due to the fertiliser drift from crop fields (Wallisdevries et al., 2012).

6.5 Conclusion

The use of the model averaging approach, which focused on the effects of variables without using an arbitrary probability threshold, provided a robust means of obtaining parameter estimates (Burnham and Anderson, 2002; Grueber et al., 2011).

Our results highlighted that the abundance of flowers is the main driver of butterfly richness and abundance. Nectar plants are mostly located in meadows and herbaceous margins, but they can be also found in uncultivated areas or urban green areas for short periods.

Intensive farmland can include different types of crops and these can have different effects on butterfly communities, probably related to different production cycles and nectar availability.

Our results confirmed the positive effect played by hedgerows and wide herbaceous margins along crop fields, and the negative effect of the number of meadow cuts on butterfly abundance. They underscore the importance to adopt correct management actions in green urban areas and in farmland, which could benefit from measures coming from agri-environmental schemes. This way, semi-natural habitats could play an important role in supporting butterfly communities, halting the general decline of populations observed in human-dominated landscape.

Finally, hedgerows and herbaceous margins could play an import role not only for butterflies, but also for the overall wildlife conservation (Bennett, 2003; Dondina et al., 2016b) and for the maintenance of ecological and agricultural services (Baudry and Burel, 1984).

To define the future development of this research, we have to consider that to counter the butterflies' decline, it is also necessary improved our knowledge of autoecological needs of species (Bonelli et al., 2011). Thus in the next studies we will focus on individual species (e.g. *Coenonympha pamphilus*, *Ochlodes sylvanus* and *Maniola jurtina*) that, although common in our study area, have showed a moderate decline in Europe in last decades (Van Swaay et al., 2013). Furthermore, the availability of detailed quantitative data on nectar sources in each sections of the transects will allow to investigated the effect of this variable on ecological groups and on some species.

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Appendix D

Tab. 6.3 Relative frequency of plant families considered in the definition of nectar index based on the cumulated abundance-score of species within each family.

Family	Frequency (%)	Family	Frequency (%)
Asteraceae	20.21	Papaveraceae	0.67
Fabaceae	16.99	Lythraceae	0.66
Rosaceae	13.31	Boraginaceae	0.59
Plantaginaceae	7.70	Celastraceae	0.42
Caryophyllaceae	4.52	Cornaceae	0.36
Ranunculaceae	4.24	Onagraceae	0.36
Lamiaceae	3.66	Dipsacaceae	0.34
Verbenaceae	3.63	Apocynaceae	0.34
Apiaceae	3.40	Solanaceae	0.29
Convolvulaceae	2.98	Primulaceae	0.27
Geraniaceae	2.79	Violaceae	0.15
Polygonaceae	2.45	Malvaceae	0.15
Phytolaccaceae	1.83	Asparagaceae	0.14
Scrophulariaceae	1.67	Valerianaceae	0.08
Caprifoliaceae	1.52	Amaryllidaceae	0.08
Balsaminaceae	0.91	Adoxaceae	0.07
Rubiaceae	0.86	Campanulaceae	0.03
Oxalidaceae	0.82	Oleaceae	0.03
Hypericaceae	0.74	Commelinaceae	0.02
Brassicaceae	0.71		

Tab. 6.4 Summary results of the effect of variables resulting from the habitat models after model averaging. Only effects that did not include the zero within the 95% confidence interval are shown. Delta<2: number of models included in top model set with a cut-off of 2 AICc and used in averaging procedure; R_{adj}^2 : mean adjusted R-squared of the averaged models. Functional groups: L (less mobile), H (highly mobile), O (open herbaceous), S (subnemoral), N (nemoral), - (overall species). See Tab. 6.1 for a description of the independent variables.

	Functional				Independe	ent variables	5				Delta<2	D 2
	groups	hedgerow	shelterB*	shelterC	shelterD	meadows	alfalfa	w-cereals	uncult	nectar	Delta<2	$\mathbf{R}_{\mathrm{adj}}^{2}$
	L				-1.439	0.373				0.495	7	0.692
	Н	0.233						-0.335		0.513	6	0.543
mi ahmaaa	O				-0.540					0.451	6	0.368
richness	S	0.163			-0.556	0.208	0.656	-0.198		0.445	3	0.687
	N			1.022	1.235						9	0.381
	-	0.146				0.244	0.435	-0.183	0.155	0.469	3	0.667
	L				-1.454	0.519				0.581	8	0.692
	Н		0.399	0.608		0.374				0.695	5	0.413
ahundanaa	O				-0.685	0.229				0.417	7	0.374
abundance	S	0.225				0.337	0.810			0.739	6	0.528
	N		0.819	1.264	1.806			-0.532			5	0.423
	-					0.313				0.623	12	0.550

^{*}shelterA was the reference category.

