Birds and climate change: possible scenarios for the European species

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INDEX

1. EXTENDED ABSTRACT

Climate Change (CC) is emerging as the greatest threat to natural communities in many, if not most, of the world's ecosystems in coming decades, with mid-range climate change scenarios expected to produce greater extinction rates than habitat loss, currently deemed the top threat to biodiversity. To foresee the biodiversity response to CC has therefore become a crucial field of research, especially in terms of management and conservation.

The aim of my PhD was to explore the impact of the CC on 542 bird species regularly breeding in Europe and Turkey.

Background

Birds are the best known of the large and adaptively diversified classes of animals. According to the last Red List of Threatened Species (IUCN, 2017), 1,375 bird species of the global 10,965 are threatened with extinction (13%). In Europe 43% of 542 regular breeding species are listed as 'threatened' or 'near threatened' (BirdLife International, 2017). CC affects birds in different ways; it can alter distribution, abundance, behavior, even genetic composition. It can also affect the timing of events like migration or breeding. Extinction rates predicted for entire communities, populations or bird species because of CC are frightening.

I had the chance to explore the impact of CC on the phenology of trans-Saharan migratory birds by analyzing the data collected for decades during spring migration across the Mediterranean and northern Europe (Jonzén *et al.*, 2006b; Saino *et al.*, 2007). The results of these analyses highlight how the constant advance of arrival dates at stop-over sites and reproductive territories is correlated with the weather conditions at wintering quarters and on the Mediterranean coasts of Africa, which influence the speed of migration.

More recently, I used species distribution models (SDM) expert-based and validated with data of presence for each of the over 500 European breeding species, and correlative bioclimatic models that, through presence data and climatic variables sets, allowed me to obtain the current ecological niche of the species. By using the results of specific global circulation models (GCM) based on different climatic future scenarios it was possible to project forward the potential climatic distribution of each species. Comparing present and future I was able to obtain indicative results of the impact of CC on the European breeding bird species.

<u>Chapters outline</u>

Where are the species and how much are exposed to climate change?

In order to obtain specific SDMs, for each species I collected spatially explicit information on the extent of occurrence (EOO) over the entire study area (BirdLife's EOOs digital database and national birds' distribution atlases), as well as habitat requirements and all freely available presence data that I could readily access. Whenever possible, habitat requirements were used to refine the EOOs using an expert-based modeling approach, while points of presence were used to evaluate the reliability of the same models.

Habitat requirements were defined by me and published literature, and I considered three environmental variables that I assumed to be informative to model species distribution: land cover, elevation and distance to water. For land cover I used *GlobCover V2.2* (offering a complete coverage of our study area with a 300m pixel size and 46 land-use/land-cover classes). I obtained data on elevation from the Shuttle Radar Topography Mission database with a 250m pixel size, while data on running and standing water bodies were obtained from the CCM2 v2.1 river and catchments database compiled by the European Joint Research Center. I used the data collected to assign to each of the 46 GlobCover land-use/land-cover classes a suitability score. Whenever possible, I recorded the maximum and the minimum elevations at which a stable population of a given species can be found, and the maximum distance to water at which they have been recorded. So, I combined the elevation range with distance to water and habitat suitability scores to refine the available EOOs and obtained a model of the current species distribution with a cell size of 300m (resolution of the available environmental layers). Finally, I collected all the readily and freely available points of presence and used them to evaluate the reliability of the expert-based distribution models.

I used the expert-based distribution models to calculate species richness maps for all breeding species together, species of conservation concern, endemic species. The top 10% richest cells in each map represented the hotspots of species richness.

Average monthly precipitation and temperature were projected using climate model outputs made available through the Intergovernmental Panel on Climate Change (IPCC) Data Distribution Centre. Following, it was defined an ensemble of forecasts of climate change considering four different global circulation models and more than one emission scenarios. In this way it was possible to generate an index of risk of exposure to extreme climates that was used to identify the areas with a significant association between hotspots of diversity and high risk of exposure to extreme climates.

The results I obtained (Maiorano *et al.*, 2013) outline that the richness hotspots for all European breeding birds are within northern central Europe and western Russia. An important hotspot for threatened species is in the eastern-central part of the study area while the species whose distribution is mainly European ('endemic' species) concentrate in northern central Europe, Greece, Alps and Iberian Peninsula.

The analyses' results suggest that the main hotspots of biodiversity for European breeding birds may be extensively influenced by the climate change projected to occur over the coming decades, especially in the Mediterranean bioregion, posing serious concerns for biodiversity conservation.

How much protected are European birds?

In order to understand the effectiveness of the current conservation tools existing for European birds, which, as already seen, are destined to undergo significant environmental changes, often in areas where high levels of biodiversity persist, a gap analysis of the entire system of European protected areas (PAs) and the Natura2000 network (N2K: the most important European biodiversity conservation effort carried out on a regional scale) was performed by using validated species distributions models for all European birds obtained as described in the previous chapter.

For each species the representativeness in terms of the suitable area falling within the protected areas network (PAs and N2K) and in Europe was calculated, and the IUCN conservation status and the presence in the annexes of the European Bird Directive were recorded. Furthermore, for each species I considered the threat status and, using the global distribution range obtained as described in the previous chapter, I calculated the percentage of the distribution included in the EU and defined as endemics all species with distributions totally encompassed in the EU.

The results of this analysis were comforting: *a)* of the 31 species with a strictly European EOO ('endemic'), 90.3% (28 species) is covered by the network of protected areas (PAs + N2K); *b)* all threatened species result protected by the network; *c)* a minimum of 74% of species reaches the representative target in the PAs and a maximum of 93% falls within the total coverage (PAs + N2K) (Maiorano *et al.*, 2015).

Because the gap analysis was performed for all species of European terrestrial vertebrates (freshwater fish excluded), I could also compare the results obtained for the birds with the ones obtained for the other classes. If the umbrella of protected areas in Europe is valid for birds, the same cannot be assessed for other European terrestrial vertebrates. In reptiles,

for example, 60.9% of threatened species are not covered by the European protection network, and even 80.4% of endemic species live outside of it. This raises serious questions, especially concerning the criteria by which a higher level of protection is granted to the territory or by which the species are annexed to conservation directives.

Combining expert-base and statistical approach

In order to build more realistic scenarios for changes in the distribution of species breeding in continental Europe, at the XVII Italian Congress of Ornithology held in Trento on 2013, I presented a proposal of a modelling approach based on the combination of state-of-the-art bioclimatic models, with expert based habitat suitability and distance to current distribution (Montemaggiori *et al.*, 2015). Thus, for each species, I developed three layers: *a)* a bioclimatic model calibrated with an ensemble forecasting approach, considering six climatic variables and species' occurrences according to European Bird Census Council (EBCC) Atlas' 50 x 50 km cells with semi-quantitative data and high coverage completeness (Hagemeijer & Blair, 1997); *b)* the expert based habitat suitability model developed as described in the first chapter of this dissertation, which considers land use, elevation and distance to water and *c)* the distance from present distribution of the species, mapped according to BirdLife EOOs digital dataset. Assuming that the three layers are largely independent, I calculated for each species a final model of the relative probability of presence by multiplying the three maps.

I evaluated the reliability of the models using independent points of presence and calculated and index of the calibration capacity of the models for both the classical bioclimatic model and for the final model of relative probability of presence. The results clearly demonstrate that this approach produces more accurate and better performing models compared to simple bioclimatic ones (79% of cases).

Combining this approach with future scenarios for land use and climate, it will be possible to build more robust models showing potential changes in species distribution. Furthermore, it will be possible to incorporate also models of species' biotic interactions and dispersal distances, providing a biologically richer outcome.

How vulnerable are European birds to climate change and why?

Besides knowing where they are, where they will move and what European birds will encounter in the coming decades, it is also important to know their degree of vulnerability to the CC.

The adopted approach was to build a vulnerability index (*Vi*) for the European birds that integrates estimations of projected range change and different proxies of species resilience

in a quantitative way. The index, originally proposed by Maggini *et al.*, (2014), is completely quantitative, and it allows ranking species so as to prioritize conservation actions.

According to Maggini, I defined the vulnerability index using five indicators expressing three operational aspects of vulnerability: the projected change in the distribution, the reservoirs for the species and the population trend. Two indicators capture the change in the species' future distribution within Europe, two measure the species resilience and one quantify the historical trend of the species over the past 30 years. I used one stressor, climate change, and one spatially explicit scenario, to represent the magnitude of the future change and to assess its impact on species distribution using MaxEnt species distribution model. The vulnerability index was developed for 499 breeding species in Europe.

The five base indicators contribute differently to the vulnerability of a species. The analysis of the single components of the index *Vi* for each species allows to highlight the relative weight of the different indicators, and a first exploration of the obtained results highlights the highest number of species with a high *Vi* value in the north-eastern part of the area study, mainly because of the strong reduction of habitat suitability for the future in that part of the study area.

The average weight of each *taxon*, its diet, its habitat suitability, some behavioral aspects and its conservation status (*sensu* IUCN) have been used to understand if there are ecological indications linked to the calculated indices, in order to highlight specific management indications. From the analysis it seems to emerge that the most specialized species in terms of habitat seem to be those with higher *Vi* indices; aquatic species are more vulnerable, as well as those nesting on the ground. The degree of vulnerability increases for the larger species and finally the increase in the degree of threat (*sensu* IUCN) increases the value of the vulnerability index.

A more in-depth exploration of these results will be the core of a contribution currently being prepared in the name of A. Montemaggiori & L. Maiorano which is expected to be submitted by April 2018.

Conclusions

The constant advance of arrival dates of migratory species at stop-over sites and reproductive territories in spring is correlated with the weather conditions at wintering quarters and on the Mediterranean coasts of Africa, which influence the speed of migration. European breeding birds are not equally distributed within continental Europe. Richness hotspots are within northern central Europe and western Russia; species of conservation concern concentrate in the eastern-central part of Europe, while species whose distribution

is mainly European are more represented in northern central Europe, Greece, Alps and Iberian Peninsula. At present, the European network of protected areas seems to be adequate to protect the current distribution of breeding birds in Europe, especially the most endangered species or the ones whose current EOO is mainly within the study area. But the main hotspots of biodiversity for European breeding birds may be extensively influenced by the climate change projected to occur over the coming decades, posing serious concerns for biodiversity conservation.

Climate change impacts on future species distribution by modifying habitat suitability and/or shrinking and displacing species EOOs, but it also affects the systemic and ecological traits of the species, seriously endangering one of the most important animal classes not only ecologically meaning, but also as an important source of inspiration and beauty for mankind.

Work in progress

While much has been said on the spatial distribution of taxonomic and phylogenetic diversity of large animals, how the associated food-web properties are distributed through geographic and environmental space is largely unknown. Together with a group of ecologists coordinated by W. Thuiller (CNRS – Grenoble) I contributed to analyze the spatial structure of terrestrial vertebrate food webs and revisit traditional diversity-environmental relationships in light of trophic interactions.

This is why I have produced a web of trophic relationships between all European bird species and each single species of European terrestrial vertebrates (mammals, birds, reptiles and amphibians). This ecological web, together with the others built for all the other classes examined, has been combined with the spatial distributions of all the species projected into the future. The results of this analysis, which flowed into a contribution recently submitted (Braga *et al.*, n.d.), show an evident effect of CC in modeling the spatial structure of trophic networks among all European terrestrial vertebrates.

Finally, together with T. Kuemmerle (Geography Dept. of Humboldt Berlin University) and L. Maiorano, I am working to a multiscale approach by using also future land use scenarios for Europe, together with climatic scenarios. This is to understand the relative importance of this component in shaping the future of European birds.

<u>Produced contributions</u>

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- Maiorano L., Amori G., Capula M., Falcucci A., Masi M., **Montemaggiori A.**, Pottier J., Psomas A., Rondinini C., Russo D., Zimmermann N.E., Boitani L. & A. Guisan. 2013. Threats from Climate Change to Terrestrial Vertebrate Hotspots in Europe. *PLoS ONE* 8(9): e74989.

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- **Montemaggiori, A.**, Guisan, A., Thuiller, W., Zimmermann, N.E. & Maiorano, L. (2015). Modelling the response of European breeding birds to climate change: combining expert-base and statistical approach. In Pedrini, P., Rossi, F., Bogliani, G. & Serra, L. (Eds). *XVII Convegno Italiano di Ornitologia: Atti del convegno di Trento.* Trento. MUSE. *Abstract of oral presentation.*

- Braga, J., Pollock, L.J., Barros, C., Galiana, N., Montoya, J., Gravel, D., Maiorano, L., **Montemaggiori, A.**, Ficetola, G.F., Dray, S. & Thuiller, W. (n.a.). Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe. *Glob. Ecol. Biogeogr.* Submitted.

- **Montemaggiori A.** & Maiorano L. (in prep.) Assessing species vulnerability to climate change within European birds.

2. INTRODUCTION

2.1 Climate change: what are we speaking about?

Earth's climate changes naturally. Changes in the intensity of sunlight reaching the earth cause cycles of warming and cooling that have been a regular feature of the Earth's climatic history. Some of these solar cycles - like the four glacial-interglacial swings during the past 400,000 years - extend over very long-time scales and can have large amplitudes of 5°C to 6°C. For the past 10,000 years, the earth has been in the warm interglacial phase of such a cycle. Other solar cycles are much shorter, with the shortest being the 11-year sunspot cycle. However, the magnitudes of changes in climate for these shorter cycles are much smaller than those for the long cycles. Within the past 1000 years, for example, such changes have been within a range of about 1°C. Other natural causes of climate change include variations in ocean currents (which can alter the distribution of heat and precipitation) and large eruptions of volcanoes (which can sporadically increase the concentration of atmospheric particles, blocking out more sunlight). Still, for thousands of years, the Earth's atmosphere has changed very little (Adedeji, Reuben & Olatoye, 2014).

Human activities are also changing the climate. The main cause of such change is the increasing atmospheric concentration of greenhouse gases. Particularly important is the increase in carbon dioxide (CO_2), which is released through the burning of fossil fuels (coal, oil and natural gas) and through deforestation and land degradation (**Fig. 1**).
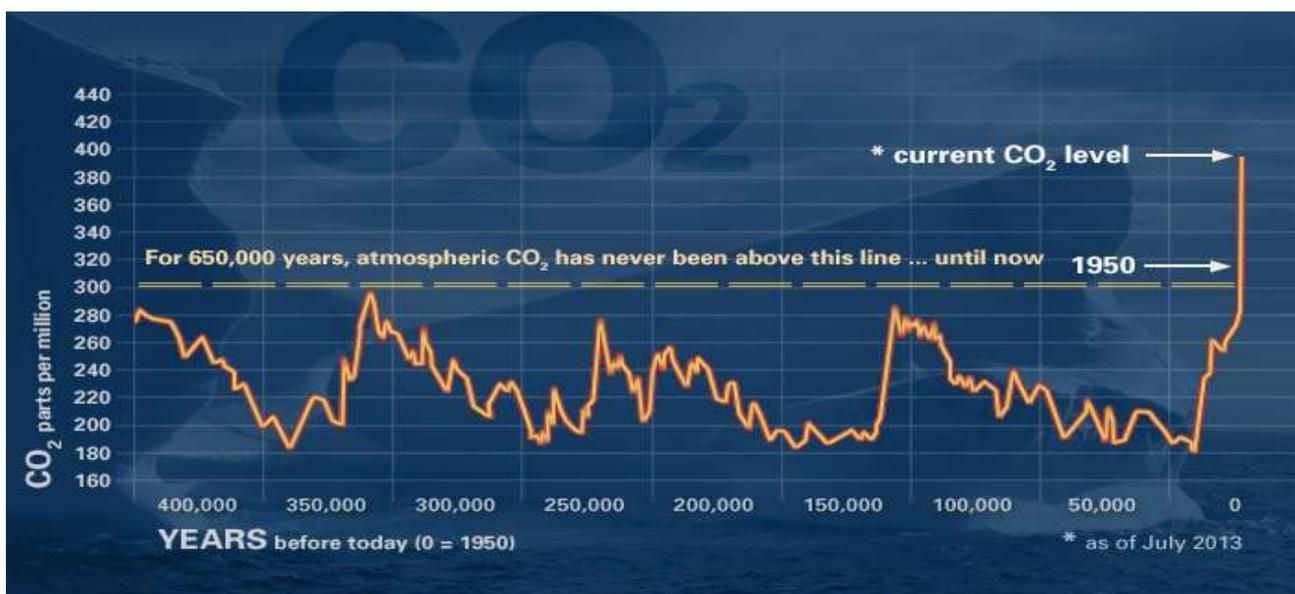
Figure 1: Rise of the carbon dioxide over the past 400.000 years to 2013 in the Earth's atmosphere. Data source: National Oceanic and Atmospheric Administration from NASA web site accessed on 10.10.2017).

Levels of carbon dioxide in the atmosphere are higher than they have been at any time in the past 400,000 years. During ice ages, CO_2 levels were around 200 parts per million (ppm), and during the warmer interglacial periods, they hovered around 280 ppm. In 2013, CO_2 levels surpassed 400 ppm for the first time in recorded history. This recent relentless rise in CO_2 shows a remarkably constant relationship with fossil-fuel burning, and can be well accounted for based on the simple premise that about 60 percent of fossil-fuel emissions stay in the air (Blunden & Arndt, 2017).

An increase in greenhouse gases like CO_2, methane and nitrous oxide enhances the natural greenhouse effect and leads to an increase in the Earth's average surface temperature (**Fig. 2**).
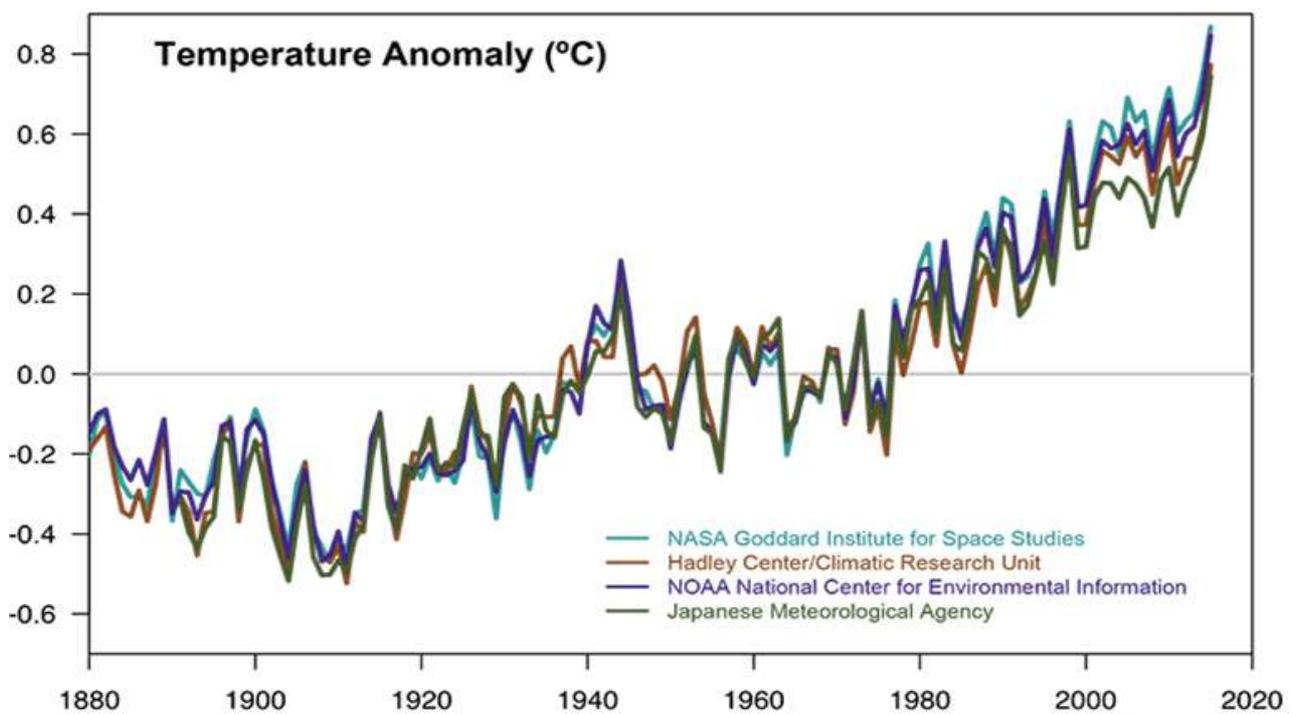
Figure 2: Temperature anomalies (°C) recorded from 1880 to date on Earth from four international science institutions. Data sources: NASA's Goddard Institute for Space Studies, NOAA National Climatic Data Center, Met Office Hadley Centre/Climatic Research Unit and the Japanese Meteorological Agency from NASA website accessed on 10.10.2017.

Consequently, artic sea ice is now declining at a rate of 13.2 percent per decade, relative to the 1981 to 2010 average (NSIDC/NASA website accessed on 10.10.2017) (**Fig 3**).
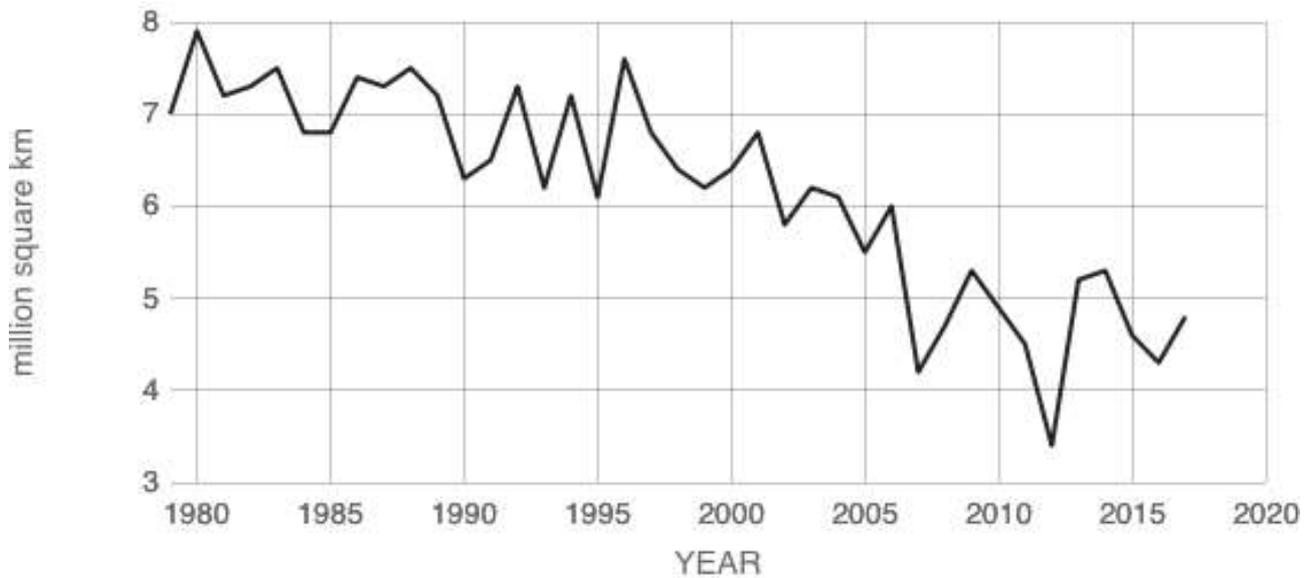
Figure 3:. Average monthly Arctic sea ice extent each September from 1979 to date, derived from satellite observations (arctic sea ice reaches its minimum each September). Data source: NASA Distributed Active Archive Center (DAAC) at National Snow and Ice Data Centre from NSIDC/DAAC website accessed on 10.10.2017.

The added water from melting ice sheets and glaciers and the expansion of sea water as it warms are causing sea level rise (**Fig. 4**).
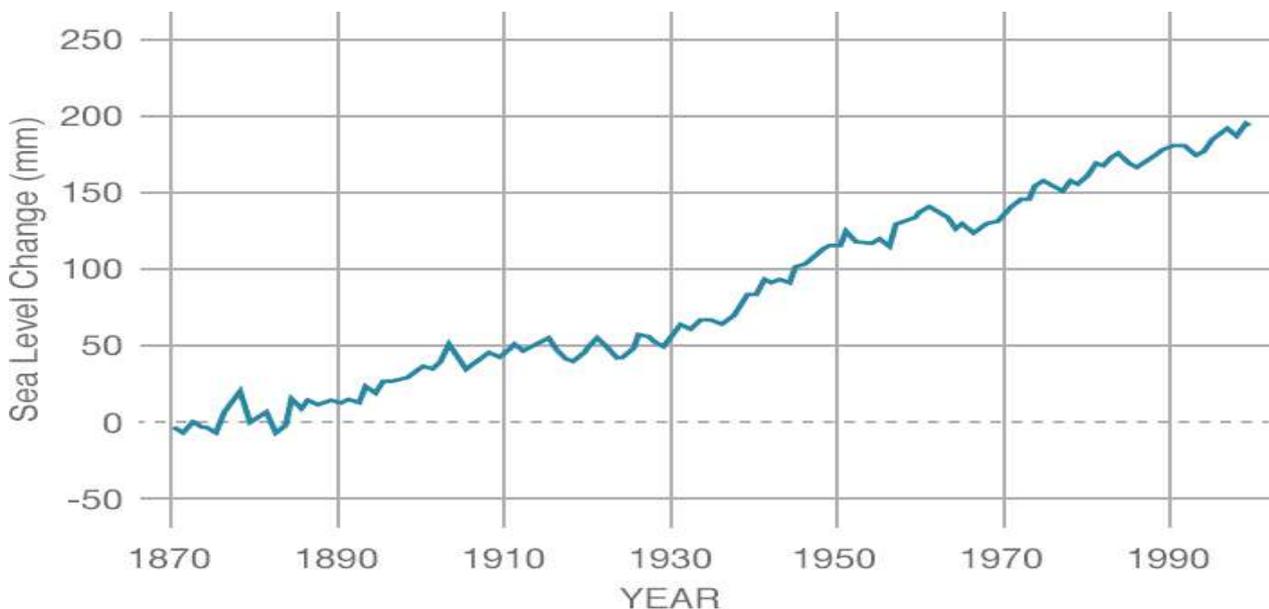
Figure 4: Sea level change (mm) on Earth from 1870 to 2000 from coastal tide gauge records. Data source: Commonwealth Scientific and Industrial Research Organization - Marine and Atmospheric Research from CSIRO website accessed on 10.10.2017.

At the regional scale, emissions of polluting gases and particles into the atmosphere can also have large effects, although some of these can have opposing impacts. Sooty aerosols, for example, tend to warm regional climates, while sulphate aerosols will cool it by reflecting more sunlight. While their direct effects will be felt primarily within the industrialized regions, these aerosols can also indirectly alter average global temperatures and wind currents. Moreover, human induced depletion of ozone in the stratosphere also tends to cool the earth's surface, while land use change can change the amount of sunlight reflected to space by the earth's surface and hence contribute to climate change (Adedeji *et al.*, 2014).

Multiple studies published in peer-reviewed scientific journals show that 97 percent or more of actively publishing climate scientists agree on the fact that climate-warming trends over the past century are extremely likely due to human activities. In addition, most of the leading scientific organizations worldwide have issued public statements endorsing this position (Oreskes, 2004; Doran & Zimmerman, 2009; Anderegg *et al.*, 2010; Cook *et al.*, 2013). Recently in its Fifth Assessment Report, the Intergovernmental Panel on Climate Change, a group of 1,300 independent scientific experts from countries all over the world under the auspices of the United Nations, concluded there's a more than 95 percent probability that human activities over the past 50 years have warmed our planet (IPCC, 2014).

2.2 Consequences of climate change on natural communities and birds

Observed and projected climatic changes for the 21st century, most notably global warming, are comparable in magnitude to the largest global changes in the past 65 million years (Diffenbaugh & Field, 2013; Kemp, Eichenseer & Kiessling, 2015). The combined rate and magnitude of climate change is already resulting in a global-scale biological response (Pecl *et al.*, 2017).
Climate change is emerging as the greatest threat to natural communities in many, if not most, of the world's ecosystems in coming decades, with mid-range climate change scenarios expected to produce greater extinction rates than habitat loss, currently deemed the top threat to biodiversity (Thomas *et al.*, 2004; Malcolm *et al.*, 2006; Foden *et al.*, 2013).

Highly sensitive to climate and weather, birds are pioneer indicators of climate change (Moller, Fiedler & Berthold, 2011) , the quintessential "canaries in the coal mine."

Climate change affects birds in different ways; it can alter distribution, abundance, behavior, even genetic composition. It can also affect the timing of events like migration or breeding (Pearce-Higgins & Green, 2014).

Climate change can affect birds directly, through changes in temperature or rainfall. It can also lead to increased pressure from competitors, predators, parasites, diseases and disturbances like fires or storms. And climate change can act in combination with other major threats like habitat loss and alien invasive species, making the overall impact worse.

Because birds are one of the best studied groups of organisms, many studies demonstrate that birds are being affected by climate change. This is occurring in a variety of ways:

- Egg laying and hatching is occurring earlier.
  Strong evidence documents earlier egg-laying and hatching by birds in response to climate change (Lehikoinen & Sparks, 2010; Griffith *et al.*, 2016). Approximately 60 per cent of studies on egg-laying show long-term advances in laying date consistent with patterns of global warming (Pearce-Higgins & Green, 2014).

  - One large-scale study showed that birds are laying eggs up at an average rate of 6.6 days earlier per decade (Both *et al.*, 2004).
  - The Common Murre (*Uria aalge*) in North America has advanced its breeding date 24 days per decade (Root *et al.*, 2003).
  - North American Tree Swallows (*Tachycineta bicolor*) are nesting up to 9 days earlier than 30 years ago, corresponding to an increase in average spring temperatures (Hussell & Brittingham, 2003).

- Migration times are shifting.
  Spring migration of birds is generally considered more important than autumn migration because it determines their arrival timing at breeding grounds, which is in turn crucial for mating and territory choice. The number of successful spring migrants also directly affects breeding population size (Gordo, 2007; Charmantier & Gienapp, 2014).

  - Birds are migrating earlier in the spring (Jonzén et al., 2006a); a study of 63 years of data for 96 species of bird migrants in Canada showed that 27 species have altered their arrival dates significantly, with most arriving earlier, in conjunction with warming spring temperatures (Murphy-Klassen et al., 2005).
  - The autumn passage of migrants wintering south of the Sahara has advanced in recent years, presumably as a result of selection pressure to cross the Sahel before

its seasonal dry period. In contrast, migrants wintering north of the Sahara have delayed autumn passage (Jenni & Ké Ry, 2003).

- Some birds in Europe are even failing to migrate all together (Lehikoinen, Sparks & Zalakevicius, 2004; Pulido & Berthold, 2010)..

- Bird behavior and their environment are becoming mismatched.
Some bird species may not be able to alter their behavior sufficiently to match shifts in the availability of important food sources such as insects, flowers and berries (Knudsen *et al.*, 2011)

  - Much of a bird's life cycle and behavior is closely linked to cues from the environment, like changing seasons. A mismatch occurs when birds cannot shift their behavior, such as breeding times, enough to coincide with changes in environment, such as when prey is available (Both et al., 2006; Saino et al., 2011).
  - Long-distance migrants are particularly at risk of a mismatch as it is harder for them to know what conditions might be like at the end of the migration route. For example, wood warblers (Parulinae) in North America aren't migrating earlier from their neotropical wintering grounds, despite earlier springs in their northern breeding ranges – this risks a late arrival, after spring food sources on breeding grounds are gone (Strode, 2003).

- Distributions are changing.
The strong relationship between bird distribution and climate means that when climatic boundaries change, bird distributions are expected to shift too (Parmesan & Yohe, 2003; Thomas, 2010).