Tab. 6.5 Summary results of the effect of variables resulting from the management models after model averaging. Only effects that did not include the zero within the 95% confidence interval are shown. Delta<2: number of models included in top model set with a cut-off of 2 AICc and used in averaging procedure; R_{adj} ²: mean adjusted R-squared of the averaged models. Functional groups: L (less mobile), H (highly mobile), O (open herbaceous), S (subnemoral), N (nemoral), - (overall species). See Table 2 for a description of the independent variables.

	Functional groups	Management variables							R_{adj}^2
Meadows		mowingB*	mowingC						
	L	-0.482	-0.469					2	0.632
ahaan dan aa	Н	-0.551	-0.474					1 1 1 2 4 2 2 2 2 1 2 2 2 2 2 1 1 2 2 2 2	0.437
abundance	S	-0.315	-0.549					1	0.446
	-	-0.282	-0.523					1	0.475
Herbaceous margin		height_ma2*	height_ma3	width_ma2*	width_ma3	perc_dic2*	perc_dic3		
	S	0.682	0.913	0.250	0.417			2	0.639
richness	N					0.753	0.904	4	0.339
	-	0.408	0.605	0.306	0.410			2	0.622
	L			0.626	0.975			2	0.638
	Н					0.521	0.524	2	0.243
ahundanaa	O	0.586	0.837	0.308				1	0.383
abundance	S	0.627	0.847			0.575	0.501	2	0.490
	N						0.675	2	0.265
	-	0.350	0.580			0.469	0.358	2	0.501
Hedgerow		height_he2*	height_he3	height_he4	brambles4*				
_	Н	_	_	_	0.405			2	0.473
richness	S	0.202			0.327			1	0.627
	-	0.211			0.381			1	0.595
	L			-0.991				1	0.597
ahundanaa	O			-0.483				2	0.303
abundance	S		-0.397	-0.447				2	0.371
	-		-0.333	-0.501				2	0.402

^{*}mowingA, perc_dic1, width_ma1, height_he1 and brambles0 were the reference categories.

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General conclusion

In my research project, I worked on several case studies in the field of conservation biology having as a base the analysis of species distribution in time and space of birds and butterflies.

I used different techniques of analysis, choosing those that were more suitable for the specific objectives of single case studies and the type of available data. As statistical models, I always used Generalized Additive Models (GAM) that have proven to adapt well to deal ecological data, which by their nature are noisy and not always easy to be treated statistically.

In the last 40 years there has been a huge development of statistics, thanks to the development of regression analysis provided by generalized linear models (GLM; Nelder and Baker, 1972) and generalized additive models (GAM; Hastie and Tibshirani, 1990). These models are better able to analyse ecological data than conventional techniques (e.g., linear models) and now are widely used in scientific research.

The first publication on GAM dates back to the late '80s (Hastie and Tibshirani, 1986) and since then, these models have spread even if to a lesser extent than GLMs. A first reason is related to the statistic complexity of GAMs that determines greater computational heaviness. Another aspect is the greater difficulty in the interpretation of the outputs, seen that the relationship between the dependent variable and the covariates are not defined by coefficients, but by smooth functions. A third reason is the higher affinity between the classical linear models and the GLMs, which are extensions of linear mathematical models. This has enabled an easier passage to generalized regressions.

GAMs have, however, the advantage to deal with highly non-linear and non-monotonic relationships between the response and the explanatory variables (Guisan et al., 2002) and thus they should be more effective in describing the complexity of ecological relationships.

The spread of generalized regressions had a strong boost since 2000, thanks to the publication of some syntheses (Guisan et al., 2002; Guisan and Zimmermann, 2000), that encouraged the use of GLMs and GAMs in ecological studies. Furthermore, the use of these models has been favoured by the increasing computation capabilities of computers and by the spread of open-source software for statistical analyses (e.g. R software; R Core Team, 2015).

In recent years the use of GAMs is growing (e.g. Bates et al., 2014; Dennis et al., 2016, 2015; Harrison et al., 2014; Maggini et al., 2011; Massimino et al., 2015; Pöyry et al., 2006; Tayleur et al., 2015), thanks also to the implementation of these models in R with the creation of the *mgcv* package (Wood, 2006) that has facilitated their use.

In my research project, GAMs have shown their flexibility being able to solve spatial and temporal autocorrelation biases, to develop mixed models using a smooth function as random factor and to describe the species distribution using presence/absence and abundance data.

My PhD thesis is divided into three parts, each focused on an important issue in conservation biology. The first part concerned the study of species distribution, followed by the analysis of the relationship between species and environmental at different spatial scales of variables, in the second and third part.