  - Bird populations are expected to shift poleward, or to higher elevations, to stay with their ideal temperatures as the climate changes (Chen *et al.*, 2011; Auer & King, 2014).
  - Importantly, although range changes will vary for different species, range contractions are expected to be more frequent than range expansions (Jetz, Wilcove & Dobson, 2007). Range shifts pose major threats to birds, both directly and indirectly.
  - Ontario Breeding Bird Atlas data demonstrates that "southern" birds species such as Tufted Titmouse (*Baeolophus bicolor*), Blue-Gray Gnatcatcher (*Polioptila caerulea*), Northern Mockingbird (*Mimus polyglottos*), and Red-bellied Woodpecker (*Melanerpes carolinus*) have increased in number and have expanded their range northwards in Ontario compared to 20 years ago (Cadman, Sutherland & Beck, 2007).

- These climate-induced shifts are not always a solution to coping with a warming climate. Birds on the move could be stymied in their efforts to find new ranges by fragmentation, human development, or natural geological features like large bodies of water (Pimm, 2008).

- Ecological communities are disrupted.
With climate change, the makeup of communities will change as species track their climate space by shifting to new areas (Hannah, Lovejoy & Schneider, 2005; Walther, 2010). As a result, the type and abundance of species upon which birds depend (food sources, nesting materials, etc.) may decline, affecting birds' health. These disrupted ecological communities mean birds may also face new competitors, predators, prey and parasites to which they are not adapted (Gaston & Elliot, 2013; Barbet-Massin & Jetz, 2015; Wittwer *et al.*, 2015; Townsend *et al.*, 2016).

  - In the northern Hudson Bay area, mosquitoes now reach peak numbers earlier in the spring. Thick-billed Murres (*Uria lomvia*) breeding in the area have not adjusted their behavior, and the combination of heat and mosquitoes is causing higher egg loss and greater adult mortality (Gaston, Hipfner & Campbell, 2002).
  - 2005 saw unprecedented failures of colonies of seabirds on the Pacific coast of North America. Only 8% of the Cassin's Auklets (*Ptychoramphus aleuticus*) nesting on Triangle Island were successful. This is because late northerly winds delayed coastal upwelling, which affected plankton growth and caused a decline in the fish species on which the seabirds depend (Sydeman *et al.*, 2006).
  - Tufted Puffins at Canadian sites have breeding success near zero when water is at its warmest, which could mean that Canada's largest breeding colony for this species, Scott Islands, becomes unsuitable for Tufted Puffins as water continues to warm (Hedd *et al.*, 2006).

- Extinction risks are on the rise.
In the future, climate change will put large numbers of birds at risk of extinction. A recent meta-analysis conducted by M. C. Urban (Urban, 2015) on 131 published predictions about extinction rates all over the world, resulted that extinction risks will accelerate with future global temperatures, threatening up to one in six species under current policies. Extinction risks were highest in South America, Australia, and New Zealand, and risks did not vary by taxonomic group.

- Birds most at risk of extinction from climate change are those with restricted ranges, poor ability to move their range, small populations, or those already facing conservation challenges (Travis, 2003).
- Of 119 long-distance migrants studied in Europe, 54 per cent have already shown a sustained, often severe, decline from 1970 to 2000, with climate change implicated as a major contributing factor (Sanderson *et al.*, 2006).
- Arctic birds are particularly vulnerable – warming is occurring rapidly here, and at least 85 of the world's bird species breed in global Arctic regions. Vast areas of habitat, including tundra and sea ice, will be lost. Sea ice retreat could have severe consequences for Ivory Gulls (*Pagophila eburnea*), which forage along sea ice. Canadian Ivory Gulls have already declined in number by 90% over the past decades (Grant Gilchrist & Mallory, 2005).

Birds have served as reliable indicators of environmental change for centuries and now indicate that global warming has set in motion a powerful chain of effects in ecosystems worldwide. In this global status review there is growing evidence of climate change affecting birds' behavior, ability to reproduce and even to survive.

Furthermore, the march toward a major bird extinction may be underway, with evidence of climate change linked to unprecedented breeding crashes and declines of up to 90 per cent in some bird populations. Forecasts of bird extinction rates depend on the potential resilience of ecosystems and vary from 5 per cent to over 70 per cent, based on current emission and warming trajectories. Unfortunately, our analysis indicates that more comprehensive consideration of risk factors is likely to upgrade such extinction estimates in future (Pearce-Higgins & Green, 2014).

Given that climate change is expected to shift important, species-rich bird communities out of protected areas, continued research is crucial. Thus, if conservation efforts are to meet the climate threat, a fundamental change in approach to bird conservation will be needed if bird species diversity is to be maintained.

The most fundamental variable in the future impacts on birds will be the extent of global warming, which is dependent on to what extent and how quickly emissions of greenhouse gases are reduced. Interventions that reduce future greenhouse gas concentrations and therefore warming levels could also lessen the extinction rates of bird species and other groups (Wormworth & Mallon, 2006).

2.3 Aim of the thesis and chapters' summary

The aim of my PhD was to explore the impact of the climate change on 542 bird species regularly breeding in Europe and Turkey.

Each regularly and naturally occurring wild bird species breeding in the study area was selected for this thesis, according to BirdLife (2017) (**Tab. I**)

Scientific name	Common name	Scientific name	Common name
Acanthis flammea	Redpoll	*Apus affinis*	Little Swift
Accipiter badius	Shikra	*Apus apus*	Common Swift
Accipiter brevipes	Levant Sparrowhawk	*Apus caffer*	White-rumped Swift
Accipiter gentilis	Northern Goshawk	*Apus pallidus*	Pallid Swift
Accipiter nisus	Eurasian Sparrowhawk	*Apus unicolor*	Plain Swift
Acrocephalus agricola	Paddyfield Warbler	*Aquila adalberti*	Spanish Imperial Eagle
Acrocephalus arundinaceus	Great Reed-warbler	*Aquila chrysaetos*	Golden Eagle
Acrocephalus dumetorum	Blyth's Reed-warbler	*Aquila fasciata*	Bonelli's Eagle
Acrocephalus melanopogon	Moustached Warbler	*Aquila heliaca*	Eastern Imperial Eagle
Acrocephalus paludicola	Aquatic Warbler	*Aquila nipalensis*	Steppe Eagle
Acrocephalus palustris	Marsh Warbler	*Ardea alba*	Great White Egret
Acrocephalus schoenobaenus	Sedge Warbler	*Ardea cinerea*	Grey Heron
Acrocephalus scirpaceus	Common Reed-warbler	*Ardea purpurea*	Purple Heron
Actitis hypoleucos	Common Sandpiper	*Ardeola ralloides*	Squacco Heron
Aegithalos caudatus	Long-tailed Tit	*Arenaria interpres*	Ruddy Turnstone
Aegolius funereus	Boreal Owl	*Argya altirostris*	Iraq Babbler
Aegypius monachus	Cinereous Vulture	*Asio flammeus*	Short-eared Owl
Alauda arvensis	Eurasian Skylark	*Asio otus*	Northern Long-eared Owl
Alauda leucoptera	White-winged Lark	*Athene noctua*	Little Owl
Alaudala rufescens	Lesser Short-toed Lark	*Aythya ferina*	Common Pochard
Alca torda	Razorbill	*Aythya fuligula*	Tufted Duck
Alcedo atthis	Common Kingfisher	*Aythya marila*	Greater Scaup
Alectoris barbara	Barbary Partridge	*Aythya nyroca*	Ferruginous Duck
Alectoris chukar	Chukar	*Bombycilla garrulus*	Bohemian Waxwing
Alectoris graeca	Rock Partridge	*Bonasa bonasia*	Hazel Grouse
Alectoris rufa	Red-legged Partridge	*Botaurus stellaris*	Eurasian Bittern
Alle alle	Little Auk	*Branta bernicla*	Brent Goose
Ammomanes deserti	Desert Lark	*Branta canadensis*	Canada Goose
Ammoperdix griseogularis	See-see Partridge	*Branta leucopsis*	Barnacle Goose
Anas acuta	Northern Pintail	*Branta ruficollis*	Red-breasted Goose
Anas crecca	Common Teal	*Bubo bubo*	Eurasian Eagle-owl
Anas platyrhynchos	Mallard	*Bubo scandiacus*	Snowy Owl
Anhinga rufa	African Darter	*Bubulcus ibis*	Cattle Egret
Anser albifrons	Greater White-fronted Goose	*Bucanetes githagineus*	Trumpeter Finch
Anser anser	Greylag Goose	*Bucanetes mongolicus*	Mongolian Finch
Anser brachyrhynchus	Pink-footed Goose	*Bucephala clangula*	Common Goldeneye
Anser caerulescens	Snow Goose	*Bucephala islandica*	Barrow's Goldeneye
Anser erythropus	Lesser White-fronted Goose	*Bulweria bulwerii*	Bulwer's Petrel
Anser fabalis	Bean Goose	*Burhinus oedicnemus*	Eurasian Thick-knee
Anthropoides virgo	Demoiselle Crane	*Buteo buteo*	Eurasian Buzzard
Anthus berthelotii	Berthelot's Pipit	*Buteo lagopus*	Rough-legged Buzzard
Anthus campestris	Tawny Pipit	*Buteo rufinus*	Long-legged Buzzard
Anthus cervinus	Red-throated Pipit	*Calandrella brachydactyla*	Greater Short-toed Lark
Anthus gustavi	Pechora Pipit	*Calcarius lapponicus*	Lapland Longspur
Anthus hodgsoni	Olive-backed Pipit	*Calidris alba*	Sanderling
Anthus petrosus	Rock Pipit	*Calidris alpina*	Dunlin
Anthus pratensis	Meadow Pipit	*Calidris bairdii*	Baird's Sandpiper
Anthus spinoletta	Water Pipit	*Calidris canutus*	Red Knot
Anthus trivialis	Tree Pipit	*Calidris falcinellus*	Broad-billed Sandpiper

Scientific name	Common name	Scientific name	Common name
Calidris ferruginea	Curlew Sandpiper	*Crex crex*	Corncrake
Calidris maritima	Purple Sandpiper	*Cuculus canorus*	Common Cuckoo
Calidris minuta	Little Stint	*Cuculus saturatus*	Oriental Cuckoo
Calidris pugnax	Ruff	*Cursorius cursor*	Cream-coloured Courser
Calidris temminckii	Temminck's Stint	*Cyanecula svecica*	Bluethroat
Calliope calliope	Siberian Rubythroat	*Cyanistes caeruleus*	Eurasian Blue Tit
Calonectris borealis	Cory's Shearwater	*Cyanistes cyanus*	Azure Tit
Calonectris diomedea	Scopoli's Shearwater	*Cyanistes teneriffae*	African Blue Tit
Caprimulgus europaeus	European Nightjar	*Cyanopica cooki*	Iberian Azure-winged Magpie
Caprimulgus ruficollis	Red-necked Nightjar	*Cygnus columbianus*	Tundra Swan
Carduelis carduelis	European Goldfinch	*Cygnus cygnus*	Whooper Swan
Carduelis citrinella	Citril Finch	*Cygnus olor*	Mute Swan
Carduelis corsicana	Corsican Finch	*Delichon urbicum*	Northern House Martin
Carpodacus erythrinus	Common Rosefinch	*Dendrocopos leucotos*	White-backed Woodpecker
Carpodacus rubicilla	Great Rosefinch	*Dendrocopos major*	Great Spotted Woodpecker
Carpospiza brachydactyla	Pale Sparrow	*Dendrocopos syriacus*	Syrian Woodpecker
Catharacta skua	Great Skua	*Dryobates minor*	Lesser Spotted Woodpecker
Cecropis daurica	Red-rumped Swallow	*Dryocopus martius*	Black Woodpecker
Cepphus grylle	Black Guillemot	*Egretta garzetta*	Little Egret
Cercotrichas galactotes	Rufous-tailed Scrub-robin	*Elanus caeruleus*	Black-winged Kite
Certhia brachydactyla	Short-toed Treecreeper	*Emberiza aureola*	Yellow-breasted Bunting
Certhia familiaris	Eurasian Treecreeper	*Emberiza bruniceps*	Red-headed Bunting
Ceryle rudis	Pied Kingfisher	*Emberiza buchanani*	Grey-necked Bunting
Cettia cetti	Cetti's Warbler	*Emberiza caesia*	Cretzschmar's Bunting
Charadrius alexandrinus	Kentish Plover	*Emberiza calandra*	Corn Bunting
Charadrius asiaticus	Caspian Plover	*Emberiza cia*	Rock Bunting
Charadrius dubius	Little Ringed Plover	*Emberiza cineracea*	Cinereous Bunting
Charadrius hiaticula	Common Ringed Plover	*Emberiza cirlus*	Cirl Bunting
Charadrius leschenaultii	Greater Sandplover	*Emberiza citrinella*	Yellowhammer
Chersophilus duponti	Dupont's Lark	*Emberiza hortulana*	Ortolan Bunting
Chlamydotis macqueenii	Asian Houbara	*Emberiza leucocephalos*	Pine Bunting
Chlamydotis undulata	African Houbara	*Emberiza melanocephala*	Black-headed Bunting
Chlidonias hybrida	Whiskered Tern	*Emberiza pallasi*	Pallas's Bunting
Chlidonias leucopterus	White-winged Tern	*Emberiza pusilla*	Little Bunting
Chlidonias niger	Black Tern	*Emberiza rustica*	Rustic Bunting
Chloris chloris	European Greenfinch	*Emberiza schoeniclus*	Reed Bunting
Ciconia ciconia	White Stork	*Eremophila alpestris*	Horned Lark
Ciconia nigra	Black Stork	*Erithacus rubecula*	European Robin
Cinclus cinclus	White-throated Dipper	*Eudromias morinellus*	Eurasian Dotterel
Circaetus gallicus	Short-toed Snake-eagle	*Falco biarmicus*	Lanner Falcon
Circus aeruginosus	Western Marsh-harrier	*Falco cherrug*	Saker Falcon
Circus cyaneus	Hen Harrier	*Falco columbarius*	Merlin
Circus macrourus	Pallid Harrier	*Falco eleonorae*	Eleonora's Falcon
Circus pygargus	Montagu's Harrier	*Falco naumanni*	Lesser Kestrel
Cisticola juncidis	Zitting Cisticola	*Falco peregrinus*	Peregrine Falcon
Clamator glandarius	Great Spotted Cuckoo	*Falco rusticolus*	Gyrfalcon
Clanga clanga	Greater Spotted Eagle	*Falco subbuteo*	Eurasian Hobby
Clanga pomarina	Lesser Spotted Eagle	*Falco tinnunculus*	Common Kestrel
Clangula hyemalis	Long-tailed Duck	*Falco vespertinus*	Red-footed Falcon
Coccothraustes coccothraustes	Hawfinch	*Ficedula albicollis*	Collared Flycatcher
Columba bollii	Dark-tailed Laurel-pigeon	*Ficedula hypoleuca*	European Pied Flycatcher
Columba junoniae	White-tailed Laurel-pigeon	*Ficedula parva*	Red-breasted Flycatcher
Columba livia	Rock Dove	*Ficedula semitorquata*	Semi-collared Flycatcher
Columba oenas	Stock Dove	*Francolinus francolinus*	Black Francolin
Columba palumbus	Common Woodpigeon	*Fratercula arctica*	Atlantic Puffin
Columba trocaz	Madeira Laurel-pigeon	*Fringilla coelebs*	Common Chaffinch
Coracias garrulus	European Roller	*Fringilla montifringilla*	Brambling
Corvus corax	Common Raven	*Fringilla polatzeki*	Gran Canaria Blue Chaffinch
Corvus corone	Carrion Crow	*Fringilla teydea*	Tenerife Blue Chaffinch
Corvus frugilegus	Rook	*Fulica atra*	Common Coot
Corvus monedula	Eurasian Jackdaw	*Fulica cristata*	Red-knobbed Coot
Coturnix coturnix	Common Quail	*Fulmarus glacialis*	Northern Fulmar

Scientific name	Common name
Galerida cristata	Crested Lark
Galerida theklae	Thekla's Lark
Gallinago gallinago	Common Snipe
Gallinago media	Great Snipe
Gallinago stenura	Pintail Snipe
Gallinula chloropus	Common Moorhen
Garrulus glandarius	Eurasian Jay
Gavia adamsii	Yellow-billed Loon
Gavia arctica	Arctic Loon
Gavia immer	Common Loon
Gavia stellata	Red-throated Loon
Gelochelidon nilotica	Common Gull-billed Tern
Geronticus eremita	Northern Bald Ibis
Glareola nordmanni	Black-winged Pratincole
Glareola pratincola	Collared Pratincole
Glaucidium passerinum	Eurasian Pygmy-owl
Grus grus	Common Crane
Gymnoris xanthocollis	Chestnut-back Bush-sparrow
Gypaetus barbatus	Bearded Vulture
Gyps fulvus	Griffon Vulture
Haematopus ostralegus	Eurasian Oystercatcher
Halcyon smyrnensis	White-breasted Kingfisher
Haliaeetus albicilla	White-tailed Sea-eagle
Hieraaetus pennatus	Booted Eagle
Himantopus himantopus	Black-winged Stilt
Hippolais icterina	Icterine Warbler
Hippolais languida	Upcher's Warbler
Hippolais olivetorum	Olive-tree Warbler
Hippolais polyglotta	Melodious Warbler
Hirundo rustica	Barn Swallow
Histrionicus histrionicus	Harlequin Duck
Hydrobates castro	Band-rumped Storm-petrel
Hydrobates leucorhous	Leach's Storm-petrel
Hydrobates monteiroi	Monteiro's Storm-petrel
Hydrobates pelagicus	European Storm-petrel
Hydrocoloeus minutus	Little Gull
Hydroprogne caspia	Caspian Tern
Iduna caligata	Booted Warbler
Iduna opaca	Isabelline Warbler
Iduna pallida	Olivaceous Warbler
Iduna rama	Sykes's Warbler
Irania gutturalis	White-throated Robin
Ixobrychus minutus	Common Little Bittern
Jynx torquilla	Eurasian Wryneck
Ketupa zeylonensis	Brown Fish-owl
Lagopus lagopus	Willow Grouse
Lagopus muta	Rock Ptarmigan
Lanius collurio	Red-backed Shrike
Lanius excubitor	Great Grey Shrike
Lanius meridionalis	Iberian Grey Shrike
Lanius minor	Lesser Grey Shrike
Lanius nubicus	Masked Shrike
Lanius senator	Woodchat Shrike
Larus argentatus	European Herring Gull
Larus armenicus	Armenian Gull
Larus audouinii	Audouin's Gull
Larus cachinnans	Caspian Gull
Larus canus	Mew Gull
Larus fuscus	Lesser Black-backed Gull
Larus genei	Slender-billed Gull
Larus glaucoides	Iceland Gull
Larus hyperboreus	Glaucous Gull

Scientific name	Common name
Larus ichthyaetus	Pallas's Gull
Larus marinus	Great Black-backed Gull
Larus melanocephalus	Mediterranean Gull
Larus michahellis	Yellow-legged Gull
Larus ridibundus	Black-headed Gull
Leiopicus medius	Middle Spotted Woodpecker
Limosa lapponica	Bar-tailed Godwit
Limosa limosa	Black-tailed Godwit
Linaria cannabina	Common Linnet
Linaria flavirostris	Twite
Locustella fluviatilis	River Warbler
Locustella lanceolata	Lanceolated Warbler
Locustella luscinioides	Savi's Warbler
Locustella naevia	Grasshopper-warbler
Lophophanes cristatus	Crested Tit
Loxia curvirostra	Red Crossbill
Loxia leucoptera	Two-barred Crossbill
Loxia pytyopsittacus	Parrot Crossbill
Loxia scotica	Scottish Crossbill
Lullula arborea	Woodlark
Luscinia luscinia	Thrush Nightingale
Luscinia megarhynchos	Common Nightingale
Lymnocryptes minimus	Jack Snipe
Lyrurus mlokosiewiczi	Caucasian Grouse
Lyrurus tetrix	Black Grouse
Mareca penelope	Eurasian Wigeon
Mareca strepera	Gadwall
Marmaronetta angustirostris	Marbled Teal
Melanitta fusca	Velvet Scoter
Melanitta nigra	Common Scoter
Melanocorypha bimaculata	Bimaculated Lark
Melanocorypha calandra	Calandra Lark
Melanocorypha yeltoniensis	Black Lark
Mergellus albellus	Smew
Mergus merganser	Goosander
Mergus serrator	Red-breasted Merganser
Merops apiaster	European Bee-eater
Merops persicus	Blue-cheeked Bee-eater
Microcarbo pygmaeus	Pygmy Cormorant
Milvus migrans	Black Kite
Milvus milvus	Red Kite
Monticola saxatilis	Rufous-tailed Rock-thrush
Monticola solitarius	Blue Rock-thrush
Montifringilla nivalis	White-winged Snowfinch
Morus bassanus	Northern Gannet
Motacilla alba	White Wagtail
Motacilla cinerea	Grey Wagtail
Motacilla citreola	Citrine Wagtail
Motacilla flava	Western Yellow Wagtail
Muscicapa striata	Spotted Flycatcher
Neophron percnopterus	Egyptian Vulture
Netta rufina	Red-crested Pochard
Nucifraga caryocatactes	Northern Nutcracker
Numenius arquata	Eurasian Curlew
Numenius phaeopus	Whimbrel
Numenius tenuirostris	Slender-billed Curlew
Nycticorax nycticorax	Black-crowned Night-heron
Oenanthe chrysopygia	Red-tailed Wheatear
Oenanthe cypriaca	Cyprus Wheatear
Oenanthe deserti	Desert Wheatear
Oenanthe finschii	Finsch's Wheatear
Oenanthe hispanica	Black-eared Wheatear

Scientific name	Common name
Oenanthe isabellina	Isabelline Wheatear
Oenanthe leucura	Black Wheatear
Oenanthe oenanthe	Northern Wheatear
Oenanthe pleschanka	Pied Wheatear
Oenanthe xanthoprymna	Kurdish Wheatear
Oriolus oriolus	Eurasian Golden Oriole
Otis tarda	Great Bustard
Otus brucei	Pallid Scops-owl
Otus scops	Eurasian Scops-owl
Oxyura leucocephala	White-headed Duck
Pagophila eburnea	Ivory Gull
Pandion haliaetus	Osprey
Panurus biarmicus	Bearded Reedling
Parus major	Great Tit
Passer domesticus	House Sparrow
Passer hispaniolensis	Spanish Sparrow
Passer italiae	Italian Sparrow
Passer moabiticus	Dead Sea Sparrow
Passer montanus	Eurasian Tree Sparrow
Pastor roseus	Rosy Starling
Pelagodroma marina	White-faced Storm-petrel
Pelecanus crispus	Dalmatian Pelican
Pelecanus onocrotalus	Great White Pelican
Perdix perdix	Grey Partridge
Periparus ater	Coal Tit
Perisoreus infaustus	Siberian Jay
Pernis apivorus	European Honey-buzzard
Petronia petronia	Rock Sparrow
Phalacrocorax aristotelis	European Shag
Phalacrocorax carbo	Great Cormorant
Phalaropus fulicarius	Red Phalarope
Phalaropus lobatus	Red-necked Phalarope
Phasianus colchicus	Common Pheasant
Phoenicopterus roseus	Greater Flamingo
Phoenicurus erythrogastrus	White-winged Redstart
Phoenicurus ochruros	Black Redstart
Phoenicurus phoenicurus	Common Redstart
Phylloscopus bonelli	Western Bonelli's Warbler
Phylloscopus borealis	Arctic Warbler
Phylloscopus canariensis	Canary Islands Chiffchaff
Phylloscopus collybita	Common Chiffchaff
Phylloscopus ibericus	Iberian Chiffchaff
Phylloscopus inornatus	Yellow-browed Warbler
Phylloscopus nitidus	Green Warbler
Phylloscopus orientalis	Eastern Bonelli's Warbler
Phylloscopus sibilatrix	Wood Warbler
Phylloscopus sindianus	Mountain Chiffchaff
Phylloscopus trochiloides	Greenish Warbler
Phylloscopus trochilus	Willow Warbler
Pica pica	Eurasian Magpie
Picoides tridactylus	Three-toed Woodpecker
Picus canus	Grey-faced Woodpecker
Picus sharpei	Iberian Green Woodpecker
Picus viridis	Eurasian Green Woodpecker
Pinicola enucleator	Pine Grosbeak
Platalea leucorodia	Eurasian Spoonbill
Plectrophenax nivalis	Snow Bunting
Plegadis falcinellus	Glossy Ibis
Pluvialis apricaria	Eurasian Golden Plover
Pluvialis squatarola	Grey Plover
Podiceps auritus	Horned Grebe
Podiceps cristatus	Great Crested Grebe

Scientific name	Common name
Podiceps grisegena	Red-necked Grebe
Podiceps nigricollis	Black-necked Grebe
Poecile cinctus	Siberian Tit
Poecile hyrcanus	Caspian Tit
Poecile lugubris	Sombre Tit
Poecile montanus	Willow Tit
Poecile palustris	Marsh Tit
Polysticta stelleri	Steller's Eider
Porphyrio porphyrio	Purple Swamphen
Porzana porzana	Spotted Crake
Prinia gracilis	Graceful Prinia
Prunella atrogularis	Black-throated Accentor
Prunella collaris	Alpine Accentor
Prunella modularis	Dunnock
Prunella montanella	Siberian Accentor
Prunella ocularis	Radde's Accentor
Pterocles alchata	Pin-tailed Sandgrouse
Pterocles orientalis	Black-bellied Sandgrouse
Pterodroma deserta	Desertas Petrel
Pterodroma madeira	Zino's Petrel
Ptyonoprogne rupestris	Eurasian Crag Martin
Puffinus lherminieri	Audubon's Shearwater
Puffinus mauretanicus	Balearic Shearwater
Puffinus puffinus	Manx Shearwater
Puffinus yelkouan	Yelkouan Shearwater
Pycnonotus xanthopygos	White-spectacled Bulbul
Pyrrhocorax graculus	Yellow-billed Chough
Pyrrhocorax pyrrhocorax	Red-billed Chough
Pyrrhula murina	Azores Bullfinch
Pyrrhula pyrrhula	Eurasian Bullfinch
Rallus aquaticus	Western Water Rail
Recurvirostra avosetta	Pied Avocet
Regulus ignicapilla	Common Firecrest
Regulus madeirensis	Madeira Firecrest
Regulus regulus	Goldcrest
Remiz pendulinus	Eurasian Penduline-tit
Rhodopechys sanguineus	Crimson-winged Finch
Rhodospiza obsoleta	Desert Finch
Rhodostethia rosea	Ross's Gull
Riparia riparia	Collared Sand Martin
Rissa tridactyla	Black-legged Kittiwake
Saxicola dacotiae	Fuerteventura Stonechat
Saxicola rubetra	Whinchat
Saxicola torquatus	Common Stonechat
Scolopax rusticola	Eurasian Woodcock
Serinus canaria	Island Canary
Serinus pusillus	Red-fronted Serin
Serinus serinus	European Serin
Sitta europaea	Eurasian Nuthatch
Sitta krueperi	Krueper's Nuthatch
Sitta neumayer	Western Rock Nuthatch
Sitta tephronota	Eastern Rock Nuthatch
Sitta whiteheadi	Corsican Nuthatch
Somateria mollissima	Common Eider
Somateria spectabilis	King Eider
Spatula clypeata	Northern Shoveler
Spatula querquedula	Garganey
Spilopelia senegalensis	Laughing Dove
Spinus spinus	Eurasian Siskin
Stercorarius longicaudus	Long-tailed Jaeger
Stercorarius parasiticus	Arctic Jaeger
Stercorarius pomarinus	Pomarine Jaeger

Scientific name	Common name
Sterna dougallii	Roseate Tern
Sterna hirundo	Common Tern
Sterna paradisaea	Arctic Tern
Sternula albifrons	Little Tern
Streptopelia decaocto	Eurasian Collared-dove
Streptopelia turtur	European Turtle-dove
Strix aluco	Tawny Owl
Strix nebulosa	Great Grey Owl
Strix uralensis	Ural Owl
Sturnus unicolor	Spotless Starling
Sturnus vulgaris	Common Starling
Surnia ulula	Northern Hawk-owl
Sylvia atricapilla	Eurasian Blackcap
Sylvia balearica	Balearic Warbler
Sylvia borin	Garden Warbler
Sylvia cantillans	Subalpine Warbler
Sylvia communis	Common Whitethroat
Sylvia conspicillata	Spectacled Warbler
Sylvia crassirostris	Eastern Orphean Warbler
Sylvia curruca	Lesser Whitethroat
Sylvia hortensis	Western Orphean Warbler
Sylvia melanocephala	Sardinian Warbler
Sylvia melanothorax	Cyprus Warbler
Sylvia mystacea	Menetries's Warbler
Sylvia nana	Asian Desert Warbler
Sylvia nisoria	Barred Warbler
Sylvia ruppeli	Rüppell's Warbler
Sylvia sarda	Marmora's Warbler
Sylvia subalpina	Moltoni's Warbler
Sylvia undata	Dartford Warbler
Syrrhaptes paradoxus	Pallas's Sandgrouse
Tachybaptus ruficollis	Little Grebe
Tachymarptis melba	Alpine Swift
Tadorna ferruginea	Ruddy Shelduck
Tadorna tadorna	Common Shelduck
Tarsiger cyanurus	Orange-flanked Bush-robin
Tetrao urogallus	Western Capercaillie
Tetraogallus caspius	Caspian Snowcock
Tetraogallus caucasicus	Caucasian Snowcock
Tetrax tetrax	Little Bustard
Thalasseus sandvicensis	Sandwich Tern
Tichodroma muraria	Wallcreeper
Tringa erythropus	Spotted Redshank
Tringa glareola	Wood Sandpiper
Tringa nebularia	Common Greenshank
Tringa ochropus	Green Sandpiper
Tringa stagnatilis	Marsh Sandpiper
Tringa totanus	Common Redshank
Troglodytes troglodytes	Northern Wren
Turdus atrogularis	Black-throated Thrush
Turdus iliacus	Redwing
Turdus merula	Eurasian Blackbird
Turdus philomelos	Song Thrush
Turdus pilaris	Fieldfare
Turdus torquatus	Ring Ouzel
Turdus viscivorus	Mistle Thrush
Turnix sylvaticus	Common Buttonquail
Tyto alba	Common Barn-owl
Upupa epops	Common Hoopoe
Uria aalge	Common Murre
Uria lomvia	Thick-billed Murre
Vanellus gregarius	Sociable Lapwing

Scientific name	Common name
Vanellus indicus	Red-wattled Lapwing
Vanellus leucurus	White-tailed Lapwing
Vanellus spinosus	Spur-winged Lapwing
Vanellus vanellus	Northern Lapwing
Xema sabini	Sabine's Gull
Xenus cinereus	Terek Sandpiper
Zapornia parva	Little Crake
Zapornia pusilla	Baillon's Crake
Zoothera aurea	White's Thrush

Table I: List of the bird species regularly and naturally breeding in the study area according to BirdLife (2017).

The study area (Fig. 5) includes the entire European subcontinent, from Macaronesia (only the islands politically belonging to Spain and Portugal) to the Ural Mountains (west to east) and from Fennoscandia and UK islands to the Mediterranean coast (north to south). I included Turkey, geographically part of Asia, to provide a complete picture of the north-eastern Mediterranean coast. Hereafter, I will generically refer to our study area as Europe.
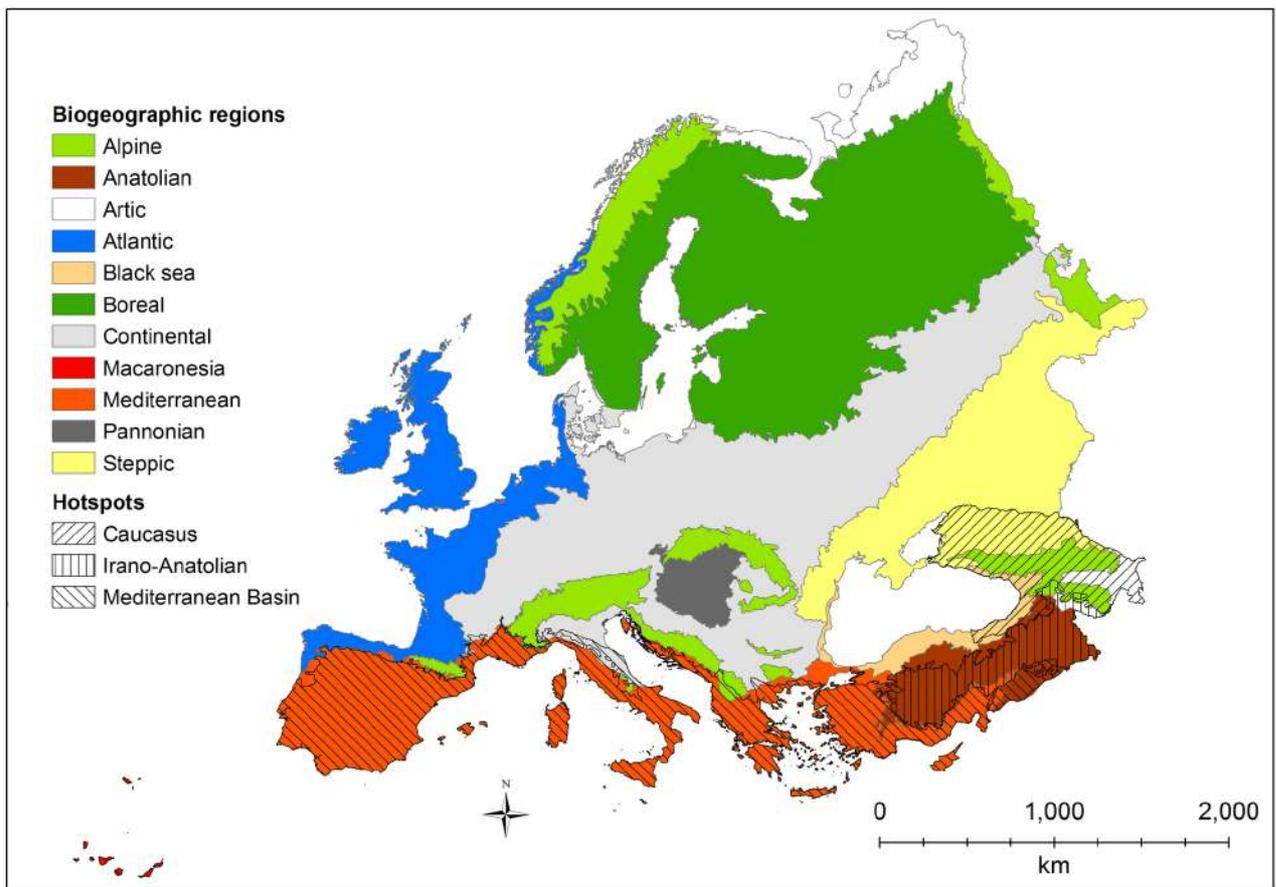
Figure 5: Study area, biogeographic regions as defined by the European Environmental Agency (http://dataservice.eea.europa.eu/dataservice/; accessed on January 2010), and biodiversity hotspots as defined by Myers et al. (2000).

Europe is one of the most densely populated sub-continents in the world, with a long history that has contributed to a high variety of cultural landscapes with their associated biodiversity. Only few areas hosting natural ecosystems remain, and as a consequence Europe has been very active in developing multi-national conservation legislations, including the Bonn and Bern Conventions, and the EU, Birds and Habitats and Species Directives (Pullin et al., 2009).

The continent covers at least 11 biogeographical regions (Fig. 5) and a significant part of three biodiversity hotspots (Myers et al., 2000): the entire northern part of the

Mediterranean basin (58.5% of the total extension of the hotspot), most of the Caucasus (89.4%) and the easternmost part of the Irano-Anatolian region (36.5%). Moreover, several of the Earth's most biologically valuable ecoregions (Olson & Dinerstein, 1998) occur on this continent.

I had the chance to explore the impact of CC on the phenology of trans-Saharan migratory birds by analyzing the data collected for decades during spring migration across the Mediterranean and northern Europe (Jonzén *et al.*, 2006b; Saino *et al.*, 2007). The results of these analyses are presented in my dissertation and highlight how the constant advance of arrival dates at stop-over sites and reproductive territories is correlated with the weather conditions at wintering quarters and on the Mediterranean coasts of Africa, which influence the speed of migration.

More recently, I used species distribution models (SDM) expert-based and validated with data of presence for each of the over 500 European breeding species, and correlative bioclimatic models that, through presence data and climatic variables sets, allowed me to obtain the current ecological niche of the species. By using the results of specific global circulation models (GCM) based on different climatic future scenarios it was possible to project forward the potential climatic distribution of each species. Comparing present and future I was able to obtain indicative results of the impact of CC on the European breeding bird species.

First of all, I mapped all the species within the study area by using Species Distribution Models (SDM). In order to obtain specific SDMs, for each species I collected spatially explicit information on the extent of occurrence over the entire study area (BirdLife's EOOs digital database and national birds' distribution atlases), as well as habitat requirements and all freely available presence data that I could readily access. Whenever possible, habitat requirements were used to refine the EOOs using an expert-based modeling approach, while points of presence were used to evaluate the reliability of the same models.

Habitat requirements were defined by me and published literature, and I considered three environmental variables that I assumed to be informative to model species distribution: land cover, elevation and distance to water. For land cover I used GlobCover V2.2 (offering a complete coverage of our study area with a 300m pixel size and 46 land-use/land-cover classes). I obtained data on elevation from the Shuttle Radar Topography Mission database with a 250m pixel size, while data on running and standing water bodies were obtained from the CCM2 v2.1 river and catchments

database compiled by the European Joint Research Center. I used the data collected to assign to each of the 46 GlobCover land-use/land-cover classes a suitability score. Whenever possible, I recorded the maximum and the minimum elevations at which a stable population of a given species can be found, and the maximum distance to water at which they have been recorded. So, I combined the elevation range with distance to water and habitat suitability scores to refine the available EOOs and obtained a model of the current species distribution with a cell size of 300m (resolution of the available environmental layers). Finally, I collected all the readily and freely available points of presence and used them to evaluate the reliability of the expert-based distribution models.

I used the expert-based distribution models to calculate species richness maps for all breeding species together, species of conservation concern, endemic species. The top 10% richest cells in each map represented the hotspots of species richness.

Average monthly precipitation and temperature were projected using climate model outputs made available through the Intergovernmental Panel on Climate Change (IPCC) Data Distribution Centre. Following, it was defined an ensemble of forecasts of climate change considering four different global circulation models and more than one emission scenarios. In this way it was possible to generate an index of risk of exposure to extreme climates that was used to identify the areas with a significant association between hotspots of diversity and high risk of exposure to extreme climates.

The results I obtained (Maiorano et al., 2013) outline that the richness hotspots for all European breeding birds are within northern central Europe and western Russia. An important hotspot for threatened species is in the eastern-central part of the study area while the species whose distribution is mainly European ('endemic' species) concentrate in northern central Europe, Greece, Alps and Iberian Peninsula.

The analyses' results suggest that the main hotspots of biodiversity for European breeding birds may be extensively influenced by the climate change projected to occur over the coming decades, especially in the Mediterranean bioregion, posing serious concerns for biodiversity conservation.

Secondly, I wanted to understand the effectiveness of the current conservation tools existing for European birds, which, as already seen, are destined to undergo significant environmental changes, often in areas where high levels of biodiversity persist. Therefore, a gap analysis of the entire system of European protected areas (PAs) and the Natura2000 network (N2K: the most important European biodiversity conservation effort carried out on a regional scale) was performed by using validated

species distributions models for all European birds obtained as described before (Maiorano *et al.*, 2013). For each species the representativeness in terms of the suitable area falling within the protected areas network (PAs and N2K) and in Europe was calculated, and the IUCN conservation status and the presence in the annexes of the European Bird Directive were recorded. Furthermore, for each species I considered the threat status and, using the global distribution range obtained as described in the previous chapter, I calculated the percentage of the distribution included in the EU and defined as endemics all species with distributions totally encompassed in the EU.

The results of this analysis were comforting: a) of the 31 species with a strictly European EOO ('endemic'), 90.3% (28 species) is covered by the network of protected areas (PAs + N2K); b) all threatened species result protected by the network; c) a minimum of 74% of species reaches the representative target in the PAs and a maximum of 93% falls within the total coverage (PAs + N2K) (Maiorano et al., 2015). Because the gap analysis was performed for all species of European terrestrial vertebrates (freshwater fish excluded), I could also compare the results obtained for the birds with the ones obtained for the other classes. If the umbrella of protected areas in Europe is valid for birds, the same cannot be assessed for other European terrestrial vertebrates. In reptiles, for example, 60.9% of threatened species are not covered by the European protection network, and even 80.4% of endemic species live outside of it. This raises serious questions, especially concerning the criteria by which a higher level of protection is granted to the territory or by which the species are annexed to conservation directives.

In order to build more realistic scenarios for changes in the distribution of species breeding in continental Europe, at the XVII Italian Congress of Ornithology held in Trento on 2013, I presented a proposal of a modelling approach based on the combination of state-of-the-art bioclimatic models, with expert based habitat suitability and distance to current distribution (Montemaggiori *et al.*, 2015). Thus, for each species, I developed three layers: *a)* a bioclimatic model calibrated with an ensemble forecasting approach, considering six climatic variables and species' occurrences according to European Bird Census Council (EBCC) Atlas' 50 x 50 km cells with semi-quantitative data and high coverage completeness (Hagemeijer & Blair, 1997); *b)* the expert based habitat suitability model developed as described in the first chapter of this dissertation, which considers land use, elevation and distance to water and *c)* the distance from present distribution of the species, mapped

according to BirdLife EOOs digital dataset. Assuming that the three layers are largely independent, I calculated for each species a final model of the relative probability of presence by multiplying the three maps.

I evaluated the reliability of the models using independent points of presence and calculated and index of the calibration capacity of the models for both the classical bioclimatic model and for the final model of relative probability of presence. The results clearly demonstrate that this approach produces more accurate and better performing models compared to simple bioclimatic ones (79% of cases).

Combining this approach with future scenarios for land use and climate, it will be possible to build more robust models showing potential changes in species distribution. Furthermore, it will be possible to incorporate also models of species' biotic interactions and dispersal distances, providing a biologically richer outcome.

Finally, besides knowing where they are, where they will find future EOO and what European birds will encounter in the coming decades, I also wanted to know their degree of vulnerability to the CC.

The adopted approach was to build a vulnerability index (Vi) for the European birds that integrates estimations of projected range change and different proxies of species resilience in a quantitative way. The index, originally proposed by Maggini *et al.*, (2014), is completely quantitative, and it allows ranking species so as to prioritize conservation actions. According to Maggini, I defined the vulnerability index using five indicators expressing three operational aspects of vulnerability: the projected change in the distribution, the reservoirs for the species and the population trend. Two indicators capture the change in the species' future distribution within Europe, two measure the species resilience and one quantify the historical trend of the species over the past 30 years. I used one stressor, climate change, and one spatially explicit scenario, to represent the magnitude of the future change and to assess its impact on species distribution using MaxEnt species distribution model. The vulnerability index was developed for 499 breeding species in Europe.

The five base indicators contribute differently to the vulnerability of a species. The analysis of the single components of the index Vi for each species allows to highlight the relative weight of the different indicators, and a first exploration of the obtained results highlights the highest number of species with a high Vi value in the north-eastern part of the area study, mainly because of the strong reduction of habitat suitability for the future in that area. The average weight of each *taxon*, its diet, its habitat suitability, some behavioral aspects and its conservation status (*sensu* IUCN)

have been used to understand if there are ecological indications linked to the calculated indices, in order to highlight specific management indications. From the analysis it seems to emerge that the most specialized species in terms of habitat seem to be those with higher *Vi* indices; aquatic species are more vulnerable, as well as those nesting on the ground. The degree of vulnerability increases for the larger species and finally the increase in the degree of threat (*sensu* IUCN) increases the value of the vulnerability index.

A more in-depth exploration of these results will be the core of a contribution currently being prepared in the name of A. Montemaggiori & L. Maiorano which is expected to be submitted by April 2018.

Very recently I also started to explore new territories.

While much has been said on the spatial distribution of taxonomic and phylogenetic diversity of large animals, how the associated food-web properties are distributed through geographic and environmental space is largely unknown. So, together with a group of ecologists coordinated by W. Thuiller (CNRS – Grenoble) I contributed to analyze the spatial structure of terrestrial vertebrate food webs and revisit traditional diversity-environmental relationships in light of trophic interactions.

I therefore produced a web of trophic relationships between all European bird species and each single species of European terrestrial vertebrates (mammals, birds, reptiles and amphibians). This ecological web, together with the others built for all the other classes examined, has been combined with the spatial distributions of all the species projected into the future. The results of this analysis, which flowed into a contribution recently submitted (Braga *et al.*, n.d.) and here presented, show an evident effect of CC in modeling the spatial structure of trophic networks among all European terrestrial vertebrates.

Finally, together with T. Kuemmerle (Geography Dept. of Humboldt Berlin University) and L. Maiorano, I am working to a multiscale approach by using also future land use scenarios for Europe, together with climatic scenarios. This is to understand the relative importance of this component in shaping the future of European birds.

3. CLIMATE CHANGE AND MIGRATION #1:

The timing of spring migration in trans-Saharan migrants: a comparison between Ottenby, Sweden and Capri, Italy

Niklas Jonzen, Dario Piacentini, Arne Andersson, Alessandro Montemaggiori, Martin Stervander, Diego Rubolini, Jonas Waldenstrom, Fernando Spina (2006) - *Ornis Svecica* 16, 27-33.

Barbarossa Castle in Capri (NA), where the Ornithological station for bird ringing operated from 1956 to date, thanks to Swedish and Italian researchers (credits Anders Lindströ)

The timing of spring migration in trans-Saharan migrants: a comparison between Ottenby, Sweden and Capri, Italy

Vårflyttningens tidsmönster hos tropikflyttare: en jämförelse mellan Ottenby, Sverige och Capri, Italien

NICLAS JONZÉN, DARIO PIACENTINI, ARNE ANDERSSON, ALESSANDRO MONTEMAGGIORI, MARTIN STERVANDER, DIEGO RUBOLINI, JONAS WALDENSTRÖM & FERNANDO SPINA

─────────── **Abstract** ───────────

Some migratory birds have advanced their spring arrival to Northern Europe, possibly by increasing the speed of migration through Europe in response to increased temperature en route. In this paper we compare the phenology of spring arrival of seven trans-Saharan migrants along their migration route and test for patterns indicating that migration speed varied over the season using long-term data collected on the Italian island of Capri and at Ottenby Bird Observatory, Sweden. There was a linear relationship between median arrival dates on Capri and at Ottenby. The slope was not significantly different from one. On average, the seven species arrived 15 days later at Ottenby compared to Capri. There was a (non-significant) negative relationship between the species-specific arrival dates at Capri and the differences in median arrival dates between Capri and Ottenby, possibly indicating a tendency towards faster migration through Europe later in the season. To what extent different species are able to speed up their migration to benefit from the advancement of spring events is unknown.

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Introduction

Over the past decades many organisms have advanced the timing of spring events, most likely in response to recent climate change (e.g. Stenseth et al. 2002, Walther et al. 2002, Parmesan & Yohe 2003). For instance, recent empirical work has demonstrated changing phenology patterns in the flowering of plant species (Fitter & Fitter 2002), in the emergence from pupae in insects (Roy & Sparks 2000), and in earlier breeding by amphibians (Beebee 1995) and birds (Crick et al. 1997). Most ornithological studies demonstrating temporal trends towards earlier spring arrival or egg-laying dates have been carried out in the temperate region of Europe and North America (reviewed by Lehikoinen et al. 2004, Dunn 2004), whereas only a few publications cover the Mediterranean region or Africa (e.g. Peñuelas et al. 2002, Sanz et al. 2003, Gordo et al. 2005). Thus, at present our understanding of these patterns in migrant birds is somewhat biased towards the situation close to the breeding areas, which makes it difficult to identify to what extent arrival patterns in Northern Europe are caused by processes in Africa or along the migration route through Europe.

One hypothesis to explain how tropical migrants can advance their spring arrival to Northern Europe is that the migration speed through Europe has increased, as suggested by e.g. Hüppop & Hüppop (2003). A more rapid spring migration in response to increased temperature *en route* has recently been demonstrated in the Pied Flycatcher *Ficedula hypoleuca* (Both et al. 2005). However, the ability to speed up migration may be affected

27

by the "normal" speed of migration, which in turn may vary across species.

In this paper, we compare the phenology of spring arrival of seven trans-Saharan migrants along their migration route by analysing long-term data collected on the island of Capri, Italy, and at Ottenby Bird Observatory, Sweden. By analysing the relationship between arrival dates at Ottenby and on Capri we tested for patterns indicating whether migration speed varied over season. Late migrating species may be more time constrained than early migrating species, and they may therefore migrate faster.

Material and methods

Study sites

The island of Capri is situated c. 5 km off mainland Italy, in the bay of Naples, with the trapping site (40°33'N, 14°15'E) located about 400m above sea level (Pettersson et al. 1990, Hjort 2006). In spring, many migrating birds stop to rest, at least for a short time (Holmgren & Engström 2006), on this island after their passage over the Mediterranean Sea. The trapping area on Capri lies mainly within the perimeter of the walls of the old castle Castello Barbarossa and comprises c. 2 ha of macchia vegetation typical for this region of the Mediterranean. However, the plant species and especially the structural composition of the vegetation has changed over the study period, most dramatically by fires (the latest occurred in 1989), which killed the larger pine trees and favoured lower bush vegetation. This could potentially have had an effect on the species composition of the birds trapped, considering that different species have different habitat preferences and the trapping efficiencies of the nets may have changed.

On Capri data have been collected during 45 springs from 1956 to 2004 (no trapping in the period 1982–1985), with the coverage varying from 13 to 89 days per season (Table 1). Birds were trapped with mist nets throughout the study, but the number of nets used varied considerably between, and sometimes also within, years. However, we could not take into account variation in trapping effort in this study. The spring trapping season on Capri is included in the Progetto Piccole Isole, run by the Istituto Nazionale per la Fauna Selvatica (Ozzano Emilia, BO) (Spina 2006).

Ottenby Bird Observatory (56°12' N, 16°24' E) is situated at the southernmost point of Öland, a 137 km long island c.10 km off the coast of south-eastern Sweden. The trapping area in the observatory garden is 1.2 hectares and contains most of the higher vegetation within the nearest 2 km. It is surrounded by water on three sides and by grazed meadows to the north. Birds have been caught at Ottenby in funnel traps of Helgoland-type since the first year of trapping in 1946, and mist nets have been used since 1959. Since 1980 the numbers of nets and traps, their position and use in spring have been strictly standardised. We considered data for 53 spring seasons from 1952–2004 as reliable for the purpose of this study. Details on the data collection at Ottenby Bird Observatory are given elsewhere, e.g. in Stervander et al. (2005).

Species analysed

We have compiled data for seven of the most numerously trapped bird species on Capri: Redstart *Phoenicurus phoenicurus*, Willow Warbler *Phylloscopus trochilus*, Icterine Warbler *Hippolais icterina*, Garden Warbler *Sylvia borin*, Common Whitethroat *Sylvia communis*, Spotted Flycatcher *Muscicapa striata* and Pied Flycatcher *Ficedula hypoleuca*. We have used ringing recoveries from birds ringed on Capri and elsewhere in the Campania region (Naples, Sorrento, Amalfi; Scebba (1993)), and recoveries of birds ringed at Ottenby to sketch putative breeding areas, migration flyways and possible wintering areas of the investigated species. An underlying assumption when comparing arrival times between Capri and Ottenby is that the species trapped belong roughly to the same population.

Statistical analyses

We estimated the median spring arrival date for each of the seven species. The estimated medians were not dependent on whether we only analysed data from years including ringing activity on both Capri and at Ottenby, and we therefore decided to keep data from all years. Due to the large samples, any effect of variability in ringing activity within and between seasons was effectively smoothened out.

Because there are observation errors in both the Capri and the Ottenby data sets we performed a reduced major axis (RMA) to test whether the relationship between median arrival on Capri and at Ottenby differed from unity. RMA regression minimize the product of the deviations from the regression line across both the x (Capri) and the y (Ottenby) variables.

28

Table 1. Ringing details and trapping data from Capri. No ringing in 1982–1985. Species: P.p. = Common Redstart *Phoenicurus phoenicurus*, H.i. = Icterine Warbler *Hippolais icterina*, S.c. = Common Whitethroat *Sylvia communis*, S.b. = Garden Warbler *Sylvia borin*, P.t. = Willow Warbler *Phylloscopus trochilus*, M.s. = Spotted Flycatcher *Muscicapa striata*, F.h. = Pied Flycatcher *Ficedula hypoleuca*.
Fångsuppgifter från ringmärkningen på Capri. Ingen ringmärkning åren 1982–1985. Arter: P.p. = rödstjärt, H.i. = härmsångare, S.c. = törnsångare, S.b. = trädgårdssångare, P.t. = lövsångare, M.s. = grå flugsnappare, F.h. = svartvit flugsnappare.

	Catch period *Fångstperiod*			Number of birds ringed *Antal märkta fåglar*						
Year	Start	Stop	Days	*P.p.*	*H.i.*	*S.c.*	*S.b.*	*P.t.*	*M.s.*	*F.h.*
1956	May 1	May 31	31	25	52	57	77	1	14	16
1957	Apr 1	May 30	60	164	320	227	445	69	125	88
1958	May 1	Jun 11	42	177	501	361	1248	26	339	54
1959	Apr 26	Jun 20	56	199	934	450	1305	53	664	264
1960	Apr 15	May 23	39	618	405	661	1327	235	347	539
1961	Mar 23	Jun 3	73	257	880	563	1472	89	880	286
1962	Mar 9	Jun 5	89	105	103	524	170	204	429	152
1963	Mar 24	May 31	69	196	436	330	683	135	578	343
1964	May 2	May 27	26	44	608	289	993	33	229	37
1965	Apr 14	May 27	44	178	420	451	557	378	203	138
1966	Apr 8	May 27	50	146	427	331	505	108	470	153
1967	Apr 11	Jun 7	58	286	368	240	384	257	194	355
1968	Apr 9	May 23	45	231	265	401	381	288	346	351
1969	Apr 1	May 25	55	197	213	408	163	384	294	180
1970	Apr 7	May 29	53	101	403	593	603	200	382	219
1971	Mar 24	Jun 5	74	140	195	305	223	140	300	144
1972	Apr 25	May 26	32	194	250	200	387	225	193	140
1973	Apr 8	May 26	49	89	403	178	266	101	327	114
1974	Apr 19	May 27	39	75	979	364	910	250	444	89
1975	Apr 11	Jun 2	53	160	374	401	546	124	722	261
1976	Apr 4	May 28	55	44	457	221	233	74	310	108
1977	Apr 19	May 23	35	94	149	188	206	70	241	110
1978	Apr 23	May 30	38	84	358	159	272	81	174	116
1979	Apr 14	May 23	40	108	624	368	666	282	58	183
1980	May 2	May 27	26	37	876	174	423	65	176	46
1981	Apr 15	May 23	39	88	485	171	180	97	195	174
1986	Apr 15	May 22	38	122	730	570	1113	273	474	465
1987	Apr 11	May 24	44	80	600	623	728	259	134	256
1988	Apr 16	May 23	38	41	366	185	237	125	280	176
1989	Mar 18	May 24	68	60	707	614	457	350	258	131
1990	Apr 5	May 23	49	95	757	902	614	197	572	465
1991	Apr 2	May 23	52	90	218	221	170	286	126	341
1992	Apr 5	May 22	48	69	798	419	350	364	538	188
1993	Apr 1	May 21	51	103	522	1105	748	433	324	453
1994	Apr 16	May 15	30	82	314	299	418	226	337	429
1995	Apr 17	May 15	29	81	236	314	302	241	199	357
1996	Apr 16	May 15	30	63	71	262	431	245	49	275
1997	Apr 16	May 15	30	185	334	519	367	422	291	358
1998	Apr 16	May 15	27	83	178	336	338	396	156	362
1999	Apr 16	May 15	29	79	451	448	876	321	245	286
2000	May 1	May 14	13	15	245	287	355	25	117	107
2001	Apr 16	May 15	27	119	79	314	284	457	298	497
2002	Apr 16	May 15	26	133	321	380	266	433	215	297
2003	Apr 16	May 15	30	74	876	320	487	317	260	566
2004	Apr 16	May 15	30	105	448	273	282	364	228	450
Total			1959	5716	19736	17006	23448	9703	13735	11119
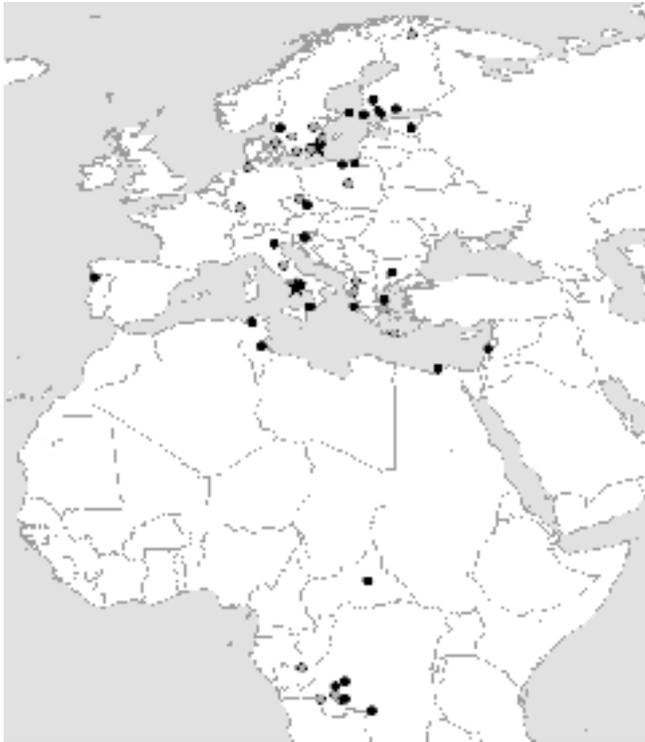
Figure 1. Map showing the recoveries of Spotted Flycatchers *Muscicapa striata* ringed or controlled at Ottenby (grey circles) and Capri (black circles). The black stars indicate the location of Ottenby and Capri. The sample from Capri also includes recoveries of birds ringed or recovered elsewhere in the Campania region (from Scebba 1993).

Återfyndskarta för grå flugsnappare Muscicapa *striata som ringmärkts eller kontrollerats vid Ottenby (grå cirklar) eller Capri (svarta cirklar). De svarta stjärnorna anger Ottenbys och Capris geografiska läge. Caprimaterialet inkluderar återfynd från hela Campania regionen (från Scebba 1993).*

Figure 2. Map showing the recoveries of Icterine Warblers *Hippolais icterina* ringed or controlled at Ottenby (grey circles) and Capri (black circles). The black stars indicate the location of Ottenby and Capri. The sample from Capri also includes recoveries of birds ringed or recovered elsewhere in the Campania region (from Scebba 1993).

Återfyndskarta för Härmsångare Hippolais icterina *som ringmärkts eller kontrollerats vid Ottenby (grå cirklar) eller Capri (svarta cirklar). De svarta stjärnorna anger Ottenbys och Capris geografiska läge. Caprimaterialet inkluderar återfynd från hela Campania regionen (från Scebba 1993).*

Figure 3. Map showing the recoveries of Garden Warblers *Sylvia borin* ringed or controlled at Ottenby (grey circles) and Capri (black circles). The black stars indicate the location of Ottenby and Capri. The sample from Capri also includes recoveries of birds ringed or recovered elsewhere in the Campania region (from Scebba 1993).
Återfyndskarta för Trädgårdssångare Sylvia borin *som ringmärkts eller kontrollerats vid Ottenby (grå cirklar) eller Capri (svarta cirklar). De svarta stjärnorna anger Ottenbys och Capris geografiska läge. Caprimaterialet inkluderar återfynd från hela Campania regionen (från Scebba 1993).*
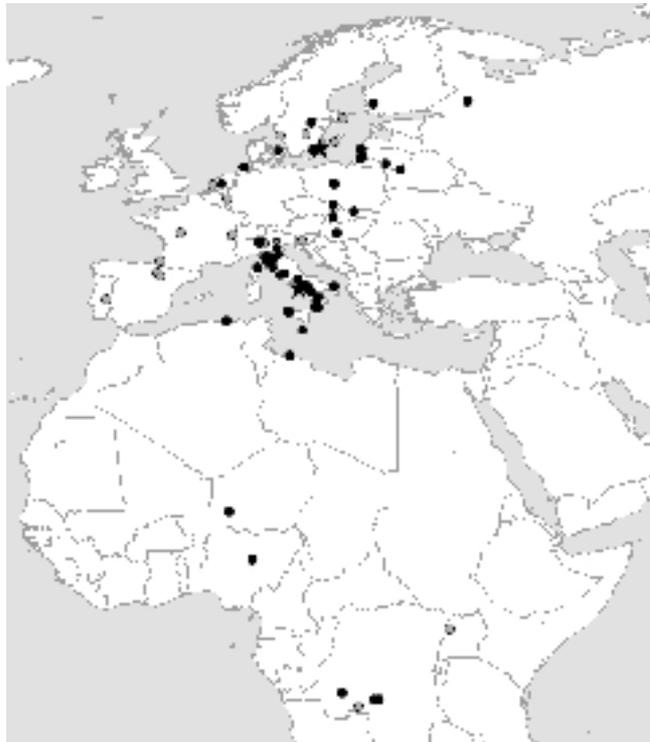
Results

The ringing recoveries indicate that Spotted Flycatchers and Icterine Warblers (Figures 1 and 2) passing Capri follow a central flyway in Europe and Africa, and are later found in the general direction of Ottenby. A similar pattern was also found for Redstarts, Willow Warblers, Common Whitethroats and Pied Flycatchers (not shown). On the other hand, the recoveries of Garden Warblers suggest a more eastern origin of the birds trapped at Capri compared with those trapped at Ottenby (Figure 3).

Figure 4 shows the linear relationship between median arrival dates on Capri and at Ottenby for each species. The point estimate of the slope was 0.87 (t_5 = 8.45, P < 0.001), which is not significantly different from one (95% confidence interval: 0.61–1.14). On average, the seven species migrated 15 days (0.79 SE) later at Ottenby compared to Capri. In order to see if migration speed varied over the season we tested if there was a relationship between species-specific arrival dates on Capri and the differences in median ar-

rival dates between Capri and Ottenby. There was a non-significant negative correlation between the species-specific arrival dates on Capri and the differences in median arrival dates between Capri and Ottenby (r = -0.57, P = 0.18; Figure 5).

Discussion

The strong and positive relationship between migration dates at Ottenby and on Capri suggests that there are either common underlying environmental factors affecting long-distance migrants along their migration route, or that arrival dates are mainly reflecting a specific endogenous time-programme. In long-distance migrants, the onset of migration is known to be under strong endogenous control (Berthold 1996, Gwinner 1996), although the speed of migration through Europe can be affected by local conditions en route, as recently shown in the Pied Flycatcher (Both et al. 2005).

The difference in median arrival date on Capri and at Ottenby may indicate variation in migration speed between species. We find that the Willow Warbler, being the earliest migrant of the species

31
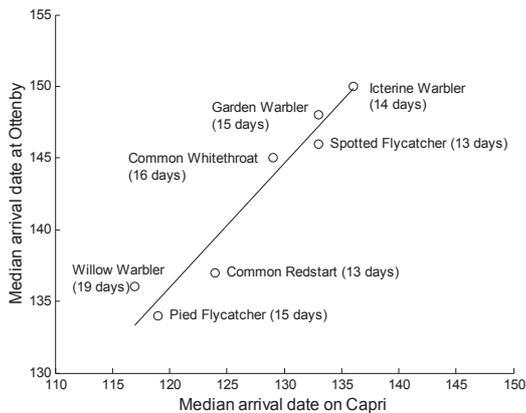
Figure 4. The relationship between median arrival dates on Capri and at Ottenby for seven trans-Sahara migrants, as well as the difference (in days). The line is the estimated slope in a reduced major axis regression (RMA).
Förhållandet mellan mediandatum för vårfångst av sju trans-Saharaflyttare på Capri och vid Ottenby, liksom skillnaden i antal dagar. Den heldragna linjen är den skattade regressionslinjen i en RMA regression.