In the Part I of my thesis, the results confirmed the decline of many farmland bird species, probably due to the impact of intensive farming and the consequent reduction in habitat quality (Donald et al., 2006, 2001). At the same time, in the alpine areas, during a long-term period (1982-2016), all mountain bird species considered exhibited changes in at least one part of their altitudinal distribution. Moreover, different ecological groups showed different behaviour, emphasizing the importance in considering the species traits in the study of the ecological relationships. The probable drivers that are acting are habitat loss (due to forest regrowth) and climate warming (Chamberlain et al., 2016, 2013) and the current challenge is to figure out which of these factors is prevalent, considering that each species could respond differently.

In the Part II and III, I investigated the species-environment relationships using butterflies, a very sensitive taxa to environmental changes (Thomas, 2005). The use of a multi-scale approach allowed to identify the most important drivers shaping butterfly communities in a human-dominated area, both at a landscape scale (i.e. considering the surrounding land cover) and at a local scale (i.e. taking into account the local habitat and its management).

My study confirmed the effect of land cover at a landscape scale on butterfly communities. In fact, the effect of variables at the local scale (e.g. meadows) on butterflies was not constant, but it varied according to the land cover in the landscape context. The study area is placed in a highly urbanized area that generally host lower butterfly richness and abundance (Di Mauro et al., 2007; Olivier et al., 2016) than natural areas or low-intensity agricultural landscapes (Loos et al., 2014). However, our results showed that urban cover not always has a negative effect, but, in areas with intensive agriculture, can improve the environmental suitability for butterfly communities (Öckinger et al., 2009), through a possible increase of both landscape and habitat heterogeneity.

The analysis at local scale confirmed the findings of other studies (e.g. Curtis et al., 2015; Milberg et al., 2016; Pywell et al., 2004), identifying the abundance of nectar sources as the main habitat driver explaining the butterfly species richness and abundance. This result is important because the loss of food sources (i.e. flowers) in intensive farmland is one of the possible causes of the decline of butterflies in Europe (Wallisdevries et al., 2012). Moreover, this result emphasizes the importance of

adopting appropriate management techniques in both farmland and urban green areas favouring the presence of butterflies and enhancing the overall biodiversity.

In my study, the analysis of the effect of management practices highlighted the negative effect of an increase in the number of cuts in meadows, which represent the breeding habitat for many butterfly species (WallisdeVries and Van Swaay, 2009). Moreover, the results also emphasizes the importance of linear features, such as hedgerows and herbaceous margins, and their characteristics (e.g. grass height, margin width and hedgerow height).

In conclusion, in my PhD research, I have highlighted the potential of modelling to address the problem of biodiversity decline, which need a response on how to set up effective conservation actions. The human impact on the global environment has become important enough to rename the current Holocene geological epoch as "Anthropocene" (Crutzen, 2002; Crutzen and Stoermer, 2000). Man has become the main direct and indirect driver of ecosystem changes and therefore only man can halt the consequent biodiversity decline. The commitment should begin at a local scale with the adoption of proper management measures in urban and agricultural areas, being both important to ensure the conservation of biodiversity. Actions should be pursued at a wider scale (e.g. regional scale) where the planning and management policies (e.g. CAP in European Union) can make an important support to local actions. Finally, at a global scale, the issue of climate change, which is affecting ecosystems already weakened by human action, can find answers only by global policies.

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Publications and Conference proceedings

Papers

The results of my research project are included in two articles:

Rocchia E., Luppi M., Dondina O., Orioli V., Bani L. Long- and medium-term changes in the altitudinal distribution of breeding birds in the Italian Alps. Ibis, under review.

Luppi M., Bani L., Orioli V. Local and landscape drivers of butterfly richness and abundance in a human-dominated area. In preparation. Agriculture, Ecosystems and Environment, under review.

Furthermore, during the PhD period, I participated in another study that was published in the following article:

Bani L., Pisa G., Luppi M., Spilotros G., Fabbri E., Randi E., Orioli V. 2015. Ecological connectivity assessment in a strongly structured fire salamander (*Salamandra salamandra*) population. Ecology and Evolution, 5, 3472–3485.

Conference proceedings

During my PhD, I have participated at two international conferences:

Student Conference on Conservation Science. University of Cambridge. Cambridge (UK), 24-26 March 2015.

POSTER

Luppi M., Bani L., Orioli V. 2015. Species distribution modelling and population trends of breeding birds in agro-ecosystems: the case of Lombardy (Italy).

Conference: International Symposium: Future 4 Butterflies in Europe. Wageningen (Netherlands), from the 31st of March to April 2nd 2016.

POSTER

Luppi M., Bani L., Orioli V. 2016. Local and landscape drivers of butterfly richness and abundance in a human-dominated area.

The butterfly counts not months but moments, and has time enough. Rabindranath Tagore

PLATE 17 2 Venessa polychloros Large Fortotse-shell B 1. Vanessa C-album. Comma B.

Duncan, J., Cuvier, J. L. N. F. 1835. The Natural History of British Butterflies. WH Lizars.