Figure 5. The differences in median arrival dates between Ottenby and Capri plotted against the species-specific arrival dates on Capri. r = −0.57, P = 0.18
Skillnad i medianankomst mellan Ottenby och Capri vid olika (artspecifik) medianankomst på Capri. r = −0.57, P = 0.18

analysed, is also the species having the largest difference (19 days) in median arrival dates between the two sites. In the same vein, late migrating species such as the Spotted Flycatcher and the Icterine Warbler show a difference of only 13 and 14 days, respectively. However, the overall pattern is weak even though some of the extremes are behaving as expected. It would be interesting to know to what extent the migration speed is limited by the time needed to stop-over. A number of recent studies (e.g. Saino et al. 2004, Both et al. 2005) have shown that arrival time is affected by environmental conditions en route, such that migration speed increases when conditions en route are favourable. If this is a general pattern the timing of migration may not constrain adaptations to climate change as much as previously thought (e.g. Both & Visser 2001, Both et al. 2005).

Competition for territories is an important factor affecting the timing of migration (Kokko 1999). A close look at Figure 4 shows that all species falling below the regression line (i.e., migrating faster than predicted by the linear model) are using cavities as nesting sites. If cavities are limited one may expect severe competition for territories. In fact, comparative evidence indicates that, among trans-Saharan migrants, hole-nesting species migrate earlier than other species in the Mediterranean (Rubolini et al. 2005). However, to

what extent different species are able to speed up their migration to benefit from the advancement of spring events is currently unknown.

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32

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Sammanfattning

Klimatförändringar har gjort att många organismers fenologi har tidigarelagts i norra Europa. Flera tropikflyttande fågelarter anländer allt tidigare och en förklaring till hur detta är möjligt är att flyttningen genom Europa går allt snabbare då vårtemperaturen ökar. Hur pass mycket olika arter kan öka sin flyttningshastighet är okänt och borde bero på deras "normala" hastighet. I denna artikel jämför vi datum för medianankomst på Capri (Italien) och Ottenby (Sverige) på våren hos sju arter som alla övervintrar söder om Sahara. Ringmärkningsåterfynd visar att några arter (t.ex. grå flugsnappare och härmsångare; Figur 1 resp. Figur 2) passerar Capri längs en central flyttningsväg genom Europa och återfinns senare i riktning mot Ottenby. Återfynd av andra arter ringmärkta på Capri (t.ex. trädgårdssångare; Figur 3) pekar på ett östligare ursprung än Ottenby. I Tabell 1 redovisas fångstperioder och antal fångade fåglar under våren på Capri för de sju arter vilkas ankomsttider analyseras i denna uppsats.

Jämför man medianankomst på Capri och Ottenby (Figur 4) finner man att det är ett linjärt förhållande med en lutning på 0.87 som dock inte skiljer sig statistiskt från 1. I genomsnitt passerar de sju studerade arterna 15 dagar senare på Ottenby än på Capri. Det finns även en icke-signifikant antydan till att ju senare en art flyttar desto snabbare flyttar den genom Europa, att döma av skillnader i medianankomst på Ottenby och Capri (Figur 5). Det är okänt i vilken utsträckning olika arter skulle kunna öka sin flyttningshastighet för att dra nytta av vårens allt tidigare ankomst i norra Europa. Det är därför viktigt att man studerar vilka egenskaper som gör att en art har (eller saknar) förmågan att anpassa sig till klimatförändringar.

33

4. CLIMATE CHANGE AND MIGRATION #2:

Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds

Nicola Saino, Diego Rubolini, Niclas Jonzén, Torbjørn Ergon, Alessandro Montemaggiori, Nils Chr. Stenseth, Fernando Spina (2007) - *Climate Research* 35:123-134.

Whitethroat (*Sylvia communis*): very common migrant through Sahel (credits Roger Tiddman).

Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds

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ABSTRACT: The long-term advance in the timing of bird spring migration in the Northern Hemisphere is associated with global climate change. The extent to which changes in bird phenology reflect responses to weather conditions in the wintering or breeding areas, or during migration, however, remains to be elucidated. We analyse the relationships between the timing of spring migration of 9 species of trans-Saharan migratory birds across the Mediterranean, and thermal and precipitation anomalies in the main wintering areas south of the Sahara Desert and in North African stopover areas. Median migration dates were collected on the island of Capri (southern Italy) by standardized mist-netting during 1981 to 2004. High temperatures in sub-Saharan Africa (Sahel and Gulf of Guinea) prior to northward migration (February and March) were associated with advanced migration. Moreover, birds migrated earlier when winter rainfall in North Africa was more abundant. The relationships between relevant meteorological variables and timing of migration were remarkably consistent among species, suggesting a coherent response to the same extrinsic stimuli. All these results were obtained while statistically controlling for the long-term trend towards the earlier timing of spring migration across the Mediterranean that has been documented in previous analyses of the same dataset, a trend that was confirmed by the present analyses. In conclusion, our results suggest that thermal conditions in the wintering quarters, as well as rainfall in North African stopover areas, can influence interannual variation in migration phenology of trans-Saharan migratory birds, although the ecological mechanisms that causally link meteorological conditions to the timing of migration remain a matter of speculation.

KEY WORDS: Arrival date · Long-distance migration · Mediterranean · Sahel · Weather

1. INTRODUCTION

The phenology of bird migration in the Northern Hemisphere has shown remarkable changes during the last decades (see reviews in Møller et al. 2004, Gordo 2007, this issue, Rubolini et al. 2007a, this issue). A general pattern of advanced spring migration and arrival dates to the European breeding areas has been demonstrated for short-distance migratory species, as well as for long-distance migrants that overwinter south of the Sahara desert (Tryjanowski et al. 2002, Cotton 2003, Hüppop & Hüppop 2003, Both et al. 2004, Gordo & Sanz 2005, 2006, Sparks et al. 2005, Jonzén et al. 2006a, Zalakevicius et al. 2006), although excep-

tions have also been documented (Mason 1995, Loxton & Sparks 1999, Peñuelas et al. 2002, Gordo et al. 2005, Peintinger & Schuster 2005). Rapid shifts in migration phenology have been paralleled by a shift in timing of phenological events of other organisms, such as leafing and flowering, or first appearance date of insects (Gordo & Sanz 2005, Menzel et al. 2006, Schwartz et al. 2006).

The consistency of the pattern of phenological shifts across diverse animal and plant taxa and its association with warming, which has occurred during the last decades in the Northern Hemisphere (IPCC 2001), have led to the hypothesis that climatic changes are directly driving the observed trends in phenological events (Both & Visser 2001, Parmesan & Yohe 2003, Root et al. 2003, Ahola et al. 2004, Jonzén et al. 2006a, Schwartz et al. 2006, Gienapp et al. 2007, this issue, Gordo 2007, Rubolini et al. 2007a).

The mechanism that mediates this association may consist of a rapid evolutionary change in the populations of organisms driven by the increasing advantage of early arrival at the breeding grounds (Pulido & Berthold 2004, Jonzén et al. 2006a, 2007, this issue, Pulido 2007, this issue; but see Both 2007), which, in turn, may arise as a consequence of phenological shifts of species (e.g. prey) that are ecologically linked to migratory birds.

Natural selection, however, is also expected to have led to the evolution of mechanisms that allow for phenotypically plastic responses to varying ecological conditions (Schlichting & Pigliucci 1998). Individual migratory birds may thus adjust their decisions on timing of departure from the wintering grounds, migration speed and route, and timing of arrival at the breeding grounds according to contingent ecological conditions (Przybylo et al. 2000, Møller & Merilä 2004, Gordo 2007).

Several studies that have investigated interannual variation in first or mean arrival dates at the breeding grounds in relation to ecological (mainly thermal) conditions at destination upon arrival or along the migration route have demonstrated that in years with relatively high spring temperatures migrants arrive earlier (Huin & Sparks 1998, 2000, Loxton et al. 1998, Sokolov et al. 1998, Sparks & Mason 2001, Tryjanowski et al. 2002, Croxton et al. 2006, Gordo & Sanz 2006, Rubolini et al. 2007b, Sparks & Tryjanowski 2007, this issue). Whatever the mechanisms that allow birds to tune their arrival schedule based on current conditions 100s or 1000s of kilometres ahead, these studies suggest that birds can balance the ecological or socio-sexual costs and benefits of early departure from the wintering areas and arrival at the breeding grounds.

The analysis of the covariation between arrival dates and conditions at destination is made relatively easy by the obvious association between the phenological datum and the area, and thus the ecological conditions to which it refers. Conversely, the analysis of the covariation between arrival or migration dates and conditions in the wintering grounds or en route is hampered by the only superficial knowledge of the spatio-temporal distribution of most migratory species during migration or wintering (Gordo 2007). In a few instances where the wintering areas of a specific breeding population could be identified with reasonable accuracy, variation in ecological conditions during wintering or migration have been shown to result in phenotypic adjustment of the individuals' phenology (e.g. Saino et al. 2004). In other studies, the problem of fuzziness in the identification of wintering areas has been circumvented by analysing the statistical effect of winter conditions in Africa at wide, sub-continental scales (Cotton 2003, Gordo et al. 2005, Rodríguez-Teijeiro et al. 2005, Gordo & Sanz 2006).

In the present study, we analyse the relationships between the median spring migration dates of 9 species of long-distance passerine migrants in southern Italy (island of Capri, Tyrrhenian Sea) and weather conditions at the African wintering/staging grounds. Most of these species breed mainly in Europe, overwinter in the Sahel or south of it, and migrate through southern Europe in April/May (Cramp 1998). Those populations that winter farther south in Africa, however, may stopover in the Sahel during late winter to early spring (Moreau 1972, Morel & Morel 1992, Pilastro & Spina 1997). During spring stopover in the Sahel region, migratory passerines are known to feed on invertebrates but chiefly on a variety of berries (Moreau 1972, Morel 1973, Morel & Morel 1992, Stoate & Moreby 1995). However, from March onwards, ecological conditions deteriorate because of the advancement of the dry season and a marked increase of temperatures (Morel 1973, Morel & Morel 1992). Therefore, thermal conditions in the Sahel in February and March, just before the bulk of migratory movements, may influence the timing of departure of long-distance European migrants because they can affect body condition either directly (e.g. by reducing energy requirements for fattening; Morel 1973), or via an effect on resource availability. Similarly, the amount of Sahel rainfall during the previous year's wet season (June to October), which is known to profoundly influence population dynamics of trans-Saharan migrants (e.g. Peach et al. 1991, Baillie & Peach 1992, Szép 1995), may affect ecological conditions and the timing of departure of migrants from the wintering grounds (e.g. Saino et al. 2004). Thus, we analysed migration dates in relation to temperature in winter to early spring in an African area comprising the Sahel and a region south of it and north of 3° N (hereafter 'Sahel' for sim-

plicity), and in relation to the wet season rainfall of the previous year in the Sahel.

Long-distance spring migrants that fly across the Tyrrhenian Sea depart from the coasts of eastern Algeria, Tunisia and the western Gulf of Sirte to cross the southern central Mediterranean (Pilastro & Spina 1997, Spina et al. 2006). To test for an effect of conditions that migrants encounter en route, we considered temperature and rainfall data from a North African region centred on Tunisia. We used the February to April mean temperature anomalies for Tunisia, because we assume that temperatures in these passage areas do not directly modulate the timing of migration, but rather that general temperature conditions prior to, and during, passage could influence habitat quality for stopover migrants. For precipitation, we considered the Sahel rainfall index (Janowiak 1988) and the mean November to April rainfall anomalies for North Africa. In fact, most rainfall in Tunisia occurs during late autumn to early winter (Wellens 1997), and we speculated that this amount of rainfall can directly affect vegetation and animals (e.g. prey), and thus habitat quality for transient migrants, up to several months later.

2. METHODS

2.1. Study site and species

Migratory birds were captured on the island of Capri (40° 33′ N, 14° 15′ E) (Fig. 1) in the period from 1981 to 2004 (except 1982 to 1985, and 2000) by means of standardized mist-netting (see Jonzén et al. 2006a,b for details). In order to homogenize the trapping effort across years, the data included in this study were restricted to the period April 17 to May 15, which corresponds to the peak migratory period of most trans-Saharan migrants across the central Mediterranean (Spina et al. 1993, Rubolini et al. 2005), when trapping occurred in all years. During spring, long-distance migratory birds stopover at Capri to rest, mainly for a short time (Holmgren & Engström 2006), after the crossing of the Sahara desert and of the Mediterranean Sea (Spina et al. 2006). The trapping area consists of ca. 2 ha of dry and bushy vegetation (*garrigue* and *macchia*). Trapping activities were carried out every day (from dawn to dusk), except in cases of heavy wind or rain (see Jonzén et al. 2006a for details).

The species considered in the present study were 9 common long-distance passerine migrants breeding in Eurasia and wintering in sub-Saharan Africa (see Table 1) (Cramp 1998). All species therefore winter or migrate through the Sahel region before crossing the Sahara Desert and the Mediterranean. The number of yearly captures ranged from 14 to 1153 ind. per species, for a total of 47 352 ind. No data were available for the tree pipit *Anthus trivialis* in 1981.

2.2. Estimating median migration dates

Since the proportion of migrants arriving outside the April 17 to May 15 period may vary from year to year, empirical percentiles from ringing dates may be biased, and may underestimate the variation in measures of the migration distribution. We therefore fitted a Gaussian seasonal distribution curve in a Poisson regression on the daily numbers of trapped birds and used the distribution derived from this analysis to estimate median arrival date of the yearly migratory distributions of each species.
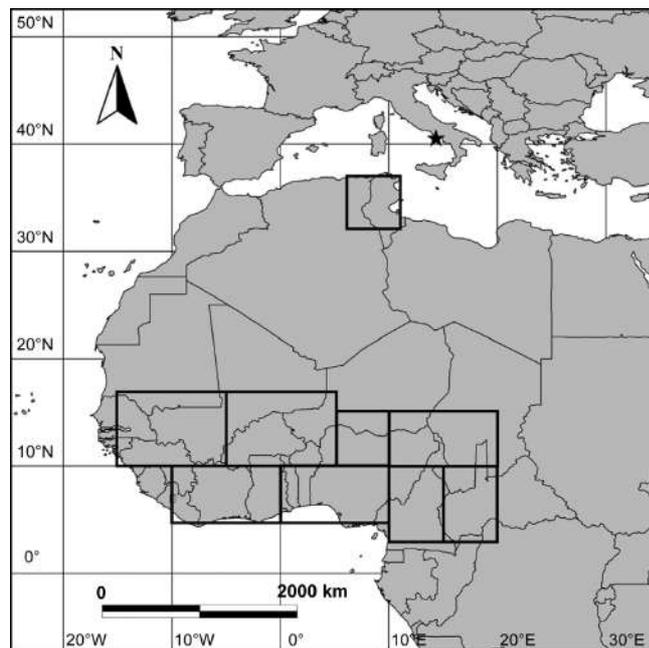
Fig. 1. Map of Africa and southern Europe showing the 8 Sahel regions (from W to E, upper row: Guinea, Burkina Faso, Niger, Chad; lower row: Ivory Coast, Nigeria, Cameroon, Central African Republic). The Tunisia region in North Africa and Capri (star) where migrants were captured are also shown

To account for large extra-Poisson variation in the data due to the huge day-to-day variation in the number of trapped birds, we used Bayesian Markov chain Monte Carlo (MCMC) methods, as implemented in the software WinBUGS 1.4 (Spiegelhalter et al. 2003).

A Gaussian seasonal distribution curve can be fitted as a quadratic function on a logarithmic scale [log (expected number on Day x_i) = $\mu_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2$]. However, the following re-parameterisation gave lower autocorrelations in the MCMC simulations: 'mean' = $\tau = -\beta_1/(2\beta_2)$, 'peak' = $\rho = \beta_0 + \beta_1\tau + \beta_2\tau^2$, and 'standard deviation' = $\kappa = 1/\sqrt{-2\beta_2}$. Two alternative models were considered for modelling the over-dispersion in the data, either a log-normal component of the Poisson parameter [$\log(\lambda_i) = \mu_i + \varepsilon_i$, where $\varepsilon_i \sim N(0,\sigma^2)$], or a stochastic day-effect from a Gamma distribution with the shape parameter being 1/scale parameter [$\lambda_i = e^{\mu_i}v_i$, where $v_i \sim \Gamma(\alpha,1/\alpha)$, $E(v_i) = 1$]. In the first model, the expected number of ringed birds on Day i is $E(\lambda_i) = e^{\mu_i + \sigma^2/2}$. In the latter model, the expected number is $E(\lambda_i) = e^{\mu_i}$. The Gamma model gave better goodness-of-fit statistics (details not shown) and a lower deviance information criterion value, and was hence used in the analyses. The model was fitted for each species separately, and all parameters except α were year specific (α was constant across years). As estimates of migration dates, we used the medians of posterior distributions of the parameter τ.

To facilitate numerical convergence and eliminate nonsensical parameter values from the a posteriori distributions, we constrained the parameter space by using uniform and rather vague priors for the parameters τ (mean passage date) and κ (standard deviation in passage date). For κ of all years and species, we used a uniform (0.25, 10) prior. The priors for mean ringing dates (τ) varied among species and spanned over what we considered the maximum reasonable range for that species (Table 1). The peak of the expectation curve (ρ)

was allowed to vary between 0 and 10 times the maximum observed daily count of the species, which is an almost uninformative prior. The prior of the parameter in the Gamma term accounting for over-dispersion, α, was set to an uninformative Γ(scale = 1/1000, shape = 1000) distribution.

We used relatively long chains in the MCMC simulations due to persistent long-lagged autocorrelations in some parameters (6 parallel chains of 80 000 iterations with an initial burn-in period of 10 000 iterations and thereafter sampling at every 5th iteration). Convergence was confirmed by the Gelman and Rubin statistic (Gelman 1996).

Goodness-of-fit was assessed by using Bayesian p-values (Gelman et al. 1995). An acceptable fit was verified with respect to deviance, skewness and kurtosis of deviance residuals, correlation between deviance residuals and day of the year (x_i), and correlation between the deviance residuals and the fitted expectations e^{μ_i}.

2.3. Weather data

African temperature and rainfall anomalies (TA and RA, respectively) were obtained from the NOAA Satellite and Information Service of the U.S. Department of Commerce (GHCN Land Surface Data, www.ncdc. noaa.gov/gcag/gcag.html). Anomalies are expressed as the deviation from the 1961 to 1990 mean value. We obtained monthly (February and March) TA for 8 regions of sub-Saharan Africa, located between 3° to 17° N and 15° W to 20° E (Fig. 1). Regions were identified by the name of 1 country encompassing each area (Fig. 1). Four of these regions (Guinea, Burkina Faso, Niger, Chad) are mostly within the 'true' Sahel region, whereas the other 4 are in adjacent areas with tropical climate (Morel & Morel 1992).

Table 1. Priors for mean passage dates on Capri. The parameters τ were constrained to fall within the intervals indicated for each species by using a uniform prior value. The range of estimated values of τ (based on the medians of the posterior distributions over all years) are shown to the right (see Section 2.2 and Jonzén et al. 2006a)

Taxon	Common name	Earliest allowed mean date	Latest allowed mean date	Range in estimated median date
Sylvia borin	Garden warbler	Apr 15	May 30	May 8 to May 17
Hippolais icterina	Icterine warbler	Apr 25	May 25	May 7 to May 21
Ficedula hypoleuca	Pied flycatcher	Apr 15	May 20	Apr 19 to May 2
Phoenicurus phoenicurus	Redstart	Mar 10	May 15	Apr 24 to May 6
Muscicapa striata	Spotted flycatcher	Apr 20	May 25	May 3 to May 18
Anthus trivialis	Tree pipit	Mar 25	May 10	Apr 21 to May 6
Saxicola rubetra	Whinchat	Apr 5	May 20	Apr 23 to May 11
Sylvia communis	Whitethroat	Mar 25	May 25	Apr 29 to May 14
Phylloscopus trochilus	Willow warbler	Mar 15	May 15	Apr 20 to May 3

As an indication of the amount of rainfall in the Sahel, which could be an indicator of habitat quality for migratory birds (Møller 1989, Peach et al. 1991, Szép 1995), we used the Sahel wet season rainfall index (RI) (June to October) of the year preceding the arrival of migrants to Capri (jisao.washington.edu/ data_sets/sahel).

We also obtained TA and RA for the area of North Africa that is crossed by birds before landing at Capri, broadly defined as Tunisia (Fig. 1; extreme coordinates, 32° to 37° N and 6° to 11° E). RA were calculated as the mean values from November of the preceding year to April of the year of arrival at Capri.

2.4. Statistical analyses

In order to reduce the number of meteorological variables, we subjected TA for the 8 Sahel regions to principal component analyses (PCA) based on correlation matrices for February and March separately, including TA for the 19 yr that had phenological information from Capri. However, PCA for the tree pipit was based on 18 yr, as phenological data from 1981 were not available (see Section 2.1). To analyse the effect of weather variables on median timing of spring migration for each species, we ran multiple regression analyses, where the principal components (PCs) of the Sahel temperature were included as predictors. Year was always included to control for any long-term temporal trend in the timing of spring migration (Jonzén et al. 2006a). Other weather variables (i.e. Tunisia TA, Sahel RI and Tunisia RA) were added separately to models containing year and PCs to test for concomitant additional effects of weather conditions along the migration route (Tunisia anomalies) or winter ecological conditions in the passage areas (Sahel rainfall).

The relationships between median timing of spring migration at Capri and weather conditions were analysed across all species, by calculating the mean slopes for each predictor included in the multiple regression models for each species. We then calculated the 95 % CI of these effects based on the sampling variance of each of the estimated slopes (i.e. considering the set of species as given, and not a random sample; see formula in Table 4), and the significance of the relationships was evaluated by checking whether estimated confidence intervals included 0. The strength of the effects of weather variables across all species for a given set of models was expressed as the mean of Zr-transformed standardized regression coefficients of each species and variable (Rosenthal 1991). No significant temporal autocorrelation in median migration dates emerged for all species at Box-Ljung tests (details not shown).

3. RESULTS

3.1. Correlations among temperature and rainfall in the Sahel and Tunisia

TA in February or March for the 8 sub-Saharan regions were subjected to separate PCA. Both analyses extracted 2 PCs with an associated eigenvalue >1, which collectively explained >90 % of the variance; these were used in subsequent analyses. The factor loadings for February indicated that PC1 was a vector of increasing TA, mainly in the 6 easternmost regions, while PC2 was mainly a vector of increasing TA in western Guinea and the Ivory Coast (Table 2). The analysis on TA in March led to similar results, with the exception that TA for Burkina Faso also had a high loading on PC2 (Table 2). Overall, these analyses suggest that the pattern of variation in TA in western 'Sahel' during late winter varied along a west to east axis.

The PC1 for February was negatively correlated with the Sahel RI (r = −0.50, n = 19, p = 0.031) and positively correlated with TA (r = 0.65, n = 19, p = 0.002), but not with RA in Tunisia (r = −0.21, n = 19, p = 0.38). A significant positive correlation existed also between PC2 in March and TA in Tunisia (r = 0.67, n = 19, p = 0.002). The correlations between the PCs and Sahel RI and TA or RA in Tunisia were far from statistical significance in all the other cases (unsigned r < 0.36, n = 19, p > 0.13).

TA in the Sahel did not show any significant temporal trend of variation during the study years (regression of PC1 or PC2 for February or March on year was always nonsignificant; p > 0.05). TA in Tunisia increased significantly by 0.11°C (0.02 SE) per year ($t_{17} = 5.14$, p < 0.001). The Sahel RI increased by 0.062 units (0.023 SE) per year ($t_{17} = 2.66$, p = 0.017), whereas no significant temporal variation existed in Tunisia RA ($t_{17} = 0.64$, p = 0.53).

Table 2. Principal component loadings of February or March temperature anomalies (TA) computed over the 19 study yr (see Section 2.4) for 8 sub-Saharan regions (see Fig. 1). The percentage of variance explained by each component is given in parentheses. The principal component analysis (PCA) of TA during the 18 yr when the tree pipit *Anthus trivialis* was studied (see Section 2.1) gave strictly similar results and is not reported for brevity

Region	Feb		Mar	
	PC1 (66.5)	PC2 (24.8)	PC1 (57.7)	PC2 (32.3)
Guinea	0.29	0.86	−0.19	0.89
Burkina Faso	0.82	0.47	0.63	0.72
Niger	0.97	−0.17	0.96	−0.18
Chad	0.92	−0.34	0.90	−0.40
Ivory Coast	0.64	0.72	0.37	0.90
Nigeria	0.94	0.12	0.90	0.37
Cameroon	0.90	−0.40	0.91	−0.35
Central African Republic	0.83	−0.44	0.83	−0.11

3.2. Median migration dates in relation to temperature and rainfall anomalies

We first computed simple correlation coefficients between year or meteorological variables and migration date for each species. Mean Fisher *z*-transformed correlation coefficients (Zr) computed across species were significantly <0 for year, PC1 and PC2 from March TA in Sahel, and TA and RA in Tunisia (Table 3).

Because the primary focus of the present study was on the relationship between migration timing and temperature in the Sahel, we initially ran multiple regression analyses of median migration date of the 9 species with year and PC1 and PC2 scores of TA for February or March as independent variables. Mean partial regression coefficients computed across the 9 species were significantly negative for PC1 in both months and PC2 in February (Model 1 in Table 4). The sign of partial regression coefficients for the PCs (Table 4) in combination with that of factor loadings (Table 2) indicates that migration occurred earlier when March temperatures in the Sahel were high; in addition, it

occurred earlier when February temperatures in the western Sahel were high compared to those in the eastern Sahel, as indicated by the sign of the loadings on PC2, which were positive for western and negative for eastern Sahel regions (see Table 2). In these models, the mean partial regression coefficient for the effect of year was also significantly <0, implying a general advancement of migration date in recent years (Jonzén et al. 2006a) (Table 4).

The effects of Sahel RI and RA/TA in Tunisia on median migration dates were tested by adding these terms to Model 1 in Table 4. Each additional term was tested in separate models to reduce the risk of over-parameterisation. The mean of the regression coefficients of March PC1 and February PC2 was significantly <0 in all 3 additional sets of analyses, whereas the mean regression coefficient for February PC1 became nonsignificantly different from 0.

The mean regression coefficients of the Sahel RI and TA in Tunisia were nonsignificantly different from 0 (Table 4; Models 2 and 3), whereas the mean regression coefficient of the RA in Tunisia was <0 (Table 4; Model 4), indicating that migration was advanced in springs that were preceded by autumns and winters with relatively large precipitation. In Models 2 to 4 (Table 4), year retained its significantly negative mean effect, as in Model 1.

The sign of the partial regression coefficients of migration date on the PC1 of March TA and that of RA in Tunisia was negative for all the species considered, and this was the case also for February PC2, with the exception of the spotted flycatcher *Muscicapa striata* (Table 5).

To test for a differential effect of temperature and rainfall data in Africa on the 9 species we ran an analysis of covariance in which we initially included species, year and meteorological variables. None of the interac-

Table 3. Mean Zr-values, 95% confidence limits (CL) from simple correlation analyses of median migration date and meteorological variables. *95% CL excluded 0

Variable	Zr	95% CL
Year	−0.45	−0.59 to −0.30*
PC1 Feb Sahel TA	−0.17	−0.37 to 0.02
PC2 Feb Sahel TA	0.09	−0.06 to 0.23
PC1 Mar Sahel TA	−0.33	−0.44 to −0.22*
PC2 Mar Sahel TA	−0.18	−0.34 to −0.02*
Tunisia TA (Feb–Apr)	−0.22	−0.33 to −0.11*
Sahel RI	−0.18	−0.41 to 0.05
Tunisia RA (Nov–Apr)	−0.38	−0.53 to −0.23*

Table 4. Mean partial regression coefficients (Slope), 95% confidence limits (CL) of median migration date and mean Zr reflecting effect size computed across the 9 species from multiple regression models including year, PCs of February and March temperature anomalies (TA), and Tunisia TA or Sahel rainfall index (RI) or Tunisia rainfall anomalies (RA). Confidence interval is based on the sampling variance of each of the estimated slopes (i.e. considering the set of species as given, and not a random sample). Variance of the mean equals $(1/9)^2 \sum_{i=1}^{9} V_i$, where V_i is the sampling variance of the slope estimate for species i (separate regressions for each species). Mean regression coefficients in bold print significantly differ from 0

Variable	Fits to Model 1			Fits to Model 2			Fits to Model 3			Fits to Model 4		
	Slope	95% CL	Zr	Slope	95% CL	Zr	Slope	95% CL	Zr	Slope	95% CL	Zr
Year	**−0.25**	−0.35 to −0.14	−0.44	**−0.33**	−0.50 to −0.17	−0.66	**−0.24**	−0.37 to −0.11	−0.44	**−0.18**	−0.29 to −0.07	−0.32
PC1 Feb Sahel TA	**−0.60**	−1.18 to −0.01	−0.14	−0.44	−1.08 to 0.21	−0.10	−0.66	−1.36 to 0.03	0.15	0.50	−0.32 to 1.32	0.16
PC2 Feb Sahel TA	**−0.94**	−1.71 to −0.16	−0.26	**−0.94**	−1.73 to −0.15	−0.26	**−0.93**	−1.71 to −0.16	−0.26	**−1.30**	−2.07 to −0.52	−0.36
PC1 Mar Sahel TA	**−1.44**	−2.23 to −0.64	−0.38	**−1.36**	−2.18 to −0.53	−0.35	**−1.42**	−2.22 to −0.62	−0.37	**−1.61**	−2.38 to −0.83	−0.43
PC2 Mar Sahel TA	0.06	−0.59 to 0.70	0.02	−0.32	−1.15 to 0.52	−0.08	0.05	−0.61 to 0.71	0.02	−0.15	−0.79 to 0.48	−0.03
Tunisia TA Feb–Apr		–		1.02	−0.39 to 2.44	0.25		–			–	
Sahel RI		–			–		−0.21	−1.34 to 0.92	−0.02		–	
Tunisia RA Nov–Apr		–			–			–		**−0.14**	−0.21 to −0.06	−0.42

Table 5. Estimates (SE) of multiple regression coefficients for each species (taxonomic names in Table 1) from Model 4 of Table 4 (first row of each cell) and Zr-transformed partial regression coefficients (second row of each cell) reflecting effect size. TA: temperature anomalies; RA: rainfall anomalies. Statistically significant coefficients are indicated in bold print

| Species | Year | Sahel TA | | | | Tunisia RA | Multiple R^2 |
		PC1 Feb	PC2 Feb	PC1 Mar	PC2 Mar		
Garden warbler	−0.22 (0.15) −0.44	0.17 (1.12) 0.05	−0.78 (1.06) −0.23	−1.18 (1.07) −0.36	−0.46 (0.86) −0.14	−0.07 (0.10) −0.24	0.43
Icterine warbler	−0.36 (0.20) −0.59	−0.60 (1.53) −0.14	−0.69 (1.46) −0.16	−0.58 (1.46) −0.14	0.32 (1.18) 0.07	−0.05 (0.14) −0.12	0.33
Pied flycatcher	−0.24 (0.14) −0.42	0.28 (1.04) 0.07	−2.00 (0.99) −0.57	−1.00 (1.00) −0.26	0.24 (0.80) 0.06	**−0.23** (0.09) −0.77	0.62
Redstart	−0.16 (0.13) −0.28	**2.82** (0.97) 0.97	−1.08 (0.92) −0.29	−1.74 (0.93) −0.50	1.39 (0.75) 0.39	**−0.23** (0.09) −0.80	0.65
Spotted flycatcher	0.17 (0.19) 0.23	0.00 (1.47) 0.00	0.05 (1.40) 0.01	−2.26 (1.41) −0.52	**−2.54** (1.13) −0.61	−0.07 (0.13) −0.17	0.48
Tree pipit	0.00 (0.22) 0.01	0.03 (1.38) 0.01	**−2.79** (1.23) −0.95	−2.19 (1.23) −0.66	−0.48 (1.10) −0.13	−0.12 (0.12) −0.37	0.43
Whinchat	−0.27 (0.17) −0.36	0.54 (1.33) 0.11	−2.13 (1.27) −0.47	−2.30 (1.27) −0.51	−0.13 (1.03) −0.03	−0.25 (0.12) −0.64	0.60
Whitethroat	−0.25 (0.15) −0.41	−0.20 (1.18) −0.05	−1.18 (1.12) −0.30	−2.01 (1.13) −0.54	−0.16 (0.91) −0.04	−0.12 (0.11) −0.34	0.56
Willow warbler	−0.30 (0.15) −0.59	1.46 (1.15) 0.43	−1.08 (1.10) −0.31	−1.22 (1.10) −0.35	0.44 (0.89) 0.12	−0.09 (0.10) −0.29	0.46

tion terms significantly predicted variation in migration date, implying that the effect of year and meteorological conditions on migration date did not vary among species (Table 6). The simplified model including only main effects showed significant negative effects of February PC2 and March PC1 of TA in the Sahel, and of RA in Tunisia (Table 6), consistent with the analyses presented in Table 4.

Table 6. Analysis of variance of median migration date of the 9 species over 19 study years (18 yr for the tree pipit *Anthus trivialis*) in relation to year and meteorological data in the Sahel and Tunisia. The interactions between species and year or meteorological variables were invariably nonsignificant and were therefore excluded from the model on the right side of the table. Degrees of freedom of factor and covariates were the same for the 3 models. The model with interactions explained 88% of the total variance, while the other 2 explained 82% of the total variance. Partial eta-squared (η^2_p) is a measure of effect size that is defined as the proportion of the effect plus the error variance that is attributable to the effect. TA: temperature anomalies; RA: rainfall anomalies; RI: rainfall index

| | | Model with interactions | | Model without interactions | | | Step-down model | | | η^2_p |
	df	F	p	F	p	η^2_p	F	p	Coefficient (SE)	
Species	8	0.57	0.80	78.32	0.001	0.80	79.43	0.001		0.80
Year	1	4.39	0.04	5.95	0.02	0.04	23.72	0.001	−0.22 (0.04)	0.13
PC1 Feb Sahel TA	1	0.92	0.34	1.03	0.31	0.01				
PC2 Feb Sahel TA	1	9.60	0.003	10.72	0.001	0.07	10.14	0.002	−1.16 (0.37)	0.06
PC1 Mar Sahel TA	1	13.73	0.001	15.49	0.001	0.09	15.89	0.001	−1.47 (0.37)	0.09
PC2 Mar Sahel TA	1	0.44	0.51	0.50	0.48	0.00				
Tunisia TA (Feb–Apr)	1	0.28	0.60	0.38	0.54	0.00				
Sahel RI	1	0.03	0.87	0.02	0.87	0.00				
Tunisia RA (Nov–Apr)	1	9.72	0.002	11.13	0.001	0.07	16.62	0.001	−0.10 (0.03)	0.10
Species × Year	8	0.57	0.80							
Species × PC1 Feb Sahel TA	8	0.67	0.72							
Species × PC2 Feb Sahel TA	8	0.53	0.83							
Species × PC1 Mar Sahel TA	8	0.24	0.98							
Species × PC2 Mar Sahel TA	8	0.80	0.60							
Species × Tunisia TA (Feb–Apr)	8	0.18	0.99							
Species × Sahel RI	8	0.98	0.46							
Species × Tunisia RA (Nov–Apr)	8	0.41	0.91							
Error df										
Model with interactions	89									
Model without interactions	153									
Step-down model	157									

When the model excluding the interactions (Table 6) was further simplified by step-down removal of non-significant covariates, the effect sizes of PCs of Sahel TA remained virtually unchanged, whereas the effect size associated with RA in Tunisia and that associated with year markedly increased (Table 6).

4. DISCUSSION

The timing of spring migration at a Mediterranean island in 9 European passerine species that winter south of the Sahara was predicted by TA during the pre-migratory period in sub-Saharan wintering/staging regions and by RA during winter and spring in North African areas, where migrants pass before crossing the Mediterranean. Median migration date was anticipated when TA in the Sahel and RA in North Africa were high. The long-term trend towards earlier migration across the Mediterranean (see also Jonzén et al. 2006a, 2007) was further confirmed by our analyses accounting for meteorological conditions during wintering or en route. These associations between meteorological variables and migration date were observed while controlling statistically for temporal trends of variation in median migration date, since the effect of year was partialled out in multiple regression and analysis of covariance models of the effect of meteorological conditions. The strength of the significant effect of TA in the Sahel or RA in Tunisia averaged across species varied from smaller than that of year (see Model 1 in Tables 4 & 6) to larger (see Model 4 in Table 4) and, on average, was of similar magnitude to the year effect. Thus, temporal factors and meteorological conditions appeared to explain partly different components of the total variance in median migration dates.

The pattern of covariation of migration date with meteorological variables was consistent among species. Partial regression coefficients of migration dates on PC1 of March TA in the Sahel and RA in Tunisia were negative for all 9 species (Table 5), and the extent of anticipation of migration date for any given increase of temperatures in the Sahel or rainfall in Tunisia did not vary among the species. The 9 trans-Saharan migrants, therefore, appeared to react with the similar intensity to variation in ecological conditions in the wintering areas and those encountered en route.

Like the few previous studies of the relationships between phenology of migration and conditions in the wintering or stopover areas of trans-Saharan migratory birds (e.g. Cotton 2003, Saino et al. 2004, Both et al. 2005, Gordo et al. 2005, Rodríguez-Teijeiro et al. 2005, Gordo & Sanz 2006, Jonzén et al. 2006a, Sparks & Tryjanowski 2007), the present study is entirely corre-lational. This implies that the observed patterns of covariation between migration dates and meteorological variables in Africa cannot be assumed to reflect causation. Under the yet unverified assumption that the meteorological variables that we considered are ultimate determinants of phenological response, diverse pathways of causation can be envisaged. For instance, relatively high temperatures may act directly on physiological control of the onset of migration in the winter quarters. A perhaps more likely, alternative interpretation is that relatively high temperatures in the Sahel affect proximate ecological factors (e.g. food availability), which promote migrants' physiological conditions before migration, or reduce energy requirements associated with pre-migratory fattening (Morel 1973), thus allowing for earlier departure. An opposite, and, to our knowledge, novel perspective is that high temperatures result in a deterioration of ecological conditions, which prompt birds to depart earlier. Primary production in the Sahel is very low in late winter and further declines until late spring (Morel 1973, Morel & Morel 1992, Philippon et al. 2005). Relatively high temperatures in early spring may further depress primary and secondary productivity in the Sahel, thus accelerating the establishment of unfavourable conditions for migrants. This implies that there would be little scope for birds to remain longer in this area, and they may thus depart even in suboptimal conditions. It may therefore be predicted that the conditions of migrants at arrival in southern Europe should be inferior in years when Sahel spring temperatures are relatively high. This hypothesis has broad implications for the interpretation of the evolutionary and ecological mechanisms that may lead to the prevailing patterns of advancement of migration dates, which have been documented for trans-Saharan migrants over longer periods than those considered in the present study. Temperatures in the Sahel since 1960 have been increasing significantly, as shown by an analysis of February and March TA (mean $Zr = 0.33$; 95% CI 0.15 to 0.51). Thus, the advancement of migration may partly result from the fact that the decline of ecological conditions for migrants wintering in the Sahel tends to start earlier, thus prompting birds to leave the wintering areas in advance. The negative effect of February TA, as reflected by PC2, on migration dates may suggest that migrants start to move earlier from the westernmost parts of the Sahel when temperatures are relatively high and this results in anticipated median migration dates across the Mediterranean.

However, it should be stressed that analyses of time series of first arrival dates, rather than median migration dates as in the present study, of 7 species (only 2 of which were also included in the present study) to diverse European areas has been shown to be posi-

tively, rather than negatively, related to TA in the Sahel (Saino & Ambrosini 2007). This apparent discrepancy may result from species-specific variation in the effects of temperature in the Sahel on migration and arrival, regional variation in these relationships, and/or uncoupling of the phenological information content of *median* migration dates across a single Mediterranean isle and arrival dates of the earliest arriving individual migrants.

Positive RA in North Africa during the main rain season resulted in earlier migration in all 9 species we considered. In this case, the causal effect, if any, on migration is unlikely to be a direct one, because most of the rainfall in North Africa occurs when migrants are still south of the Sahara (Wellens 1997). Relatively rainy winters and early springs may obviously result in enhanced primary and secondary production and, proximately, in more abundant food for migrants. Migrants may simply refuel in North Africa without undergoing any significant fattening (Pilastro & Spina 1997), and refuelling might occur more rapidly in springs following rainy winters with high primary and secondary production (by taking advantage of, e.g., nectar; Schwilch et al. 2001). In a study of the trans-Saharan migratory barn swallow *Hirundo rustica*, it has been shown that high winter NDVI (normalised difference vetatation index) in Algeria is associated with delayed arrival to the breeding areas in Denmark (Møller & Merilä 2004). That study provided evidence of phenotypic plasticity, because changes in arrival date of the same individuals in consecutive years, rather than mean migration dates at population level were analysed. However, the 2 studies seem to point in a different direction, because we observed earlier migration after rainy winters, whereas the study of barn swallows showed a delay after winters with high NDVI, which is associated with high precipitation.

The interpretation of the present findings is also complicated by the possible spatial and temporal autocorrelation of meteorological variables at continental or intercontinental scale. TA in the Sahel and RA in Tunisia may simply be proxies, which correlate with other ecological factors that act either locally or in distant areas and cause the phenology of migration to change (see Forchhammer et al. 2002, Saino & Ambrosini 2007). Such large-scale climate connections (e.g. Visbeck et al. 2001) may result in a correlation between meteorological conditions in different regions at different times of the year. Given the strong selection advantage of adjustment of migration schedules, migrants may have evolved to exploit environmental (e.g. temperature) cues in Africa to predict conditions months later in their breeding range, and fine-tune timing of migration accordingly, an idea which, to date, has never been tested empirically.

Studies of the putative effects of conditions in Africa on the phenology of migration of European birds are scarce. In fact, this is the first study where median migration dates have been analysed in relation to meteorological variables in sub-Saharan and Mediterranean Africa. Four previous studies have investigated the relationships between meteorological variables and first arrival dates, rather than migration dates (Cotton 2003, Gordo et al. 2005, Rodríguez-Teijeiro et al. 2005, Gordo & Sanz 2006). The use of first arrival rather than mean/median migration dates as descriptors of migration phenology has diverse advantages as well as drawbacks (see Sparks et al. 2001). However, first arrival dates may be expected to respond more strongly to variation in extrinsic ecological factors, because the risks associated with anticipating arrival to the breeding grounds can be expected to be higher for individuals that arrive early (Lehikoinen et al. 2004, Rubolini et al. 2007a). The patterns of response to ecological conditions may therefore be expected to differ between these 2 aspects of the migration phenology.

Cotton (2003) found that, in England, first arrival dates of 20 migrant species had advanced with increasing temperatures in sub-Saharan Africa. In that study, correlation analyses of arrival dates and conditions during wintering were based on temperatures in Africa measured on a very large scale and did not statistically control for the effect of temporal trends in both arrival dates and conditions in Africa. Thus, it is not clear whether those associations were mediated by a concomitant effect of year on both migration phenology and conditions in Africa. Gordo et al. (2005) analysed first arrival dates of 6 migratory species in Spain in relation to temperature and precipitation in 5 broad regions encompassing all of sub-Saharan Africa. Consistent with the assumptions of the present study, they found that weather conditions in the Sahel and the coastal areas south of it had a largely prevailing effect on arrival dates. However, high temperatures in the Sahel were associated with delayed arrival of the nightingale *Luscinia megarhynchos*, a species not considered in our study. In addition, Gordo et al. (2005) and Gordo & Sanz (2006) found negative effects of precipitation in the Sahel on arrival dates, whereas we failed to find an association between rainfall in the Sahel and phenology. This discrepancy could arise because of the correlation between year and Sahel rainfall index, which could have obscured a significant effect of Sahel precipitation in multiple regressions where we simultaneously accounted for long-term trends in median migration dates. However, simple correlation analyses between median migration dates of each species and Sahel rainfall failed to reveal any consis-

tent relationship between the 2 variables (see Table 3). Similarly to the present study, Rodríguez-Teijeiro et al. (2005) showed that first arrival dates of the quail *Coturnix coturnix* in Spain were earlier following high temperatures during late winter to early spring in the western (but not eastern) Sahel and North Africa. Finally, Saino et al. (2004) showed that the same individual barn swallows returned earlier from migration after winters with relatively high NDVI in the Sahel and sub-Sahel region, where Italian barn swallows winter.

Thus, the few existing studies of the correlations between conditions in Africa during winter and spring migration phenology have led to different results, although differences in the specific phenological variable under scrutiny, set of species concerned, meteorological or ecological variables considered, and analytical approach strongly suggest caution in comparing these findings.

In conclusion, we showed that variation in migration phenology of 9 common species of trans-Saharan migratory birds at a Mediterranean island is related to temperature in the Sahel wintering areas and rainfall in North African passage areas. Median migration date was earlier when temperatures and precipitation were high. These effects were independent of long-term temporal trends in migration phenology, and were consistent among species. Present results therefore suggest that annual variation in migration phenology partly results from phenotypic adjustment of migration schedules driven by meteorological conditions in Africa during the wintering period, although this does not preclude that microevolutionary changes in migration phenology are occurring in trans-Saharan migrants (Jonzén et al. 2006a, 2007). In our opinion, these findings have obvious relevance to conservation of declining populations of trans-Saharan European migratory birds (e.g. Robinson et al. 2005), as they strongly suggest that migration schedules of trans-Saharan migrants may be influenced by meteorological conditions in the wintering and staging areas. Any differential long-term climatic change in the breeding, wintering and passage areas of these migrants may further jeopardize these declining populations by, for example, uncoupling migration phenology to ecological facts relevant to successful reproduction in Europe.

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5. CLIMATE CHANGE AND SPECIES DISTRIBUTION:

Threats from Climate Change to Terrestrial Vertebrate Hotspots in Europe

Luigi Maiorano, Giovanni Amori, Massimo Capula, Alessandra Falcucci, Monica Masi, Alessandro Montemaggiori, Julien Pottier, Achilleas Psomas, Carlo Rondinini, Danilo Russo, Niklaus E. Zimmermann, Luigi Boitani, Antoine Guisan (2013) – *PLoS ONE* 8(9): e74989.

Siberian jay (*Perisoreus infaustus*) (credits Zsombor Károlyi).

Threats from Climate Change to Terrestrial Vertebrate Hotspots in Europe

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Abstract

We identified hotspots of terrestrial vertebrate species diversity in Europe and adjacent islands. Moreover, we assessed the extent to which by the end of the 21st century such hotspots will be exposed to average monthly temperature and precipitation patterns which can be regarded as extreme if compared to the climate experienced during 1950-2000. In particular, we considered the entire European sub-continent plus Turkey and a total of 1149 species of terrestrial vertebrates. For each species, we developed species-specific expert-based distribution models (validated against field data) which we used to calculate species richness maps for mammals, breeding birds, amphibians, and reptiles. Considering four global circulation model outputs and three emission scenarios, we generated an index of risk of exposure to extreme climates, and we used a bivariate local Moran's *I* to identify the areas with a significant association between hotspots of diversity and high risk of exposure to extreme climates. Our results outline that the Mediterranean basin represents both an important hotspot for biodiversity and especially for threatened species for all taxa. In particular, the Iberian and Italian peninsulas host particularly high species richness as measured over all groups, while the eastern Mediterranean basin is particularly rich in amphibians and reptiles; the islands (both Macaronesian and Mediterranean) host the highest richness of threatened species for all taxa occurs. Our results suggest that the main hotspots of biodiversity for terrestrial vertebrates may be extensively influenced by the climate change projected to occur over the coming decades, especially in the Mediterranean bioregion, posing serious concerns for biodiversity conservation.

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Introduction

Over the 21st century, climate change is projected to be a major driver of species extinction, particularly in combination with additional stressors [1]. Several impacts of climate change on species and ecosystems have already been addressed [2], namely shifts in species' phenology [3], distribution [4,5] or morphology [6]. Obviously, the responses of single species and ecosystems to future climate change will depend on intrinsic characteristics of the taxa considered (e.g., dispersal capacity, phenotypic plasticity, rapid evolutionary changes [7]), on the natural resistance and resilience of biological systems, and on the extent to which future climate regimes will present conditions beyond those previously experienced [8].

The identification of biodiversity hotspots [9], i.e. regions with distinctly high levels of species richness, is particularly important in the conservation arena, as most national and international conservation efforts are usually concentrated in these areas. Hotspot analyses have been performed at regional, continental and global scales, using many databases on species distribution whose availability, at least for vertebrates, has increased exponentially in the last few years (e.g. [10]). The identification of areas with exceptionally high levels of species richness is particularly relevant for Europe, with its considerable political fragmentation, long history of conservation as well as habitat modification and species persecution [11]. Here conservation has to focus on small patches of remnant natural and/or semi-natural habitats

embedded into human-dominated landscapes, often highly threatened by human activities even inside protected areas [12].

Exposure of biodiversity hotspots to significant climate change, and particularly to novel climate conditions [13] will further undermine conservation efforts, potentially leading to high vulnerability for many of the species they host [14]. Therefore the identification of areas with high species richness that in the future may be jeopardized by extreme changes in climate is crucial [8].

Several assessments of future exposure of species and biodiversity to climate change have so far considered at least parts of the European continent, especially focusing on vascular plants [15], terrestrial vertebrates [4,15,16] and selected groups of invertebrates [17]. However, these assessments have usually only relied on a limited set of global change scenarios, have accounted for overall means over the entire time period considered (i.e. not considering climatic extremes), and have all been restricted to a sector of the European continent, most often western Europe (with the exception of [16]). Furthermore, no attention has been paid to environmental factors other than climate (e.g. land-cover), which are often important in determining vertebrate distribution at a higher spatial resolution [18].

Here we considered the entire European continent including Turkey focusing on all terrestrial vertebrates (over 1,100 species of amphibians, reptiles, breeding birds and mammals) and on their ecological requirements to 1) identify hotspots of species richness (for threatened, endemic, and all species) by applying expert-based distribution models (e.g. [19]) and 2) assess the extent to which these diversity hotspots will be exposed, by the end of the 21st century, to average monthly temperature and precipitation patterns which can be regarded as extreme in their deviation from the climate they experienced in 1950-2000. Most previous studies focused on areas of high species turnover or extinction following climate change (e.g., [4]), or addressed primarily the expected impact of climate change on species diversity, turnover and invasion/extinction in nature conservation sites [20], examining the responses of single species and assuming climate change will mainly cause changes in their distribution. In our study we do not make any assumption on species-specific responses, but simply assesses to what degree terrestrial vertebrate hotspots are exposed to extreme climates by the end of the century as projected by global circulation models. Such information is crucial to better develop mitigation actions and plan conservation management for biodiversity hotspots, and biodiversity in general, at large spatial scales.

Materials and Methods

Study area

The study area (Figure 1) includes the entire European sub-continent, from *Macaronesia* (only the islands politically belonging to Spain and Portugal) to the Ural Mountains (west to east) and from Fennoscandia and UK islands to the Mediterranean coast (north to south). We included Turkey, geographically part of Asia, to provide a complete picture of the

north-eastern Mediterranean coast. Hereafter, we will generically refer to our study area as Europe.

Europe is one of the most densely populated sub-continents in the world, with a long history that has contributed to a high variety of cultural landscapes with their associated biodiversity. Only few areas hosting natural ecosystems remain, and as a consequence Europe has been very active in developing multi-national conservation legislations, including the Bonn and Bern Conventions, and the EU, Birds and Habitats and Species Directives [11].

The continent covers at least 11 biogeographical regions (Figure 1) and a significant part of three biodiversity hotspots [9]: the entire northern part of the Mediterranean basin (58.5% of the total extension of the hotspot), most of the Caucasus (89.4%) and the easternmost part of the Irano-Anatolian region (36.5%). Moreover, several of the Earth's most biologically valuable ecoregions [21] and many centers of plant diversity [22] occur on this continent.

Species data

We considered 104 species of amphibians, 248 of reptiles, 288 of mammals and 509 of breeding birds naturally occurring in the study area (1,149 species in total; see Appendix S1 in Supporting Information for more details on the available data). We excluded all introduced species, with the exception of historical introductions today part of the naturally occurring European fauna (e.g. *Genetta genetta*). For each species we collected spatially explicit information on the extent of occurrence (EOO) over the entire study area, as well as habitat requirements and all freely available presence data that we could readily access (more details on data sources below). Whenever possible, habitat requirements were used to refine the EOOs using an expert-based modeling approach, while points of presence were used to evaluate the reliability of the same models (more details below).

We obtained data on the EOO directly in a digital format from the Global Mammal Assessment (http://www.iucnredlist.org/initiatives/mammals; accessed 15 August 2013) and the Global Amphibian Assessment (http://www.iucnredlist.org/initiatives/amphibians; accessed 15 August 2013.) For a few species, these were integrated and corrected with more updated and detailed sources (Appendix S2). For 47 endangered breeding birds we obtained the EOOs from Birdlife International; for the remnant 464 species we combined the data on EOO made available by [23] with those from the Birds of the Western Palearctic interactive DVD-ROM 2006, version 2.0.1; for these species the final EOO was represented by the union of the two data sources. For reptiles, we combined data from [24] with those of the Global Reptile Assessment [25] and other sources (Appendix S2).

Expert-based distribution models and hotspots of diversity

Habitat requirements for 1,018 species (88.6% of all species; 95 amphibians, 483 breeding birds, 272 mammals, and 168 reptiles) were defined by experts (M. Capula for amphibians and reptiles; A. Montemaggiori for breeding birds; G. Amori, D. Russo, and L. Boitani for mammals) and published literature
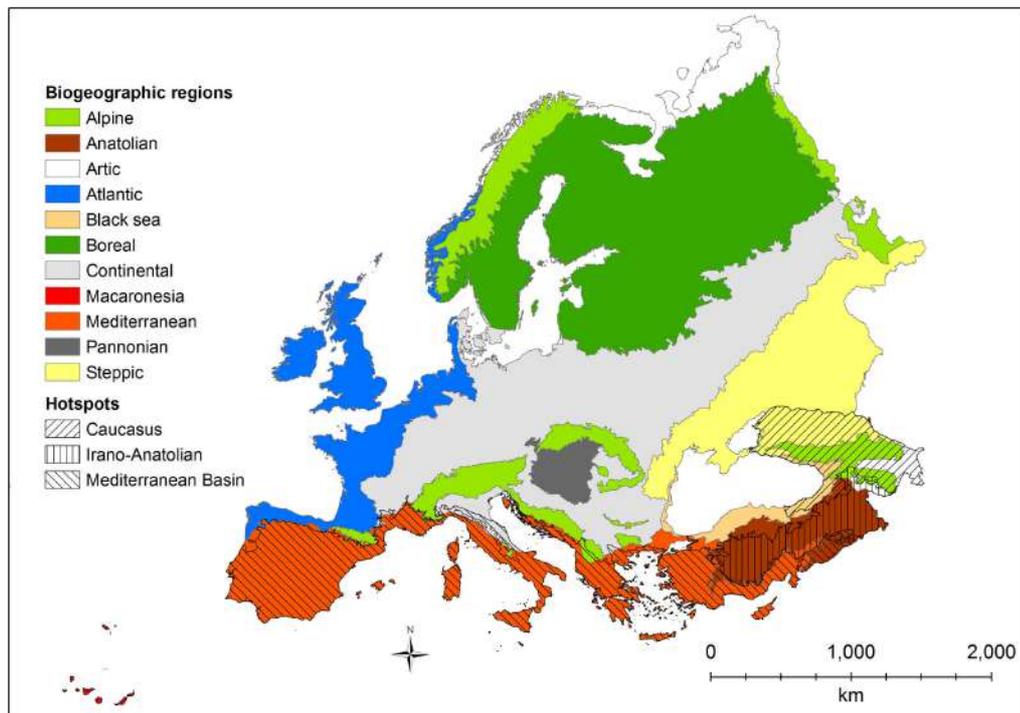
Figure 1.   Study area, biogeographic regions as defined by the European Environmental Agency (http://
dataservice.eea.europa.eu/dataservice/**; accessed on January 2010), and biodiversity hotspots as defined by Myers et al.
(2000).**
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(Appendix S2). For the remaining 131 species either no
information on the ecology was available or the EOO was so
small (for some species below 12 km^2) and detailed that no
further refinement was possible on a continental scale. Each
expert considered three environmental variables that we
assumed to be informative to model species distribution: land
cover, elevation and distance to water. Although such variables
do not all represent direct predictors of species occurrences,
they are more appropriate to derive expert-based rules on
species ecological requirements and additionally offer a
reasonable alternative to the lack of spatially explicit
information on more direct and ecologically important variables
(e.g. prey abundance to model the distribution of predators).
Moreover, the same type of data has already been used
successfully in comparable models applied to a range of study
areas [10,26] and spatial scales [27,28].

We obtained data on land cover from GlobCover V2.2,
offering a complete coverage of our study area with a 300m
pixel size and 46 land-use/land-cover classes (http://
ionia1.esrin.esa.int/; accessed 15 August 2013). We obtained
data on elevation from the Shuttle Radar Topography Mission

database   (http://gisdata.usgs.gov/website/seamless/
viewer.htm; accessed 15 August 2013) with a 250m pixel size,
and resampled the dataset to the same cell size and origin as
the available land cover layer. We obtained data on running
and standing water bodies from the CCM2 v2.1 river and
catchments database compiled by the European Joint
Research Center (http://ccm.jrc.ec.europa.eu/; accessed 15
August 2013).

Setting the same origin and cell size as GlobCover, we used
the CCM2 v2.1 database to calculate a layer of distance to
water.

We used the data collected to assign to each of the 46
GlobCover land-use/land-cover classes a suitability score with
3 possible values: 0, for land-use/land-cover classes which do
not represent a habitat for the species (i.e. habitat where the
species cannot be found except for vagrant individuals); 1, for a
secondary habitat (i.e. habitat where the species can be
present, but does not persist in the absence of primary habitat);
2, for a primary habitat (i.e. habitat where the species can
persist). For 849 species (97 amphibians, 359 breeding birds,
226 mammals, and 167 reptiles) we also recorded the

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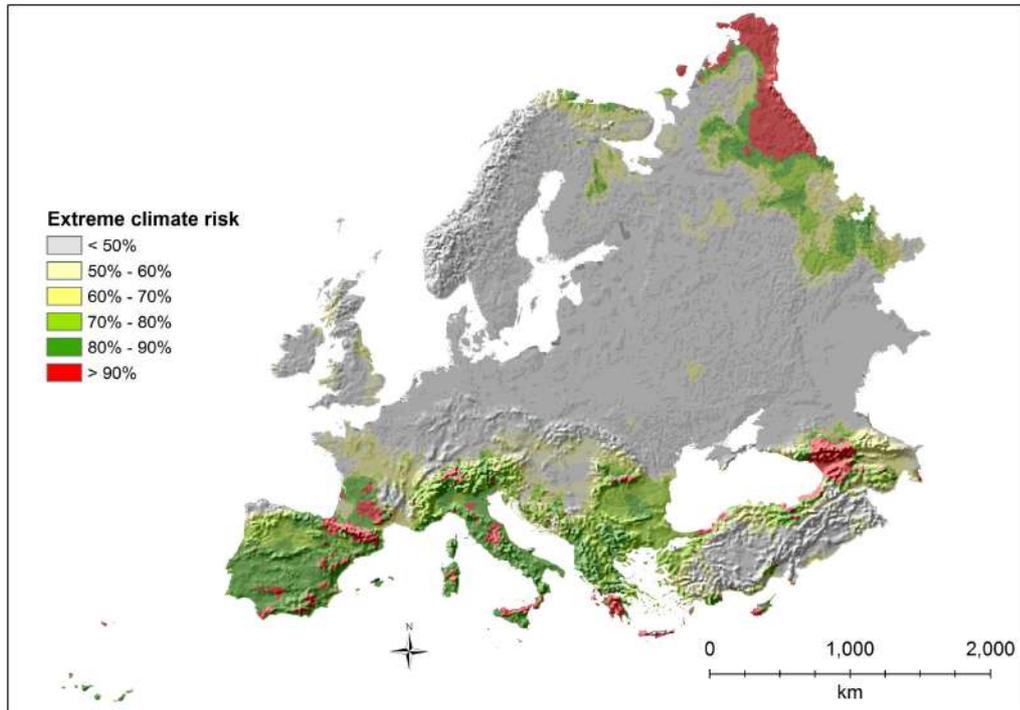
Figure 2. Risk of exposure to extreme climates (expressed in percentage).

maximum and the minimum elevations at which a stable population of a given species can be found, and for 268 species (81 amphibians, 163 breeding birds, 18 mammals, and 6 reptiles) we also obtained the maximum distance to water at which they have been recorded.

We combined the elevation range with distance to water and habitat suitability scores to refine the available EOOs and obtained a model of the current species distribution with a cell size of 300m (resolution of the available environmental layers). In particular, we considered as areas of presence all those within the EOO matching at the same time the elevation range and the distance to water and being classified with a habitat score = 2 (primary habitat). When no reliable information on elevation range, distance to water and habitat preferences was available, we considered the entire EOO for further analyses. All analyses described below were performed considering also secondary plus primary habitats together. Results were similar to those obtained considering only primary habitats and are available as Appendix S3.

For 450 species (44.2% of all expert-based models: 38 amphibians, 283 breeding birds, 93 mammals, 36 reptiles) we collected all the readily and freely available points of presence (list of references in Appendix S4), obtaining on average 663

points per species (minimum = 10 points, maximum = 6187 points), for a total of almost 290,000 points (Figure 2) with associated location errors (minimum ≤ 100m; maximum = 3km). We retrieved points of presence for 22 countries (Austria, Belarus, Cyprus, Czech Republic, Denmark, France, Germany, Greece, Italy, Luxembourg, Montenegro, Netherlands, Norway, Poland, Portugal, Slovenia, Spain, Svalbard, Sweden, Switzerland, Turkey, United Kingdom), with one point only for Belarus, Czech Republic and Slovenia and over 40,000 points each for the UK, Sweden and Italy.

We used the available points of presence to evaluate the reliability of the expert-based distribution models. In particular, if the models are effectively refining the available EOO, the percentage of primary habitat around points of known presence should be significantly higher than that surrounding a similar set of random points (i.e. the expert-based distribution model should be able to discriminate between real presences and background data). To test this hypothesis, for each species we generated 499 sets of random points with the same characteristics as the available points of presence (i.e. number of random points per country equal to the number of available points of presence; distribution of location errors for random points corresponding to the distribution of location errors in the

available points of presence). We generated a circular buffer around each point of presence (radius of the buffer corresponding to the location error) and measured the amount of primary habitat included in all buffers. We performed the same analysis for the 499 sets of random points and measured the statistical significance of the results by a randomization test (H_0: percentage of primary habitat around the points of known presence is not significantly different from the percentage of primary habitat around random points; H_1: percentage of primary habitat around the points of known presence is significantly higher than the percentage of primary habitat around random points).

We used the expert-based distribution models to calculate a species richness map for each taxon separately (amphibians, breeding birds, mammals and reptiles) with a cell size of 10 minutes (same resolution as the climate layers; see below). In particular, we considered a species as present in a 10-minute cell when the latter contained at least one 300m-cell being classified as presence by the original expert-based model. All species richness maps were rescaled from 0 to 100 to make them directly comparable. The top 10% richest cells in each map represented the hotspots of species richness. The same procedure was followed considering only species of conservation concern (IUCN categories: critically endangered, endangered, vulnerable, near threatened) and thus identifying hotspots of threat for each class of vertebrates. Moreover, to highlight the area with a high concentration of endemic or restricted-range species, we also calculated a map of species richness in which each species was weighted considering the percentage of its distribution range included in our study area (hereafter termed endemic species richness). In particular, all presence/absence maps were multiplied by the proportion of their global distribution range included in our study area and then summed together. In this way endemic or almost-endemic species gained a much higher weight in the final map compared to species with a wider distribution. The global distribution range for each species was obtained from the IUCN Global Initiatives (http://www.iucnredlist.org/technical-documents/spatial-data; accessed 15 August 2013).

Exposure to extreme climates

To account for current climate, we considered average monthly precipitation and temperature as given by WORLDCLIM (10' resolution [29];). Future projections for the same variables were derived using climate model outputs made available through the Intergovernmental Panel on Climate Change (IPCC) Data Distribution Centre (http://ipcc-ddc.cru.uea.ac.uk; accessed 15 August 2013). Following [30,31], we defined an ensemble of forecasts of climate change considering different global circulation models and more than one emission scenarios. In particular, we used four global circulation model (GCM) outputs (CGCM31 run by the CCMA, CSIRO's MK35, UKMO's HADCM3, MPI's ECHAM5) that are part of the fourth assessment report [32] for three of the IPCC's emission scenarios: B1 describing a world with reduced use of natural resources and the use of clean and resource-efficient technologies; A2: where the greenhouse gas emission rate continues to increase; and α1B intermediate between the other

two [32]. Climate variables were averaged over the period 2071–2100 for each global circulation models and emission scenarios.

The original global circulation models came with varying resolutions of roughly 2 x 2°, corresponding to 180 x 200 km in our study area. To downscale the climate model output to 10 'we used the change factor method [33-36], commonly used in climatology. To do so, we first calculated anomalies of the future monthly average temperature and precipitation values against the 1950–2000 means generated from the same GCMs, where the latter represents the WORLDCLIM base period. Anomalies represent absolute temperature (Δ°C) and relative precipitation (% change) differences per coarse resolution pixel measured directly from the model output. Second, we downscaled these anomalies to 10' of spatial resolution, using bilinear interpolation. Third, we added the absolute temperature anomalies to WORLDCLIM temperatures and multiplied precipitation by the respective relative anomalies to obtain maps of future monthly mean temperature and precipitation sum for each model and scenario at a 10' spatial resolution. The advantage offered by this procedure is that a possible model offset under current climate is not added to the projected climate trends.

To generate an index of risk of exposure to extreme climates for each 10' cell (same resolution used to calculate species richness) we calculated the standardized Euclidean distance (stD) for both average monthly temperature and precipitation as the distance between the mean (μ) 21st century value and the mean value of the baseline (WORLDCLIM), standardized by the standard deviation (σ) of the baseline climate [37]. The standard deviation values for both precipitation and temperature were calculated using the CRU TS2.1 global database [38] and considering a time frame going from 1950 to 2000. A value of 2σ has been proposed as a good approximation for identifying extreme climate [8] and thus we defined extreme monthly temperature and precipitation where the future climate exceeds the current by 2σ of the baseline μ (i.e., stD > 2σ). For each 10' cell, we calculated an index of risk of exposure to extreme climates as the number of times an extreme temperature and/or precipitation was predicted. Considering the maximum possible number of times an extreme climate is predicted for a given cell (4 global circulation models by 6 climate variables by 12 months by 3 emission scenarios), the results were rescaled from 0 to 100. We assumed that the higher the number of times an extreme climate event is predicted, the higher the risk of exposure to extreme climates for a given cell at the end of the 21st century.

Analyses

We calculated a bivariate global Moran's I [39] for each combination of species richness (all species, threatened species, endemic species) and risk of exposure to extreme climates. Using a spatial randomization approach (9,999 permutations) as implemented in OpenGeoDa 0.9.9.13 (see 39 for all details), we tested whether the global spatial correlation between species richness and the risk of extreme climate was significantly different from what would be expected in case of spatial randomness.

56

To identify the areas with a significant association between hotspots of diversity and high risk of exposure to extreme climates we used a bivariate local Moran's *I* as calculated in OpenGeoDa 0.9.9.13 [39]. The bivariate local Moran's *I* is a simple extension of the univariate local Moran's *I* [39]. While the latter involves the crossproduct of the standardized value of a variable in one location with the value of the same variable averaged over a neighborhood, the bivariate version takes the crossproduct of the standardized value of one variable (species richness in our case) in one location with the value of another variable (risk of extreme climate in our case) averaged over a neighborhood. The bivariate local Moran's *I* tests whether local correlations between values at location *i* and those of its neighbors are significantly different from what would be observed under conditions of random spatial allocation of the value range of our variables.

Given the relatively coarse cell size we adopted, we chose the smallest neighborhood structure possible (acting as a smoothing factor [40]), corresponding to 9 cells. Then, using the same spatial randomization approach [39] with 9,999 permutations, we tested whether local correlation between species richness in one pixel and the risk of extreme climate averaged over the 9 neighboring pixels was significantly different from what would be expected in case of spatial randomness. Areas inside the hotspots of diversity with positive local Moran's *I* and *p*≤0.0001 were considered as particularly critical for the possible effects of climate change on vertebrate biodiversity.

Results

Model evaluation

For almost 95% of the 450 expert-based distribution models considered for the evaluation, the percentage of primary habitat around the points of known presence was significantly higher than the percentage of primary habitat around random points at the α=0.05 level. When each taxon was considered alone, we found no difference, with all groups showing a statistically significant result for more than 90% of the distribution models at the α=0.05 level (amphibians: 92.3%; breeding birds: 94.7%; mammals: 94.7%; reptiles: 97.2%).

Risk of exposure to extreme climates and diversity hotspots

The areas with the highest risk of exposure to extreme climates are concentrated in two main blocks: southern and north-eastern Europe (Figure 2). Almost the entire Mediterranean basin and the surrounding mountain chains, with high probabilities, are predicted to be exposed to extreme climates, with particularly high risks in a few areas of Spain (particularly southern Spain and Pyrenees), south western France, Italy (central Apennines, Sardinia, and northern Sicily), Switzerland, Greece (all Peloponnese and Crete), Cyprus, Turkey (Mediterranean bioregion), and the Caucasus. Especially high risks of extreme climates are also predicted for the far north-east in the Boreal and Arctic bioregions and for the Urals.

Table 1. Global spatial correlation (as measured with Monran's *I* values) between species richness and risk of exposure to extreme climates.

Taxon	Moran's *I*	P-value
All mammals	0.062	0.0001
Threatened mammals	0.172	0.0001
Endemic mammals	0.106	0.0001
All birds	-0.249	0.0001
Threatened birds	-0.036	0.0001
Endemic birds	-0.033	0.0001
All reptiles	0.252	0.0001
Threatened reptiles	0.342	0.0001
Endemic reptiles	0.434	0.0001
All amphibians	-0.004	0.0171
Threatened amphibians	0.317	0.0001
Endemic amphibians	0.145	0.0001

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Overall, species richness for all taxa showed a significant relationship with the risk of exposure to extreme climates (Table 1; see Appendix S5 for the scatter plots). However, given the extremely large sample size that characterizes our analysis, almost every Moran's *I* value would be statistically significant. Therefore, we focused our interpretation of global spatial autocorrelation patterns on Moran's *I* values themselves, not on the associated P values. Considering all species, reptiles showed a relatively strong positive correlation between species richness and high exposure to extreme climates (Table 1; Appendix S5), while no correlation was found for mammals and amphibians. Birds, on the contrary, showed a negative correlation between species richness and high risk of exposure to extreme climates (Table 1; Appendix S5). Considering endemic and threatened species, the relationship did not change for reptiles, but it was positive for mammals and amphibians and non-existing for breeding birds (Table 1; Appendix S5).

Hotspots of species richness for amphibians (Figure 3a) were identified in central Europe (Atlantic and western Continental regions, mainly France and Germany), and in a few, relatively small areas of Spain and Italy (within the Mediterranean basin hotspot). Basically the entire French part of the hotspot is predicted to be exposed to high risks of extreme climates (Figure 3a), together with southern Germany, the Czech Republic, Austria, Croatia, Slovenia, and all the areas in Spain and Italy.

Hotspots of threatened species richness for amphibians (Figure 3b) are almost completely shifted towards the Mediterranean, with the entire Iberian and Italian peninsulas being part of the top 10% richest areas, together with southern France, the coastal areas of the Balkans, the southern coasts of the Black Sea (in Turkey), the Caucasus, and a few areas in southern Turkey. The main Mediterranean islands also are extremely important, particularly Corsica, Sardinia (where many endangered species are also strictly endemic), and Crete. Among these areas, those associated with high risks of extreme climates are limited to Spain, central Italy (along the

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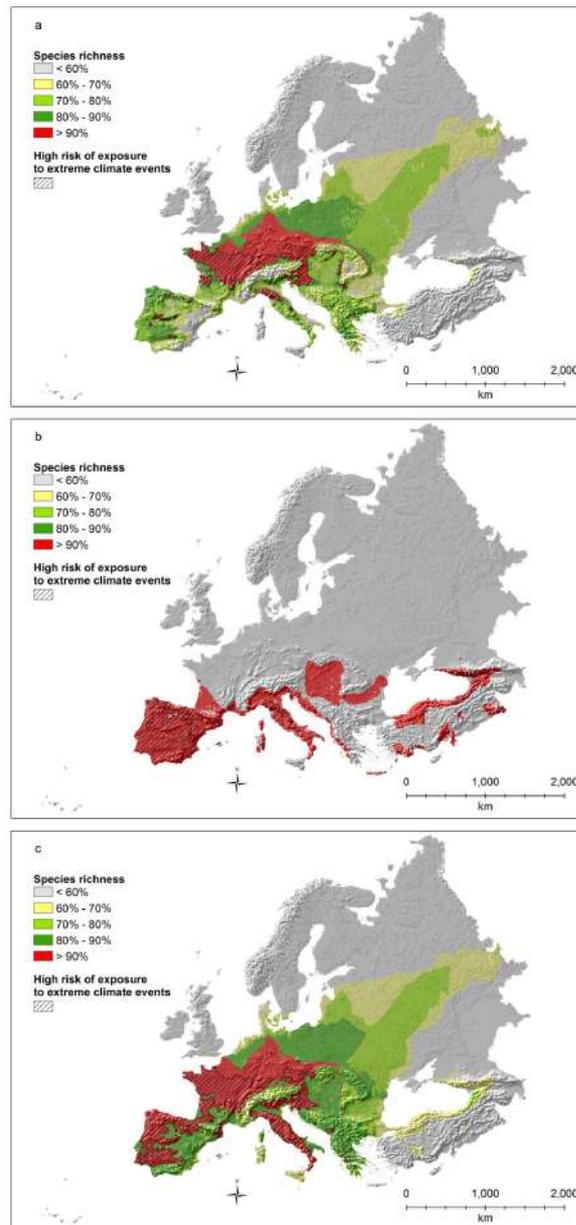
Figure 3. Amphibian species richness (richness values rescaled between 0 and 100; a: all species; b: threatened species as defined by IUCN; c: all species weighted by the percentage of the global distribution occurring inside the study area) and areas with significant overlap (p<0.0001) between risk of exposure to extreme climates and hotspots (top 10% richest cells).

58

Apennines), Sardinia, and northern Turkey/Caucasus (Figure 3b).

Hotspots of endemic species richness for amphibians (Figure 3c) include a large part of the Iberian peninsula, central Europe (mainly France and Germany), and most of the Italian peninsula. The entire Mediterranean part of the hotspot is associated with high risk of extreme climates, together with most of France. On the contrary, most of the German part of the hotspot is not exposed to any particular risk.

Hotspots of species richness for breeding birds (Figure 4a) are almost exclusively located in the eastern part of the study area (continental and boreal regions), except for a few small areas in western Europe, particularly in Greece, Bulgaria, Romania, and Spain. Many hotspots in the western part of the study area are associated with high risks of extreme climates (Figure 4a), although the bulk of the areas at high risk is found in the eastern part of the study area.

Hotspots of species richness for threatened birds (Figure 4b) are again mostly located in the eastern part of the study area and are found almost exclusively in the steppe bioregion. The areas at high risk of exposure to extreme climates are limited to the easternmost part of the study area (Figure 4b).

Hotspots of endemic species richness for birds (Figure 4c) are shifted towards the western part of the study area, including a few Mediterranean islands (like Corsica and the Balearic islands), part of the Iberian peninsula, the Pyrenees and the Alps, and northern Europe, especially along the Baltic coasts. Moreover, a few isolated spots are also present in the United Kingdom, France, central Italy, and Greece. Among these hotspots, the Pyrenees, the Alps, France, Greece, Italy, and the Mediterranean islands are all associated to high risks of extreme climates (Figure 4c).

Hotspots of species diversity for mammals (Figure 5a) clearly show the importance of mountain ranges in the Alpine, Mediterranean and Black sea biogeographic regions (from the Cantabrian mountains, to the Alps, the Apennines, the Balkans, the Rhodope, the Carpathians, and the Caucasus). All these areas are characterized by high risks of exposure to extreme climates, with the exception of the northern part of the Carpathians (Figure 5a).

Considering only threatened species (Figure 5b), almost all hotspots are located in Spain, and particularly in the Mediterranean bioregion, with a couple of small areas also in Bulgaria. Again, the entire hotspot is associated with high risks of exposure to extreme climates (Figure 5b).

Considering endemic species (Figure 5c), all hotspots are located in northern Spain, France, the whole Italy, the Dinaric Alps, the Carpathians, Bulgaria, and in a few small areas in the Caucasus and Greece. Almost all these areas are associated with high risks of exposure to extreme climates, with the exception of the northern Carpathians and of northern France and Germany.

Hotspots of species richness for reptiles (Figure 6a) are clearly located in the Mediterranean and the Anatolian biogeographic regions (Mediterranean, Irano-Anatolian, and Caucasus hotspots), particularly in Turkey, Greece and countries belonging to the former Yugoslavia. A few coastal areas and mountain ranges in Spain also stand out as being

especially important. Almost the entire surface of the hotspot for reptiles is characterized by an extremely high risk of exposure to climate change (Figure 6a), with the exception of a few areas in Turkey.

Considering only threatened species (Figure 6b), Turkey has basically no hotspots, while the Caucasus retains its importance. At the same time, only the Peloponnesus in Greece and a few spots in the former Yugoslavia remain as hotspots, while the Iberian Peninsula gains a prominent role. All these areas are associated with high risks of exposure to extreme climates (Figure 6b).

Greece and the former Yugoslavia represent the main hotspot of richness for endemic reptiles (Figure 6c). Other areas of high species richness are present in Spain, and southern Italy. A few areas are also located in southern France, Turkey, and in the Caucasus. The entire richness hotspot for endemic reptile species is associated with high risks of exposure to extreme climates.

Discussion

The impact of climate change on European biodiversity has been extensively investigated in the last few years, e.g., [5,15,41-43]. Most studies have adopted a species-specific approach, modeling changes in the distribution of single species in response to changes in average climatic conditions. However, most of these analyses account only for changes in potential climate suitability, while overlooking changes in the risk of exposure to extreme climates [44]. Moreover, species are usually considered as independent entities, posing serious concerns on the results, given the importance of biological interactions in communities and ecosystems [45-47].

Although our approach suffers from the same limitation if we consider the single species distribution models, we did not model directly the response of single species to global change, but focused on the occurrence of extreme climates [8]. In this way we are not assuming a lack of biological interactions unlike the typical single species approaches (e.g. [4]), but we identify the regions where current species diversity is extremely high and, at the same time, where climate change is projected to be extreme, thus potentially affecting biodiversity.

The identification of biodiversity hotspots *per se* represents one of the most important goals for conservation biogeography [48] and an important complement to the individual species assessments. Myers et al. [9], for example, identified 34 terrestrial hotspots at the global level (recently reassessed by [49]), and comparable analyses have been performed also for the marine environment [50]. However, most of the regions identified as hotspots are far too extensive and heterogeneous to be treated as a single conservation area, and the spatial resolution usually considered is too coarse to be useful for conservation practice [51].

Identifying key sectors or regional hotspots which warrant special consideration is an essential first step to develop conservation strategies at regional scales. Médail & Diadema [52] focused on the Mediterranean basin to develop conservation strategies and only considered vascular plants in their analysis. Our study is the first to offer a detailed analysis

59
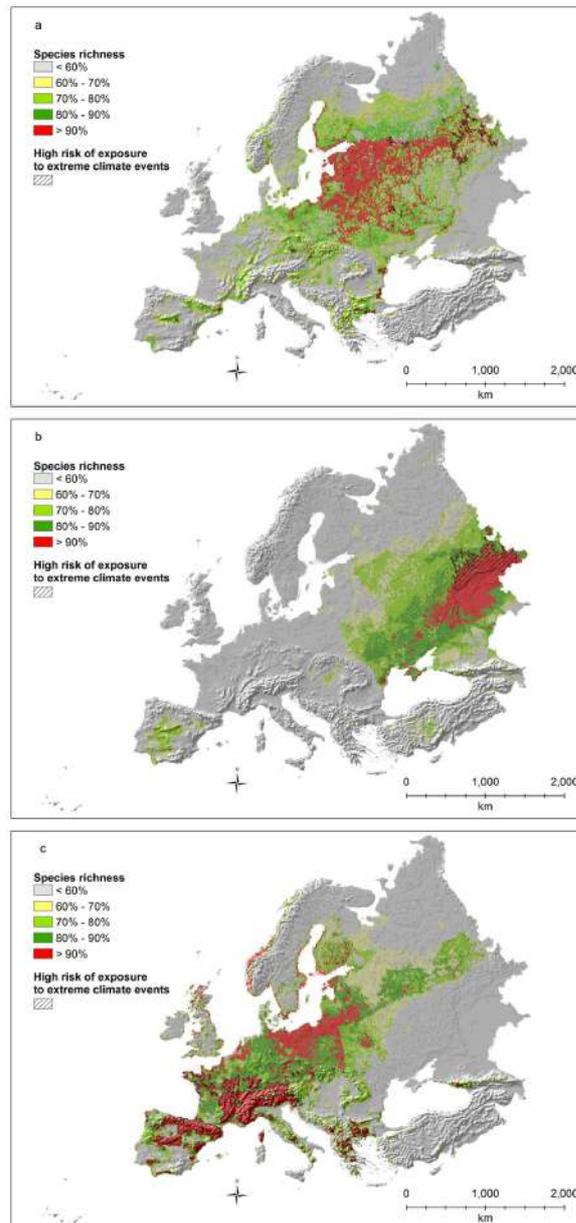
Figure 4. Breeding bird species richness (richness values rescaled between 0 and 100; a: all species; b: threatened species as defined by IUCN; c: all species weighted by the percentage of the global distribution occurring inside the study area) and areas with significant overlap (p<0.0001) between risk of exposure to extreme climates and hotspots (top 10% richest cells).

60
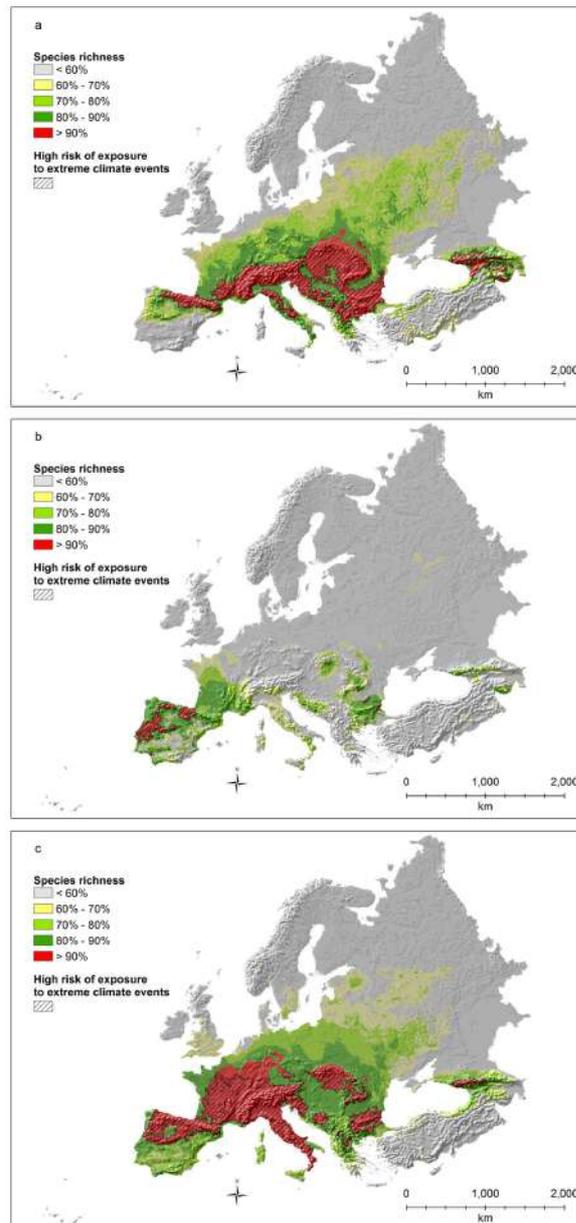
Figure 5. Mammal species richness (richness values rescaled between 0 and 100; a: all species; b: threatened species as defined by IUCN; c: all species weighted by the percentage of the global distribution occurring inside the study area) and areas with significant overlap (p<0.0001) between risk of exposure to extreme climates and hotspots (top 10% richest cells).

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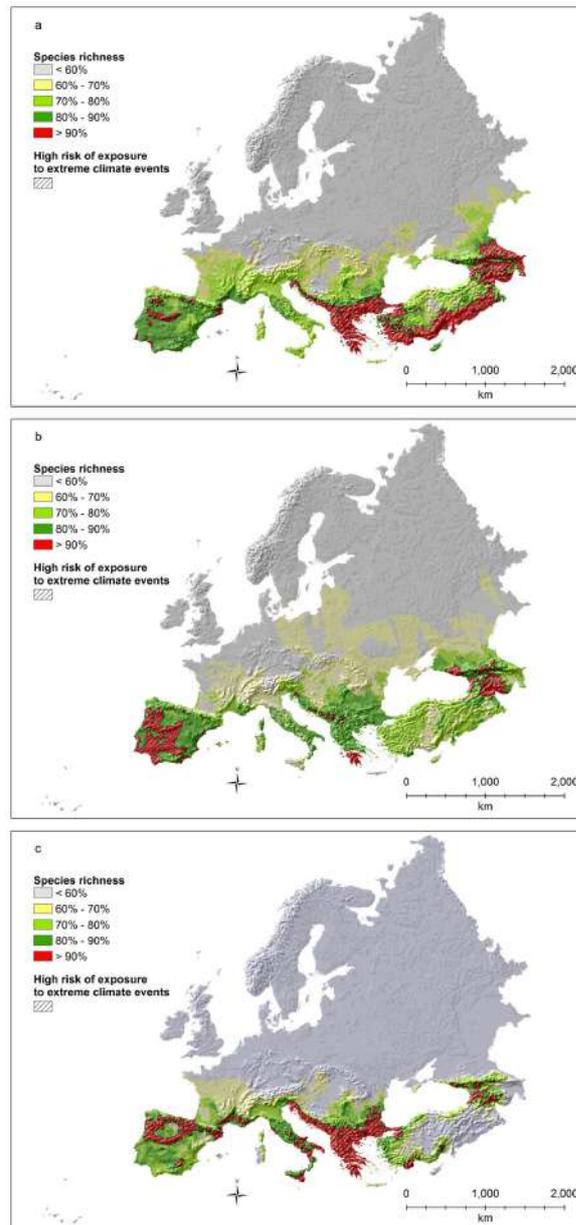
Figure 6. Reptile species richness (richness values rescaled between 0 and 100; a: all species; b: threatened species as defined by IUCN; c: all species weighted by the percentage of the global distribution occurring inside the study area) and areas with significant overlap (p<0.0001) between risk of exposure to extreme climates and hotspots (top 10% richest cells).

62

considering expert-based species distribution models for all terrestrial vertebrates and covering the entire European sub-continent.

We compared more than 44% of our expert based distributions against scarce field data, and in 95% of the cases we obtained a high sensitivity. Moreover, even excluding the 5% of the species without significant results, the general pattern of species richness did not change at all. It is possible that our model evaluation was influenced (positively or negatively) by the lack of points of presence for many countries within our study area. We were able to provide a thorough coverage mainly for Western Europe (from north-western to central and south-western Europe), but not for Eastern Europe. Particularly striking is the limited knowledge of species ranges and their ecology even within biodiversity hotspots such as the Caucasus and interior Turkey, as demonstrated by the paucity of published work on biodiversity for those areas. The same regions, and more generally eastern and south-eastern Europe (e.g. Greece, the Balkans, the Rhodope, the interior Turkey, and the Caucasus), are also characterized by a limited knowledge of species taxonomy, especially for less charismatic taxa like amphibians and reptiles, which may in fact be richer in species and endemicity than what our results show. Still, we did provide an evaluation for some species in Turkey, Cyprus and Poland, and obtained good results. We argue that our distribution models also perform well in the eastern part of the study area, albeit a complete evaluation should also cover Russia, and possibly consider a larger sample of species.

To identify diversity hotspots we applied an arbitrary threshold by identifying the pixels with the top 10% highest values. We understand that the choice of an arbitrary threshold for the identification of biodiversity hotspots is debatable [40], but several previous analyses showed that the richest 1–10% of surface could represent a substantial proportion of terrestrial species [53,54].

Overall the Mediterranean basin appears to be an important hotspot for all taxa, especially when focusing on threatened and/or endemic species. In particular, the Iberian and Italian peninsulas are important for all groups, while the eastern Mediterranean basin (Balkans, Greece, and Turkey) proved important mainly for amphibians and reptiles, but only partially for mammals. The Caucasus and the Irano-Anatolian region – the other two hotspots identified by [9] falling within our study area – proved in general to be less important for terrestrial vertebrates. These regions included only smaller areas of high richness values for mammals (the Caucasus) and reptiles (the Caucasus and Anatolia). The northern coast of Turkey along the Black sea, although not included in any internationally recognized hotspot, stands out as particularly important for amphibians, and partially for reptiles and mammals. Especially important are also the Macaronesian islands and all the major Mediterranean islands (Sardinia and Sicily in Italy, Corsica in France, the Balearic islands in Spain, Crete in Greece, Cyprus) where we identified the highest richness of threatened or endemic species, at least for some taxa.

Considering the global spatial correlation between species richness and the risk of exposure to extreme climate changes, bird species richness is associated with areas less impacted by climate change, while basically in all other cases areas of higher species richness are associated with those with high risk of exposure to extreme climate changes (with the exception of all amphibians, whose global spatial correlation is extremely close to zero; Table 1). Considering the results of the local correlation between species richness and exposure to extreme climate changes, our results suggest that the main hotspots of biodiversity for terrestrial vertebrates may be largely affected by climate change as projected to occur over the coming decades, especially in the Mediterranean bioregion and particularly if we consider endemic and/or threatened species. By the end of the 21st century, many of the hotspots will face temperature and/or precipitation conditions that can be considered as extreme compared to the 1950-2000 baseline period and its variability, as also confirmed by independent analyses performed on different sets of species and study areas [55,56]. Moreover, many of these hotspots are additionally exposed to threats from other environmental and social pressures (e.g. habitat fragmentation, land-use change, industrialization, loss of traditional agricultural practices [11]), substantially increasing the likelihood of a significant biodiversity loss. Yet, opposite results are also predicted in some particular areas, with e.g. an increase in species richness predicted by [4] for Mediterranean mammals in some of the same areas (such as the Alps), yielding uncertainty that will need to be considered in any subsequent conservation action.

However, whether and when extreme climate conditions will result in substantial changes in animal community and/or in species extinctions will depend on a number of factors. Many species will be limited in their ability to react with range shifts, such as those dwelling mountain environments or small islands (both cases fairly common in the Mediterranean basin). On the other hand, species and communities occupying vast areas with relatively homogeneous ecological conditions and limited human impacts (e.g. Russia [57]) might more easily adapt and follow climate change.

The extent of the climatic changes that are likely to occur and the large scale dynamics of species' range shifts needed to counteract the loss of species diversity on a continental scale offer clear evidence that the challenge of conserving biodiversity needs a continent-wide approach to be successful. Local- and national-scale conservation plans have intrinsic limitations in dealing with processes and patterns which concern transboundary areas and cover the entire continent [58]. While local action is necessary to implement conservation measures on the ground, an overall strategic direction must be followed on a continental scale. This is a formidable coordination challenge for the effective application of the many conservation treaties available for Europe (Bern Convention, Bonn Convention, Bird and Habitat Directives), but also a call that cannot be ignored.

Traditional conservation practices (e.g. protected areas) may not be able to counter the detrimental effects of dynamic global changes on biodiversity [12,59], and there is an urgent need for new approaches to optimize biological conservation under climate change [60]. A particularly interesting framework is offered by the Natura2000 network of protected sites of the European Union, a political counterpart that has both the

responsibility and the legal means to implement a continental vision for conservation. The Natura2000 network represents the forefront of biodiversity conservation in Europe, covering *ca* 850,000 km^2 [11]. However, a higher degree of international integration would be important to achieve biologically sound conservation objectives. Our findings could provide important inputs in this regard, especially for those countries whose networks were not assessed in previous studies [20] because they have only recently accessed the European Union (e.g. Romania, Bulgaria, and Croatia), as well as for new accession countries that will join the Union in the near future.

Ian May and Mark Balman from BirdLife International kindly provided the data on the extent of occurrence for 47 species of birds. Additional Supporting Information may be found in the online version of this article.

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Supporting Information

Appendix S1. List of species considered in the analysis.
(XLSX)

Appendix S2. List of references used to update the available extent of occurrence and to define the species' habitat requirements.
(PDF)

Appendix S3. Results obtained by defining species presences with both primary and secondary habitats.
(PDF)

Appendix S4. List of references providing points of presence for one or more species considered in the analyses.
(PDF)

Appendix S5. Scatter plots showing the global spatial correlation (as measured with Monran's *I* values) between species richness and risk of exposure to extreme climates.
(PDF)

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64

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65

6. CLIMATE CHANGE AND SPECIES CONSERVATION:

On how much biodiversity is covered in Europe by national protected areas and by the Natura 2000 network: insights from terrestrial vertebrates

Luigi Maiorano, Giovanni Amori, Alessandro Montemaggiori, Carlo Rondinini, Luca Santini, Sandra Saura, Luigi Boitani (2015) – *Conservation Biology* 29: 986-995.

Male Golden oriole (*Oriolus oriolus*) (credits Jari Peltomäki, M. & W. von Wright).

On how much biodiversity is covered in Europe by national protected areas and by the Natura 2000 network: insights from terrestrial vertebrates

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Abstract: *The European Union has made extensive biodiversity conservation efforts with the Habitats and Birds Directives and with the establishment of the Natura 2000 network of protected areas, one of the largest networks of conservation areas worldwide. We performed a gap analysis of the entire Natura 2000 system plus national protected areas and all terrestrial vertebrates (freshwater fish excluded). We also evaluated the level of connectivity of both systems, providing therefore a first estimate of the functionality of the Natura 2000 system as an effective network of protected areas. Together national protected areas and the Natura 2000 network covered more than one-third of the European Union. National protected areas did not offer protection to 13 total gap species (i.e., species not covered by any protected area) or to almost 300 partial gap species (i.e., species whose representation target is not met). Together the Natura 2000 network and national protected areas left 1 total gap species and 121 partial gap species unprotected. The terrestrial vertebrates listed in the Habitats and Birds Directives were relatively well covered (especially birds), and overall connectivity was improved considerably by Natura 2000 sites that act as stepping stones between national protected areas. Overall, we found that the Natura 2000 network represents at continental level an important network of protected areas that acts as a good complement to existing national protected areas. However, a number of problems remain that are mainly linked to the criteria used to list the species in the Habitats and Birds Directives. The European Commission initiated in 2014 a process aimed at assessing the importance of the Birds and Habitats Directives for biodiversity conservation. Our results contribute to this assessment and suggest the system is largely effective for terrestrial vertebrates but would benefit from further updating of the species lists and field management.*

Keywords: Birds Directive, connectivity, European Union, gap analysis, Habitats Directive

Cuánta Biodiversidad Europea es Tomada en Cuenta por las Áreas Protegidas Nacionales y cuánta por la Red Natura 2000: Percepciones de los Vertebrados Terrestres

Resumen: *La Unión Europea ha hecho esfuerzos extensos de conservación de la biodiversidad con las Directivas de Hábitat y de Aves y con la creación de la red de áreas protegidas Natura 2000, una de las redes más grandes de áreas de conservación a nivel mundial. Realizamos un análisis de falta de datos en todo el sistema Natura 2000 más las áreas protegidas nacionales y todos los vertebrados terrestres (excluimos a los peces de agua dulce). También evaluamos el nivel de conectividad de ambos sistemas, proporcionando así un primer estimado de la funcionalidad del sistema Natura 2000 como una red efectiva de áreas protegidas. La red Natura 2000, junto con las áreas protegidas nacionales, cubrió más de un tercio de la Unión Europea. Las áreas protegidas nacionales no ofrecieron protección para un total de 13 especies del vacío (es decir, las especies que no abarcaron ninguna área protegida) o para casi 300 especies parciales del vacío (es decir, especies cuyo objetivo de representación no es alcanzado). La red Natura 2000, junto con las áreas protegidas nacionales,*

1

dejó un total de una especie del vacío y 121 especies parciales del vacío sin protección. Los vertebrados terrestres enlistados en las Directivas de Hábitat y de Aves fueron tomados en cuenta relativamente bien (especialmente las aves), y la conectividad general mejoró considerablemente por los sitios Natura 2000, los cuales funcionan como peldaño entre las áreas protegidas nacionales. En general, encontramos que la red Natura 2000 es, a nivel continental, una red importante de áreas protegidas que actúa como un buen complemento para las áreas protegidas nacionales existentes. Sin embargo, todavía permanece un número de problemas que están conectados principalmente con la lista de especies en las Directivas de Hábitat y de Aves. La Comisión Europea inició en 2014 un proceso enfocado a la importancia de estas directivas para la conservación de la biodiversidad. Nuestros resultados contribuyen a esta evaluación y sugieren que el sistema es generalmente efectivo para los vertebrados terrestres pero que se beneficiaría de una mayor actualización de las listas de especies y del manejo en el campo.

Introduction

The Aichi Targets, adopted in 2010 by the Convention on Biological Diversity (CBD) (CBD 2011), are aimed at tackling the continuing decline in biodiversity. A key element is Aichi Target 11, which commits CBD to improve connectivity within existing networks of protected areas (PAs) and to expand the global coverage of terrestrial PAs up to 17% by 2020 (Venter et al. 2014).

The European Union (EU) is a pioneer at the global level due to its efforts toward nature conservation. Already in 1979 the EU adopted Directive 79/409/EEC (Birds Directive) aimed at the conservation of wild birds (193 endangered species and subspecies or populations) and then in 1992 adopted Directive 92/43/EEC (Habitats Directive) aimed at the conservation of natural habitats, wild faunas (other than birds), and floras (approximately 900 species, subspecies, and populations of plants and animals). Under the framework of the 2 directives, each member state has to identify specific areas for inclusion in the EU Natura 2000 conservation network, the aim of which is to conserve an extensive range of threatened habitat types and species throughout Europe, and to maintain at or restore to "favorable conservation status" listed habitat and species.

The EU clearly represents a complex and highly peculiar case study compared with other continent-wide national or international systems. With its 28 member states, the EU alone covers a total land area of about 4.5 million km^2 and contains parts of the Mediterranean biodiversity hotspot (Mittermeier et al. 2005), several of Earth's most biologically valuable ecoregions (Olson & Dinerstein 1998), and many centers of plant diversity (Davies et al. 1994). At the same time, the overall human population is currently >500 million, leaving a very limited space for natural and semi-natural ecosystems. Humans have extensively reshaped the region for at least the last 10,000 years, substantially longer than most regions globally, making it considerably different from most of Australia or North America. For example, Australia is 1.7 times bigger than EU28 and has a human population of

about 21.5 million, whereas the United States and Canada together are 4.4 times bigger and have a human population of about 350 million. The local footprint of human consumption with the related environmental impacts is many times higher in the EU than in either of these areas (Imhoff et al. 2004), leaving only limited options for conservation.

Nonetheless, the EU had implemented a unique system of PAs, and the Natura 2000 network is undoubtedly one of the largest and more articulated networks of conservation areas worldwide (EEA 2012). At present, however, it is unlikely that the Aichi Target of halting biodiversity loss by 2020 will be met. In fact, although PAs represent one of the most important responses to the global biodiversity crisis (Watson et al. 2014), their biodiversity benefits are far from guaranteed, with PAs often established in locations that are remote or have low economic value (Maiorano et al. 2006; Joppa & Pfaff 2009).

Explicitly recognizing this problems, CBD asks for the establishment of PAs in places that are of "importance for biodiversity" and "ecologically representative."

To date, many analyses focused on the national scale or smaller parts of the Natura 2000 network have been performed to assess the patterns of biodiversity coverage (Dimitrakipoulos et al. 2004; Maiorano et al. 2007; López-López et al. 2011; D'Amen et al. 2013; Lison et al. 2013; Rubio-Salcedo et al. 2013). Other analyses have considered connectivity (e.g., Gurrutxaga et al. 2011; Opermanis et al. 2012), human activities (Tsiafouli et al. 2013), and ecosystem services (Bastian 2013), but they all focused on particular areas and few species or habitats. Some analyses have considered the entire Natura 2000 network as part of a much larger study areas (e.g., Zupan et al. 2014), therefore making it impossible to evaluate the contribution of the network to biodiversity conservation. Only a few analyses have been explicitly focused on the Natura 2000 network, considering for example bird species richness (Albuquerque et al. 2013), a subset of threatened species (Trochet & Schmeller 2013), population trends for birds (Donald et al. 2007), and climate change (Araujo et al. 2011). Gruber et al. (2012)

included the entire Natura 2000 network in an analysis of the system's coverage of over 77% of the species listed in the Habitats Directive (Annex II only). However, they based their analyses on species presence data obtained from national reports, which are often of variable quality and resolution from country to country (Evans 2012) and spatially coarse (100 km^2 resolution) relative to the size of many Natura 2000 sites (often below 1 km^2) (Maiorano et al. 2007). Such mismatch in resolution between the size of PAs and the data available on biodiversity may generate problems and spurious results, especially in conservation planning and gap analysis exercises (Alagador et al. 2011).

This wealth of studies provides no information that can clearly be applied to the EU as a whole because the primary findings are relevant only to the particular study area considered and depend on the quality of the input data and the particular research question. To date, no comprehensive and reliable analysis of the Natura 2000 network aimed at evaluating its "importance for all biodiversity" or its ecological representativeness has been performed at the level of the EU.

The Natura 2000 network has been designed to protect only the species and habitats listed in the Annexes of the Habitats and Birds Directives; there is no pretense of conserving all European biodiversity. However, the network is currently considered the most effective tool for biodiversity conservation in the EU, even though the potential umbrella effect of the network in conserving more than the species listed remain untested. Therefore, the question of primary importance is what is the value of the Birds and Habitats Directives as a general tool for biodiversity conservation in the EU, especially considering the possible revision of the 2 directives in the next few years and the ongoing discussions on the need for a broad conservation tool that can be applied at the European level.

A second important point yet to be explored is the level of complementarity and overlap between the Natura 2000 network and national PAs. The Natura 2000 network has been conceived as a network of areas independent of national PAs (although with a widespread overlap); thus, Natura 2000 should be able to cover biodiversity, at least listed species, by itself. However, this point has never been tested with data that homogeneously cover the entire EU and include a substantial portion of all biodiversity.

We attempted to provide such an evaluation for all terrestrial vertebrates (freshwater fish excluded) that occur naturally in the EU. We used a database with high-resolution data on species presence that covered the entire EU. We considered species listed and not listed in the directives as well as endemicity and threat status. We determined the coverage provided by national PAs and by the Natura 2000 network to terrestrial vertebrates; the role of the Natura 2000 in adding to the coverage

provided by the national PAs; and the contribution of Natura 2000 to overall connectivity between PAs. In our examination of connectivity, we accounted only for non-flying terrestrial vertebrates (excluding birds and bats) and compared the connectivity of national PAs with that of national PAs plus the Natura 2000 areas.

Methods

To map the currently existing national PAs, we downloaded the 2014 version of the World Database on Protected Areas (Protected Planet 2014) and extracted data on International Union for Conservation of Nature (IUCN) category I-VI PAs. We excluded all proposed PAs, all areas lacking a national designation, and all areas without polygonal representation. We retained IUCN categories V and VI because, although not specifically aimed at biodiversity conservation, they can provide some protection (Venter et al. 2014). Data on the Natura 2000 network was downloaded from the European Environmental Agency for the entire EU except Croatia. The Croatian State Institute for Nature Protection (courtesy Ivana Plavac) provided the national Natura 2000 database.

We obtained validated species distributions models for all terrestrial vertebrates occurring in the study area from Maiorano et al. (2013). For each species we considered the threat status from the global IUCN Red List and defined as threatened all species classified as critically endangered, endangered, or vulnerable. Furthermore, using the global distribution range as reference (see Maiorano et al. [2013] for details on data source), we calculated the percentage of the distribution included in the EU and defined as endemics all taxa with distributions totally encompassed in the EU.

Analyses

To investigate the level of coverage offered by national PAs, by the Natura 2000 network, and by both systems to terrestrial vertebrates in the EU, we took three main steps: gap analysis considering only national PAs, gap analysis considering only the Natura 2000 network, and gap analysis considering both.

We defined for each species a representation target based on the area occupied and on the percentage of the global distribution range occurring in the EU, a modification of Rodrigues et al.'s (2004) approach. The representation target was set to a maximum of 100% of the area occupied for species with a narrow distribution (area occupied < 1000 km^2) and with more than 10% of their global distribution range in the EU and to a minimum of 10% for widespread species (area occupied > 100,000 km^2) or species only marginally present in the EU (< 10% of their global distribution range in EU). For all other species the representation target was interpolated

between the 2 extremes with a linear regression on the log-transformed area occupied. A species not represented in any PA was considered a total gap species, a species whose representation target is only partially met was considered a partial gap species, and a species whose representation target is met was considered covered.

Because functional connectivity depends on several species-specific aspects that cannot be easily generalized, we estimated connectivity based only on the role of dispersal distance and network topology. Ignoring the role of landscape matrix heterogeneity and animal behavior may result in uncertain predictions (Bender & Fahrig 2005); however, it allowed us to provide generic estimates of the functionality of the network for a range of dispersal distances representing broad species categories. To measure connectivity among PAs, we converted the layers of national PAs and of the Natura 2000 network in a raster with roughly 1 km^2 resolution and calculated the distance of each PA to all neighboring PAs. Assuming a negative exponential dispersal kernel, and considering only non-flying vertebrates, we limited our analyses to a maximum radius of 500 km. For Natura 2000 areas, we considered only areas established under the Habitats Directives because we excluded breeding birds from the connectivity analyses.

Using the software Conefor (www.conefor.org) and considering a set of 12 dispersal distances (from 180 m to 100 km), we calculated the equivalent connected area index (Saura et al. 2011), which represents the amount of reachable habitat (species-specific habitat defined in Maiorano et al. [2013]) for a given dispersal distance (i.e., the total area of habitat available in national PAs or Natura 2000 sites that a species would be able to reach by moving within and among protected sites).

Results

Our final national PA layer (Supporting Information) included 87,719 areas covering 19.5% of the study area. The Natura 2000 network was almost equivalent. It covered more than 18% of the EU (>26,000 terrestrial sites) and thus exceeded the Aichi Target 11 (Table 1). Considering the combined national PAs and Natura 2000 networks, 32.6% of EU28 was covered (almost 1,400,000 km^2). The two networks overlapped extensively; 28.9% of the area protected was covered by both systems (Supporting Information).

On average, 3133 national PAs and 943 Natura 2000 areas have been established per country, corresponding to a mean country coverage of 22.4% for national PAs and of 19.2% for Natura 2000 areas (Table 1). On average national PAs were smaller (mean area = 10.8 km^2) relative to the Natura 2000 areas (mean area = 29.8 km^2), with a large portion of PAs smaller than 1 km^2 in central and northern Europe.

Habitats and Birds Directives Species Lists

There were 842 species of terrestrial vertebrates occurring in the EU (Table 2). Among these, 33% were listed in Appendix II of the Habitats Directive or in Appendix 1 of the Birds Directive. We excluded from further analyses 3 species listed in the Habitats Directive (*Capra pyrenaica pyrenaica*, which went extinct in 2000; *Mauremys caspica* and *Capra aegagrus*, whose populations in the EU are introduced) and 9 species listed in the Birds Directive (*Numenius tenuirostris* and *Perdix perdix italica*, both extinct in EU28; *Branta ruficollis, Gavia immer, Anser albifrons flavirostris, Chlamydotis undulata, Cursorius cursor, Branta bernicla,* and *Polysticta stelleri*, all only winter in the EU). The full list of species is in the online Supporting Information.

Overall, 71 species or subspecies (8%) are strictly EU endemics. Amphibians have the highest share of endemic taxa (57.6%), and breeding birds have the lowest (7.1%) (Table 2). The Birds Directive covered endemic species extremely well; 28 species out of 31 endemics are listed in the directive. To the contrary, the Habitat Directive species list did not include many of the endemic species. In particular, 80.4% of endemic reptiles were not listed. Exactly the same pattern occurred for threatened species. All threatened breeding birds were listed, but 60.9% of threatened reptiles were not (Table 2). Overall, 29 endemic and at the same time threatened species (7 amphibians, 11 mammals, 11 reptiles) were not listed in the directives; 7 of these endemic species are critically endangered at the global level. In contrast, 79% of the species listed in the 2 directives (229 out of 288) are not categorized as threatened by the IUCN. Almost half of these species (12 mammals and 92 breeding birds) occur only marginally in the EU (<10% of their global distribution range is in the EU [mean = 3.4%, min = 0.005%, max 9.8%]).

GAP Analyses and Connectivity

Breeding birds were by far the best-covered taxon. A minimum of 74% of the species met their representation targets inside national PAs and a maximum of 93% of the species were totally covered inside national PAs plus the Natura 2000 network (Table 3). A similar pattern, although with smaller percentages, was found for mammals, whereas reptiles (closely followed by amphibians) were the least protected (Table 3).

Overall, only 13 species were not covered by any national PA in the EU, 9 of which were listed in the Habitats or Birds Directives. Amphibians (8 species, 7 of which are listed) were the main taxon among total gap species (Table 3). Nine out of the 13 total gap species are classified as threatened by IUCN and 8 are also endemic. Two of the total gap species (*Mertensiella luschani* and *Pterodroma feae*) occur marginally in the EU (0.7% and

Table 1. Country data on area of national protected areas (PAs) and Natura 2000 areas (N2k) and terrestrial vertebrate species covered by these areas.

Country	Country area (km²)	No. of PAs	No. of N2ks	Mean area PAs (km²)	Mean area N2ks (km²)	Total area PAs (km²)	Total area N2ks (km²)	Total area of PAs + N2ks (km²)	Species covered by PAs (%)	Species covered by N2ks (%)	Species covered by PAs + N2ks (%)
Austria	83,859	1,250	219	22.17	57.35	27,715	12,559	31,673	33.05	14.98	37.77
Belgium	30,528	3,398	453	1.62	8.57	5,521	3,883	7,046	18.09	12.72	23.08
Bulgaria	110,910	1,007	335	25.03	113.63	25,206	38,066	50,557	22.73	34.32	45.58
Croatia	56,594	436	577	13.52	35.83	5,895	20,675	21,580	10.42	36.53	38.13
Cyprus	5,736	45	58	75.89	28.07	3,415	1,628	3,671	59.54	28.38	64.00
Czech Rep.	78,866	4,073	1,116	4.48	9.91	18,231	11,062	23,780	23.12	14.03	30.15
Denmark	43,093	3,923	294	2.35	12.19	9,214	3,584	12,779	21.38	8.32	29.66
Estonia	45,226	12,639	557	1.07	14.50	13,479	8,076	15,326	29.80	17.86	33.89
Finland	338,145	9,270	1,803	7.59	27.09	70,363	48,851	109,148	20.81	14.45	32.28
France	549,192	1,758	1,665	36.30	41.52	63,818	69,127	125,597	11.62	12.59	22.87
Germany	357,031	17,532	5,217	11.91	10.57	208,833	55,142	232,973	58.49	15.44	65.25
Greece	131,940	794	403	27.63	88.74	21,939	35,761	44,564	16.63	27.10	33.78
Hungary	93,030	133	525	36.56	38.00	4,863	19,950	21,145	5.23	21.44	22.73
Ireland	70,280	218	544	8.06	16.95	1,757	9,222	10,587	2.50	13.12	15.06
Italy	301,333	821	2,479	38.45	23.05	31,570	57,137	75,164	10.48	18.96	24.94
Lithuania	65,301	339	484	28.21	16.30	9,562	7,890	16,392	14.64	12.08	25.10
Luxembourg	2,597	25	60	21.52	7.82	538	469	933	20.72	18.08	35.93
Latvia	64,589	701	326	10.22	22.85	7,163	7,449	11,986	11.09	11.53	18.56
Malta	316	153	35	0.64	1.16	98	41	107	31.02	12.88	33.86
Netherlands	41,526	2,099	192	4.11	28.97	8,620	5,563	9,185	20.76	13.40	22.12
Poland	312,685	1,854	978	42.25	62.43	78,338	61,059	107,355	25.05	19.53	34.33
Portugal	91,990	172	141	41.48	134.82	7,135	19,010	20,152	7.76	20.66	21.91
Romania	238,391	910	522	18.02	103.04	16,399	53,788	55,487	6.88	22.56	23.28
Slovakia	48,845	1,120	514	10.98	28.10	12,299	14,442	18,274	25.18	29.57	37.41
Slovenia	20,273	1,940	352	7.16	21.80	13,897	7,673	14,196	68.55	37.85	70.02
Spain	504,782	479	1,706	101.32	80.52	48,534	137,365	148,150	9.61	27.21	29.35
Sweden	414,864	11,860	4,020	4.26	14.28	50,559	57,410	130,249	12.19	13.84	31.40
UK	244,820	8,770	835	8.34	25.01	73,169	20,884	80,398	29.89	8.53	32.84
EU28	4,290,148	87,719	26,410	9.55	29.83	838,130	787,767	1,398,454	19.54	18.36	32.60

Table 2. Number of terrestrial vertebrate species by taxa naturally occurring in the 28 states that are part of the European Union (EU28) and, in parentheses, the number of taxa listed in the Annex II of the Habitat Directive or in Annex I of the Birds Directive.

| Taxon | Number of species in EU28 | | |
	total	endemics	threatened*
Amphibians	85 (30)	49 (20)	21 (13)
Reptiles	142 (21)	56 (11)	23 (9)
Breeding birds	435 (184)	31 (28)	17 (17)
Mammals	180 (43)	36 (12)	22 (10)

Includes all taxa listed by the International Union for Conservation of Nature as critically endangered, endangered, or vulnerable.

0.0001%, respectively, of their global range is in the EU). Almost 34% of all species (285 species) did not meet their representation target in national PAs; an average of 53.4% of the representation target was met (minimum = 43.9% for reptiles; maximum = 63.4% for breeding birds). More than 37% of these species (106) are listed in the EU Directives, 19.6% (56 species) are threatened, and 48.4% (138 species) are endemic to the EU.

On average, the Natura 2000 network offered more coverage than national PAs to each species. The mammal *Microtus bavaricus* was the only total gap species and it is not listed in the directives. The species is known only for a single locality at the German-Austrian borders and it is considered critically endangered by the IUCN. However, *M. bavaricus* was considered extinct at the time the Habitat Directive was drafted; a residual population was discovered only recently. The number of partial gap species was lower relative to national PAs, particularly in the case of breeding birds listed in the Birds Directive (Table 3).

On average, adding the Natura 2000 network to national PAs increased the coverage offered to single species by 302.3% (477.8% for amphibians, 413.7% for reptiles, 246.7% for breeding birds, 273.2% for mammals), up to an average increase of 331.4% for species listed in the Habitats or Birds Directives (573.7% for amphibians, 279.0% for reptiles, 293.9% for breeding birds, 385.1% for mammals). Considering both national PAs and the Natura 2000 network, there was 1 total gap species (the same *Microtus bavaricus* cited above) and 121 partial gap species (14.4% of all species). Again, reptiles had the lowest level of protection. On average, 57.3% of the representation target was covered for partial gap species by national PAs and Natura 2000 network; a minimum of 49.2% for amphibians and a maximum of 62.5% for breeding birds were covered.

The two networks combined provided considerably improved potential connectivity for terrestrial vertebrates relative to national PAs only. The equivalent connected area index increased from 2.6 to 4.7 times along the range of dispersal distances considered (Fig. 1). For

long dispersal distances ($\sim$ >30 km of median dispersal distance), the increase in the equivalent connected area was higher than the increase in the total area of protected habitat, whereas the opposite occurred for shorter dispersal distances. Therefore, Natura 2000 sites largely increased the amount of connected habitat and efficiently upheld connectivity for vagile species by playing a role as stepping stones among national PAs.

Discussion

We have provided the first complete gap analysis specifically tailored to the EU and on the Natura 2000 network for terrestrial vertebrates. We asked how much biodiversity is covered by national PAs, by the Natura 2000, and by the combination of both, including species listed under the Habitats or Birds Directives as well as species not listed.

The Natura 2000 network is possibly not the most efficient systems (area wise) of PAs, but this inefficiency is linked to the bottom-up process on which the network has been constructed (for a detailed description of the process see Evans [2012]). Specific problems with the Natura 2000 network are mainly related to the list of species considered in the 2 directives. The first issue is updating the lists to capture the changing species taxonomy and the definition of new species, currently a problem for 7.2% of the taxa listed (vertebrates only). Although this first point is relatively easy to solve by updating the annexes, the introduction in the listing process of more objective criteria to identify species (and habitats) with higher risk of extinction appears to be a more difficult task (Hochkirch et al. 2013a). If the list of bird species covers very well endemic and threatened species, the lists under the Habitats Directive presents several problems. Twenty-nine vertebrate species endemic to the EU and globally threatened are not listed (7 amphibians, 11 mammals, 11 reptiles), whereas more than 82% of the species listed are not threatened at the global level and more than 37% of the species listed are not threatened and occur only marginally in the EU. Similar problems have already been shown for insects (Cardoso 2012), butterflies (van Swaay et al. 2011), and dragonflies (Kalkman et al. 2010), all taxa for which the available information was (and still is) very limited when the Habitat Directive was drafted and updated.

Previous proposed amendments to the Annexes of the EU Directives have generated a polarized debate in the scientific literature (e.g., Hochkirch et al. 2013b; Maes et al. 2013). Maes et al. (2013), in particular, see the focus on the species list as a potential diversion of attention and resources from more important problems, like the implementation of the Natura 2000 network. We agree with the importance of local scale effective management measures for the Natura 2000 network such as, for

Table 3. Number of total and partial gap species[a] per taxon relative to national protected areas (PAs), to the Natura 2000 network, and to both systems (All).[b]

	National PAs		Natura 2000		All	
Taxon	total gap (%)	partial gap (%)	total gap (%)	partial gap (%)	total gap (%)	partial gap (%)
All amphibians	8 (9.4)	35 (41.2)	0 (0.0)	30 (35.3)	0 (0.0)	26 (30.6)
Endemic amphibians	7 (8.2)	28 (32.9)	0 (0.0)	26 (30.6)	0 (0.0)	24 (28.2)
Threatened amphibians	7 (8.2)	13 (15.3)	0 (0.0)	17 (20.0)	0 (0.0)	15 (17.6)
Amphibians listed in EU directives	7 (8.2)	13 (15.3)	0 (0.0)	16 (18.8)	0 (0.0)	13 (15.3)
All reptiles	1 (0.7)	82 (57.7)	0 (0.0)	51 (35.9)	0 (0.0)	47 (33.1)
Endemic reptiles	0 (0.0)	56 (39.4)	0 (0.0)	42 (29.6)	0 (0.0)	41 (28.9)
Threatened reptiles	0 (0.0)	20 (14.1)	0 (0.0)	18 (12.7)	0 (0.0)	17 (11.9)
Reptiles listed in EU directives	0 (0.0)	12 (8.5)	0 (0.0)	10 (7.0)	0 (0.0)	9 (6.3)
All birds	2 (0.5)	110 (25.3)	0 (0.0)	40 (9.2)	0 (0.0)	31 (7.1)
Endemic birds	1 (0.2)	27 (6.2)	0 (0.0)	25 (5.7)	0 (0.0)	22 (5.1)
Threatened birds	0 (0.0)	8 (1.8)	0 (0.0)	4 (0.9)	0 (0.0)	4 (0.9)
Birds listed in EU directives	2 (0.5)	62 (14.3)	0 (0.0)	28 (6.4)	0 (0.0)	21 (4.8)
All mammals	2 (1.1)	58 (32.2)	1 (0.6)	35 (19.4)	1 (0.6)	26 (14.4)
Endemic mammals	2 (1.1)	27 (15.0)	1 (0.6)	20 (11.1)	1 (0.6)	17 (9.4)
Threatened mammals	2 (1.1)	15 (8.3)	1 (0.6)	11 (6.1)	1 (0.6)	10 (5.6)
Mammals listed in EU directives	0 (0.0)	19 (10.6)	0 (0.0)	13 (7.2)	0 (0.0)	10 (5.6)

[a]*Definitions: total gap species, species not covered by any protected area; partial gap species, species whose representation target is not met.*
[b]*Percentages in parentheses are calculated considering the total number of species per taxa.*
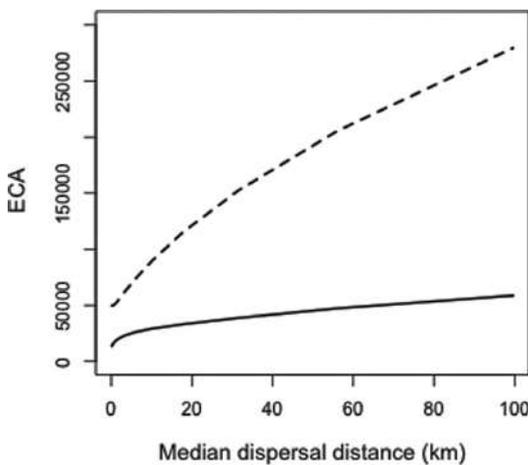
Figure 1. Equivalent connected area (ECA) index relative to dispersal distances of non-flying terrestrial vertebrates for national protected areas alone (solid line) and national protected areas plus the Natura 2000 network (dashed line). The index is a measure of the total area of habitat available in national protected areas or Natura 2000 sites that a species would be able to reach by moving within and among protected sites.

example, providing economic incentives to compensate for the losses due to productive activities limited by the conservation objectives. These measures, complemented by more effective controls, would ensure that Natura 2000 represents an effective conservation tool and not simply a system of paper parks. However, we claim that having a long list of not-threatened species and applying some of the limited resources available for conservation to species only marginally occurring in the EU could make all EU conservation efforts weaker and, in the long term, more difficult to sustain both economically and politically.

Changing the directive's annexes would clearly be a very political process and should be done very carefully as it may also open the way to proposals weakening the protection regime provided by Article 6 in the Habitat Directive. Furthermore, especially if one considers plants and insects, the list of taxa and species to include would be extremely long and basically impossible to draft based on current taxonomic and biogeographical knowledge. However, the level of knowledge we currently have on distribution, systematics, and ecology for terrestrial vertebrates in Europe clearly calls for an update of the annexes at least for these species.

Our results demonstrate that the Natura 2000 network represents at continental level an important network of PAs and provides a good complement to existing national PAs. First, when both networks are considered almost one-third of EU28 is under some form of protection, providing one of the largest networks of PAs in the world. Second, the coverage offered to single species is generally very good. One key result of our analysis is the almost complete absence of total gap species inside the Natura 2000 network, with only one exception. Furthermore, the Natura 2000 network provides overall a reasonable representation to most terrestrial vertebrates in Europe. When national PAs and the Natura 2000 network

are taken as a consolidated system, the results are even more encouraging; only 14% of all species would be considered partial gap species given our representation targets. Furthermore, on average, more than 50% of the representation target is also covered for partial gap species, a percentage that is closely approached for the least protected taxa (i.e., amphibians and reptiles). Moreover, the consolidated network provides more reachable habitat than the PAs alone and Natura 2000 alone for species dispersing long distances. This indicates that Natura 2000 sites act as stepping stones, reinforcing the connectivity of the entire system.

Our results clearly differ from previously published analyses focused on nation-wide systems (e.g., Maiorano et al. 2007), but this is not surprising because a species that may be a total gap species in Italy may at the same time be well protected elsewhere. Furthermore, our results on connectivity suggest that the Natura 2000 network presents a unique opportunity to contribute to the ecological linkages necessary for a substantial portion of biodiversity in the EU and that there is room for improvement particularly for the less mobile species that depend on fine-scale landscape features and the proximity of protected habitat at relatively short distances. The Habitat Directive (Article 10) already provides the framework within which management and conservation measures outside of Natura 2000 areas can be implemented, and other EU initiatives (e.g., the Green Infrastructures strategy adopted in 2013) can help.

However, the two networks are not managed under the same political and technical vision. While Natura 2000 responds to the policies of the European Parliament, national PAs respond to national policies. Past and recent events show that tensions between the two levels can easily occur and disrupt the necessary coordination in managing the various networks (EEA 2012).

Maintaining these vast systems of PAs is economically and politically costly, and one might ask what is the level of redundancy of the overall system and how can it be reduced to improve its efficiency? However, there are no studies, to our knowledge, on the possible level of redundancy of the individual and combined networks; moreover, having a certain amount of redundancy appears the most prudent approach against the uncertainty of the predicted global changes (Mumby et al. 2011).

Future efforts in terms of new areas being established should be focused primarily on the only total gap species, on those taxa currently less well protected (reptiles and amphibians), and on enhancing connectivity for the largest number of taxa and dispersal ranges. However, the EU is characterized by extremely high human population density and pervasive human influence even in the most remote areas, and the establishment of new PAs is difficult. Further subtraction of productive land for conservation is likely to be socially, economically, and politically costly. Therefore, any further conservation

effort should prioritize management on the ground to achieve a favorable conservation status for all species and habitats inside PAs. At the same time, it is important to focus on the habitat matrix outside PAs. It has been clearly demonstrated that PAs cannot fulfill their conservation objectives if they are small and are islands in a human dominated landscape (Maiorano et al. 2008). However, the EU potentially has the political power and the economic and technical tools to make a real impact on biodiversity conservation in unprotected areas. For example, agri-environmental policy has been implemented with increasing conviction and economic support in the last decades (Batary et al. 2015 [this issue]).

Obviously, the good representation that we measured for terrestrial vertebrates does not guarantee representation of other taxa or other biodiversity features. Yet the literature provides good support of the contention that broad taxonomic groups generally can represent the majority of species (Moore et al. 2003; Di Minin & Moilanen 2014). In this sense, our analyses should be fairly robust because we have included species as different (in ecology, morphology, physiology) as large mammalian carnivores and as salamanders.

Our results should be considered with a number of caveats. A major caution is linked to the representation targets we considered. We used a widely applied approach to set species-specific targets (Rodrigues et al. 2004; Venter et al. 2014) that is based on the assumption that species with restricted ranges require a stronger conservation effort. We recognize, however, that even a species-specific representation target can represent a problem, with inequitable assessments of PAs coverage (Santini et al. 2014). One possible solution would be to explicitly recognize the existence of spatial structuring in the populations of each species, but this is not feasible for the number of species and the study area we considered.

A second important caveat is linked to data quality. The species distribution database we used is updated, and more than 44% of the distribution maps have been positively evaluated against independent field data (Maiorano et al. 2013). Moreover, models of species distribution based on habitat suitability represent one possible solution to minimize commission errors that often plague maps of extent of occurrence (Gaston 2003). However, even if we decreased the amount of commission errors in species distributions, we could not exclude the presence of omission errors, which could have influenced our results.

The main problem linked to data quality resides, however, in the PA and Natura 2000 layers. We selected PAs on the basis of the IUCN categories and, following the approach adopted by Venter et al. (2014), we included all areas in categories I to VI. The assumption for this choice is that even multiple-use areas (such as categories V and VI) can support species conservation, but we recognize that the IUCN PA categories can potentially foster a

number of problems (Boitani et al. 2008). Furthermore, both the World Database on Protected Areas and the Natura 2000 database may have spatial errors as well as errors in their attributes. We made every effort in the initial selection of areas to correct these problems (e.g., excluding one PA in Sardinia because it was actually a Tunisian PA erroneously mapped in Italy), but other errors may have remained undetected.

The EU has initiated in 2014 a process called Fitness Check on EU Nature Legislation (Birds and Habitats Directives) aimed at assessing the effectiveness, efficiency, coherence, relevance, and EU added value of the Birds and Habitats Directives in contributing to the EU Biodiversity Strategy. Because the Natura 2000 network is central to the effort to meet the 2020 European conservation targets, our results contribute to the assessment and suggest the system is largely effective but would benefit from further updating and maintenance.

Comparing the Natura 2000 network with other PAs at the global level, the EU is clearly advanced from a conservation point of view. Watson et al. (2014) proposed a change in PA policies at the global level, a focus on expansion, management, investment, and enforcement of existing PAs. While many countries are still short of what they formally agreed to do in the 2020 CBD strategic plan (Watson et al. 2014), considering more options for expansion of the PA system in the EU is not the main issue (and could be difficult considering the level of protection already reached and the level of human pressure on the landscape). However, the EU should focus on the other aspects, particularly on management (both in and outside PAs) and enforcement (particularly inside Natura 2000). Further investments in conservation are urgently needed, and a focus on ecosystem services and the costs of habitat degradation inside PAs is particularly important.

Supporting Information

A description of the study area and the spatial distribution of national PAs and the Natura 2000 network (Appendix S1) and a list of all species considered in the analyses (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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7. CLIMATE CHANGE AND SPECIES VULNERABILTY:

Assessing species vulnerability to climate change within European birds

Alessandro Montemaggiori & Luigi Maiorano (in prep.)

Male and female Lesser kestrel (*Falco naumanni*) (credits Sameh Odeh).

The aim of this chapter was to move beyond the simple projections of likely impacts of global change to identify the most vulnerable species within the study area.

The adopted approach was to build a vulnerability index (Vi) for the European birds that integrates estimations of projected range change and different proxies of species resilience in a quantitative way. The index, originally proposed by Maggini et al., (2014) for Swiss avifauna, is completely quantitative, and it allows ranking species so as to prioritize conservation actions.

According to this algorithm, five indicators are defined to compose the vulnerability index, expressing three operational aspects of vulnerability: the projected change in the distribution, the reservoirs for the species and the population trend. Two indicators capture the change in the species' future distribution within Europe, two measure the species resilience and one quantify the historical trend of the species over the past decades. I used one stressor, climate change, and one spatially explicit scenario, to represent the magnitude of the future change and to assess its impact on species distribution using MaxEnt species distribution model.

The five base indicators contribute differently to the vulnerability of a species.
The analysis of the single components of the index Vi for each species allows to highlight the relative weight of the different indicators, and a first exploration of the obtained results highlights the highest number of species with a high Vi value in the north-eastern part of the area study, mainly because of the strong reduction of habitat suitability for the future in that area. The average weight of each taxon, its diet, its habitat suitability, some behavioral aspects and its conservation status (*sensu* IUCN) have been collected and used to understand if there are ecological indications linked to the calculated indices, in order to highlight specific management indications.

From the analysis it seems to emerge that the most specialized species in terms of habitat seem to be those with higher Vi indices; aquatic species are more vulnerable, as well as those nesting on the ground. The degree of vulnerability increases for the larger species and finally the increase in the degree of threat (*sensu* IUCN) increases the value of the vulnerability index.

Background

Vulnerability is a term applied to a variety of systems and defined in various ways across disciplines. All definitions agree that four main elements are necessary to define vulnerability: the vulnerable entity, the attribute of concern (e.g. existence, health, biodiversity), an identified hazard/stressor (e.g. climate change) and a temporal reference for the vulnerability assessment (Füssel, 2007). It is also widely accepted that the vulnerability of a system is a function of its sensitivity to stressors

and adaptive capacity to change, and its resilience, that is the ability of a system to recover from perturbations or to shift to another stable state (Folke, 2006).

Several attempts have been made to propose a generally applicable conceptual framework for assessing vulnerability across disciplines (e.g. Füssel, 2007). Often, this requires the assessment of vulnerability of single species which make up an ecosystem and its services to humans (Midgley *et al.*, 2002; Şekercioğlu, Daily & Ehrlich, 2004), and to identify regions where species might specifically become at risk *(Beaumont et al., 2011)*. A significant step forward in species vulnerability assessment was the proposition of a unified framework by Williams et al. (2008) which theoretically identifies the different components of vulnerability and their inter-relations. However, it remains an open question how these theoretical components can be translated into identifiable and measurable units applicable to practice.

Because qualitative assessment cannot account for the magnitude of impact caused by stressors. Maggini et al. (2014) proposed a quantitative vulnerability index based on the impact of two stressors, climate and land use change. I used only one stressor, climate change, and one spatially explicit scenario, the worst-case IPCC AR5 scenario (IPCC, 2014), to represent the magnitude of the stressors and to assess its impact on species distribution using MaxEnt species distribution model. I also incorporated indicators of resilience and a proxy of species- specific factors. The vulnerability index was developed for 499 breeding species in Europe.

Methods

The vulnerability index uses five indicators expressing three operational aspects of vulnerability: the projected change in the distribution, the reservoirs for the species and the population trend. Each indicator was defined as to vary between 0 (no contribution to vulnerability) and 1 (maximal contribution).

Two indicators (*IAO* and *IOverlap*) capture the change in the species' distribution within Europe.

$$(1) \quad IAO = AO/(AO+AOi)$$

IAO relates the current (*AO*, number of 10' cells) and the future area of occupancy (*AOi*) of the species and measures the relative amount of change that is projected as a consequence of the selected global change scenario. In our case, all species considered were already breeding within Europe, so that *AO* is always greater than zero.

$$(2) \quad IOverlap = 1- Overlap/AO$$

IOverlap accounts for the relative overlap between the current and future area of occupancy of the species (overlap measured in 10' cells). The indicator expresses that

the more the current and future areas are disconnected, the more difficult it is to colonize the future area.

The following two indicators (*IReEU* and *IReGL*) represent the reservoirs of a species.

$$(3) \quad IReEU = 1 - (AOi/57153)$$

IReEU expresses the size of the future area of occupancy of the species within Europe (57153 10' cells being the total area of Europe and thus the maximum content of the European reservoir). Species with restricted ranges are indeed more prone to extinction and more vulnerable to climate change (Ohlemuller et al., 2008).

The resilience of European populations will likely depend on the geographic position of Europe with respect to the global distribution of the species. If Europe is located at the southern margin of the global distribution, the recruitment possibilities from neighboring global countries will be limited as the range will generally shift towards northeast following climate warming (Huntley et al., 2007). To account for recruitment from surrounding countries, the global reservoir was defined by using BirdLife global breeding ranges digital dataset.

$$(4) \quad IReGL = 1 - (AO/AOglobal)$$

IReGL refers to the proportion of the global 10' cells occupied by a given species.

Fine-scale environmental relationships, intrinsic characteristics and population dynamics of a species are difficult to capture and quantify for a large number of species. As a proxy of these species-specific aspects, the population trend over the past 47 years was used (BirdLife International, 2004, 2017).

$$(5) \quad ITrend = 1 - (category - lower\ category)/(higher\ category - lover\ category)$$

Categories are defined by populations trend within Europe, according to BirdLife (2014; 2017). Small decline = -0,33; moderate decline = -0,66; large decline = -1; stable = 0; small increase = 0,33; moderate increase = 0,66; large increase= 1; fluctuating = 0. *ITrend* is used as a proxy for species-specific characteristics of the species.

The first four indicators assess the vulnerability of a species on the basis of the projected changes in distribution and reservoirs. However, projections only represent the potential for range expansion/ retraction on the basis of climate change, and the actual range change will in reality also depend on current population viability and dynamics, information that we approximated by population trend. Moreover, by including population trend, I indirectly incorporated the life history traits of species, more detailed aspects of the ecological and demographic relationship of the species with its environment (e.g. abundance of food, nest site availability, availability of

micro-habitats, competition with other species) and events occurring outside Europe during migration and the non- breeding season. Population trends was not extrapolated into the future because of the large uncertainty involved and because population size is deemed to be correlated with range size (O'Grady et al., 2004) which is already captured by the indicator *IAO*.

These five indicators were averaged to obtain a final vulnerability index varying between 0 (species not vulnerable) and 1 (species highly vulnerable). The final vulnerability index (*Vi*) is calculated as the mean of the three operational aspects of vulnerability (**Fig. 6**): the change in the distribution within the study area (represented by *IAO* and *IOverlap*); the reservoirs for the species (represented by *IReEU* and *IReGL*); and the population trend (represented by *ITrend*):

$$Vi = [(IAO + IOverlap)/2 + (IReEU + IReGL)/2 + ITrend]/3$$
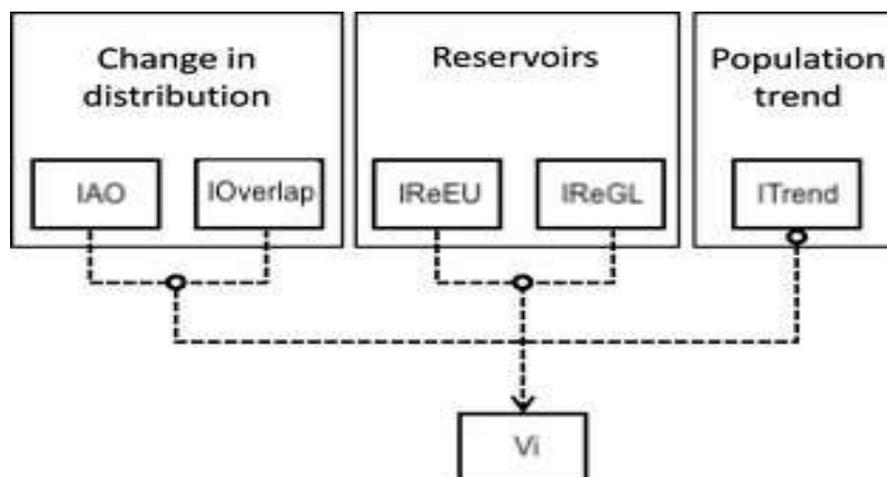
Figure 6: The contribution of the three operational aspects of vulnerability to the final vulnerability index (*Vi*): (i) the change in the distribution within Europe (represented by the mean of two indicators: the estimated relative change in the projected area of occupancy of the species under future climate and land use change, *IAO*; the proportion of overlap of the future relative to the current area of occupancy, *IOverlap*); (ii) the reservoirs for the species (represented by the mean of two indicators: extent of the future area of occupancy within Europe, i.e. the European reservoir for the species, *IReEU*; the relative position of Europe with respect to the global range of the species, i.e. the content of the 'global' reservoir defined around Europe, *IReGL*); (iii) the population trend (represented by one indicator: the trend of the European populations over the last 47 years, *ITrend*). The final *Vi* is the mean of the three operational aspects of vulnerability, that is [(*IAO* + *IOverlap*)/2 + (*IReEU* + *IReGL*)/2 + *ITrend*]/3.

Projections of species distribution into the future are highly dependent on the greenhouse gas emissions scenario considered (Dormann *et al.*, 2008). I considered the worst scenario to represent the upper bound of anthropogenic interference with

the climate system. The distribution of each species was modelled using MaxEnt SDM and then projected for the 21st century (2100) according to the worst-case IPCC AR5 scenario (IPCC, 2014).

Moreover, for each species the average weight (Snow et al., 1997), the diet, the habitat suitability (according to the expert-based database I produced in Maiorano et al., 2013), some behavioral and ecological traits (if the species is a hole nester, elevated nester or ground nester; if the species is aquatic or not (*sensu* Maiorano *et al.*, 2013), and its conservation status (*sensu* IUCN, 2017) have been collected.

Results

I calculated vulnerability indices for 499 current regular breeding bird species of Europe (91.2% of all breeding species within the study area) under one scenario of climate change.

Apart from very few exceptions, model goodness-of-fit of the underlying species distribution models showed to be good. AUC average value being 7.53.

I mapped the species by vulnerability index in the study area (**Fig. 7**) and identified the habitats of the most vulnerable species and, their different vulnerability patterns. I also combined Vi with the average weight of the species, the diet, the nesting behavior, the dependence from water. The notion of vulnerability and international importance were combined to assess conservation priorities.
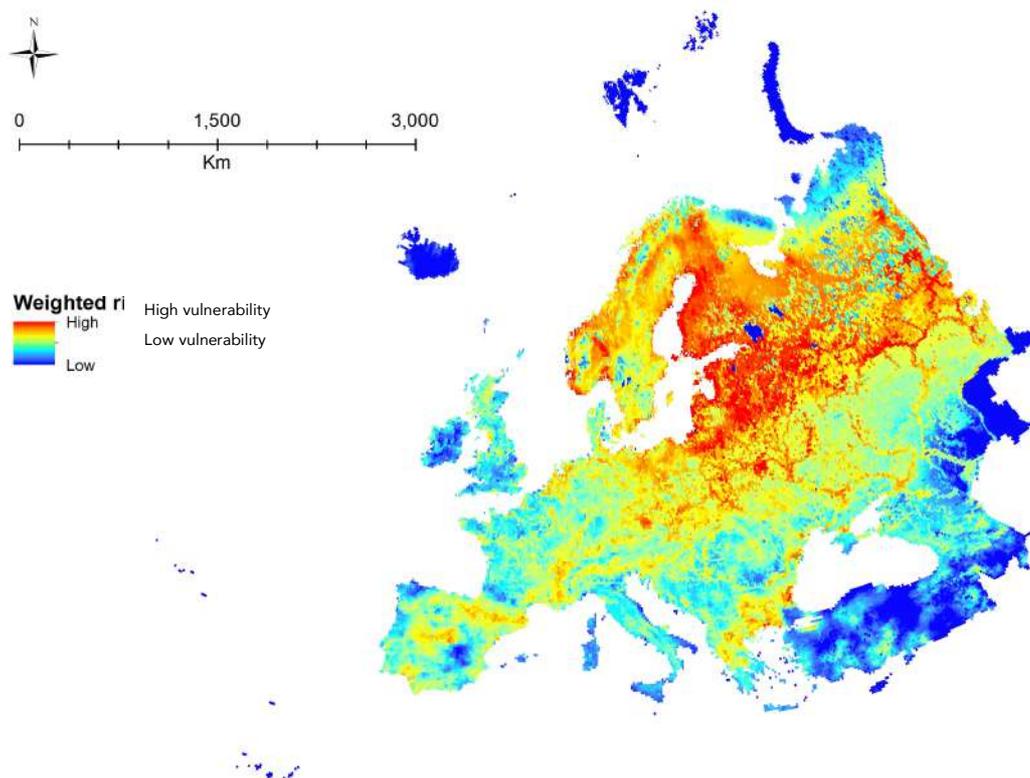
Figure 7: Vulnerability map of bird species richness (values rescaled between 0 and 100).

The vulnerability index of a species is determined by the different contributions of the five base indicators. Four typical patterns of vulnerability can be distinguished (example species given in **Fig. 8**) which represent the extremes of a continuum. The first pattern (**Fig. 8a**) is dominated by high indicator values related to changes in the area of occupancy (*IAO*, *IOverlap*, *IReEU*). The second pattern (**Fig. 8b**), characterized by low European and global reservoirs (*IReEU*, *IReGL*), is typical for species that are presently rare within the European territory, but are projected to spread under future conditions. The vulnerability of these species is also determined by the global reservoir (*IReGL*) that is partially empty. The third pattern (**Fig. 8c**) is that of non-vulnerable, widespread species, for which the values of all indicators are low. The forth pattern characterizes highly vulnerable species (**Fig. 8d**), which are projected to lose a large part or even all of their breeding area in Europe and in the neighboring countries. The vulnerability of species characterized by this pattern becomes a real threat as soon as the populations start to decrease.
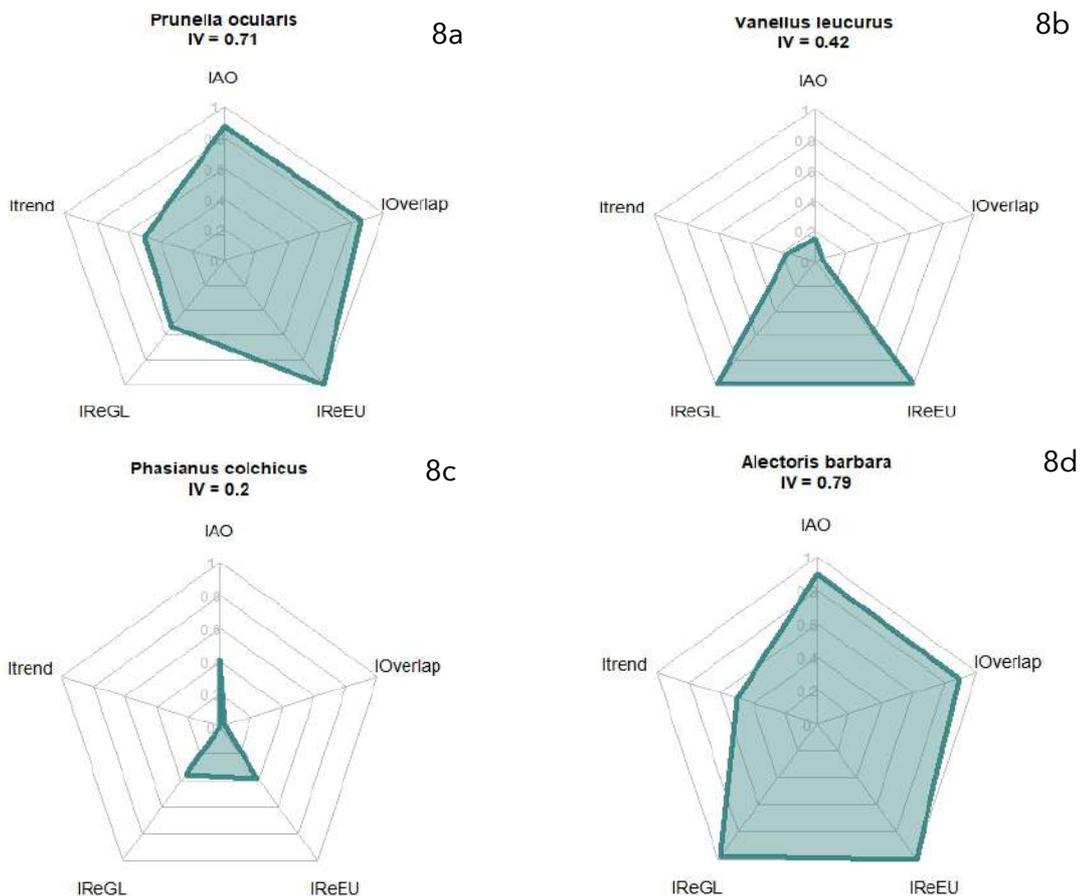
Figure 8: Spider graphs of example species representing different patterns of vulnerability with their associated contributions from the five base indicators: IAO, indicator related to the change in the area of occupancy; IOverlap, indicator accounting for the overlap between present and future area of occupancy; IReEU, indicator informing about the range of the species within Europe; IReGL, indicator informing about the relative position of Europe with respect to the global distribution of the species; ITrend, indicator related to the trend of the European populations.

To interpret both the spatial output and the Vi indices for each taxon I have considered ecological traits ranging from diet, habitat type, behavior, categories of threat, to morphology. A first results' exploration indicates that aquatic species (species that need to be less than 2 Km from water) seem to be more vulnerable to CC (**Fig. 9**).

The ground nesting species seem to be also more vulnerable (**Fig. 10**) as the more habitat selective (species that prefer only one habitat class) (**Fig. 11**).

Finally, larger species appear to be more vulnerable, than lighter ones (**Fig. 12**) together with the most threatened ones (**Fig. 13**).
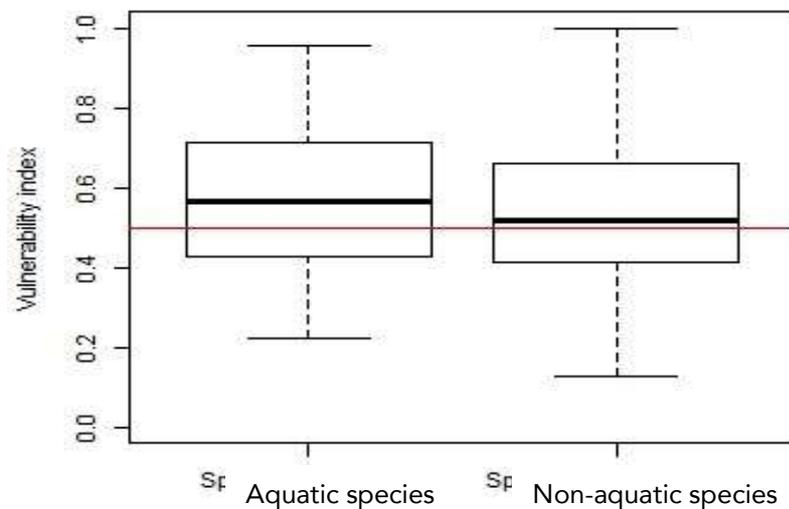
Figure 9: Boxplot of Vi index related with aquatic and non-aquatic species. Aquatic species are the ones that breed within 2 km of distance from water.
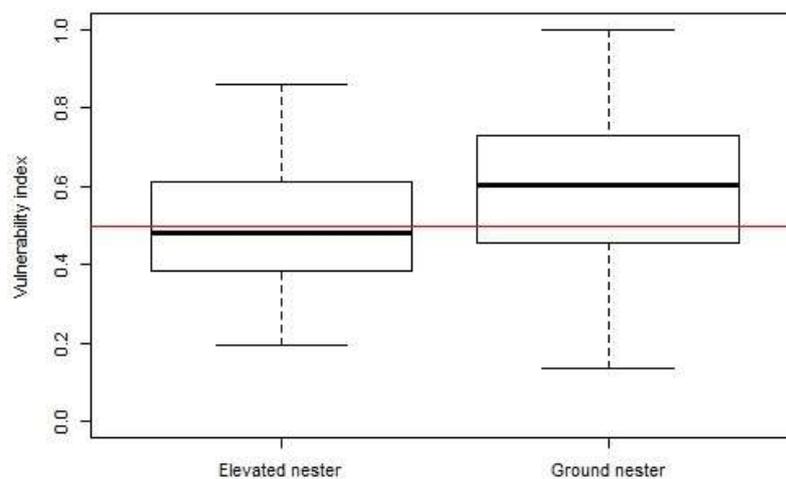
Figure 10: Boxplot of Vi index related with nesting behavior of the species. (elevated and ground nester).
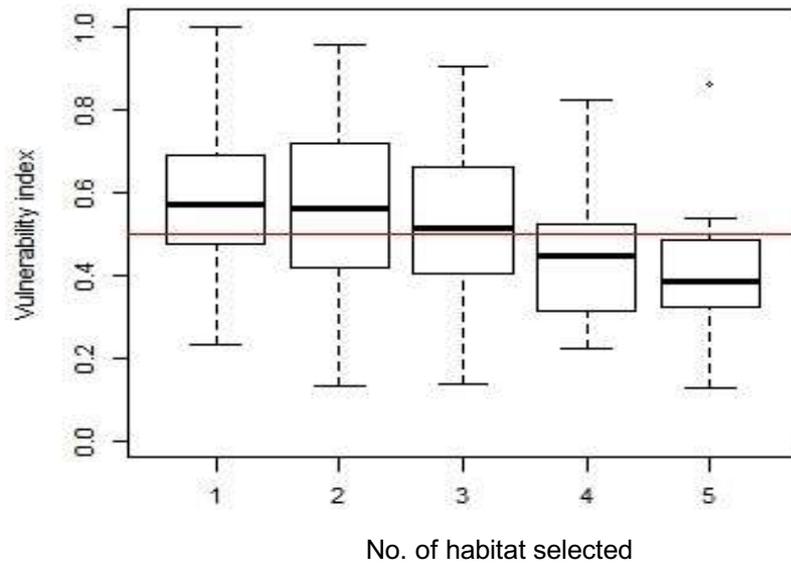
Figure 11: Boxplot of Vi index related with no. of habitat selected by the species (cultivated or anthropized areas, woods and forests - vegetation > 5 m, shrubland - vegetation < 5m, pastures/prairies/steppe/tundra, wetlands, bare areas, ice).
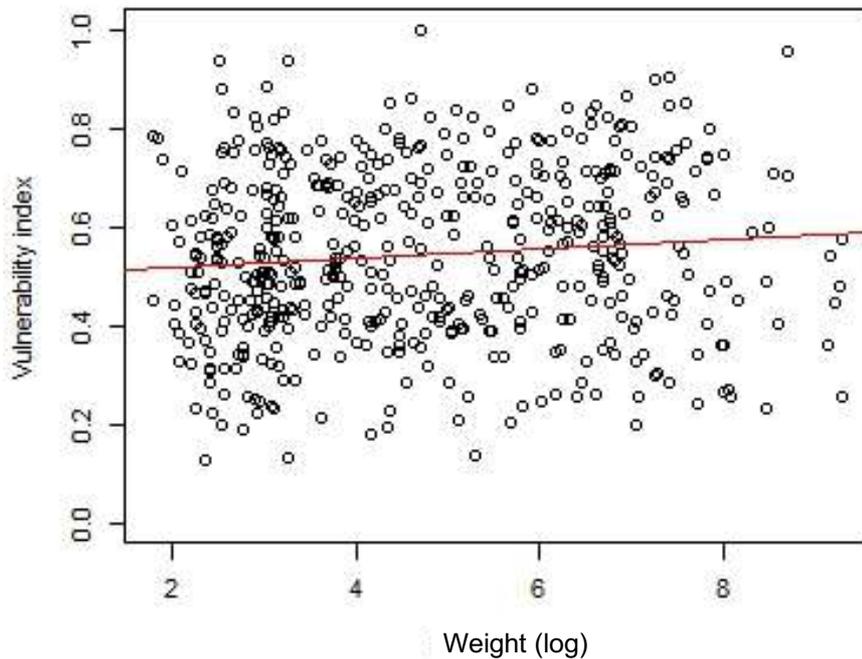
Figure 12: Scatter plot of Vi index related with weight (expressed in log). β_{weight} = 0.01 (P-value = 0.03).
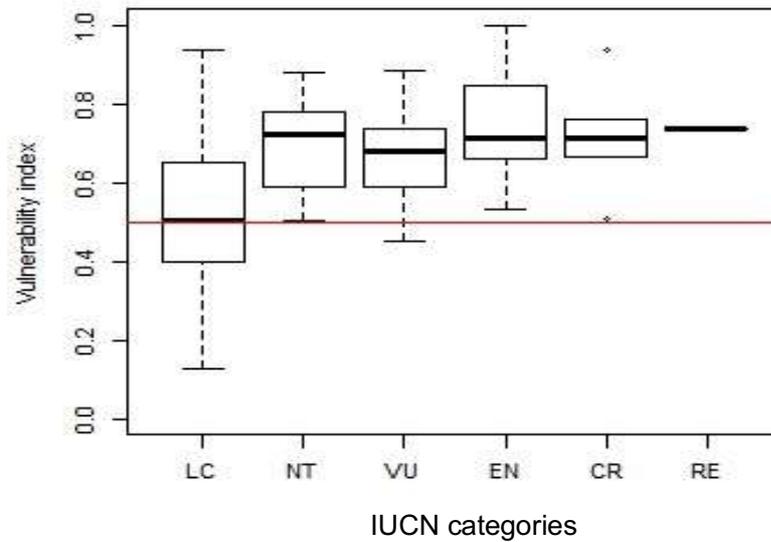
Figure 13: Boxplot of Vi index related with IUCN threat categories (LC = Least Concern, NT = Near threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, RE = Extinct in the Wild).

The proposed vulnerability index complements the assessment of extinction risk based on the IUCN European Red List. In particular, the vulnerability index points at species which are currently not threatened (LC), but are likely to become so, as for 50%, under climate change scenario. Their persistence in Europe is at risk over the next 80 years.

These are only preliminary results I started to explore. A more in deep analysis and discussion is expected by April 2018 within a pare I am preparing with my tutor L. Maiorano.

8. COMBINING EXPERT-BASE AND STATISTICAL APPROACH:

Modelling the response of European breeding birds to climate change: combining expert-base and statistical approach

Alessandro Montemaggiori, Antoine Guisan, Wilfried Thuiller, Niklaus E. Zimmermann & Luigi Maiorano (2015) – *In XVII Convegno Italiano di Ornitologia: Atti del convegno di Trento. Pedrini, P., Rossi, F., Bogliani, G. & Serra, L.& S.A. (Eds). . Trento: MUSE. Abstract of oral presentation.*

Male Rock Ptarmigan (*Lagopus muta*) (credits Paul Cools).

Alessandro Montemaggiori[1], Antoine Guisan[2], Wilfried Thuiller[3], Niklaus E. Zimmermann[4] & Luigi Maiorano[1]

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Modelling the response of European breeding birds to climate change: combining expert-base and statistical approach

Climate change is emerging as the greatest threat to natural communities in most of the world's ecosystems, with mid- and long-range scenarios expected to produce greater extinction rates than habitat loss, currently deemed the top threat to biodiversity. One in eight species of bird is pushed towards extinction by climate change, according to the latest assessment of the IUCN. Time shifting and alteration of phenology, shifting and shrinking of geographical distributions and communities' disruption are only some of the direct and indirect consequences, among the others, of climate change on bird populations. This was clearly demonstrated by many long-time scale field studies and species- and location-specific analyses.

Effects of climate change on breeding bird species are often predicted by projecting into future climate scenarios the current species' climate niche as calculated with correlative species distribution models. Although widely used and, often, highly successful, these models (and the related projections) are generally calibrated considering only climate variables, without accounting for habitat, biotic interactions and dispersal distances.

In order to build more realistic scenarios for changes in the distribution of species breeding in continental Europe, we propose a modeling approach based on the combination of state-of-the-art bioclimatic models, with expert based habitat suitability and distance to current distribution. Thus, for each species, we developed three layers: a) a bioclimatic model calibrated with an ensemble forecasting approach, considering six climatic variables (annual mean temperature, annual precipitation, mean temperature of the coldest month, growing degree days, summer and winter precipitation) and species' occurrences according to EBCC Atlas' 50 x 50 km cells with semi-quantitative data and high coverage completeness; b) an expert based habitat suitability model which considers land use (Globe Cover), elevation (SRTM) and distance to water (as mapped by CCM21 database) and c) the distance from present distribution of the species, mapped according to BirdLife. Assuming that the three layers are largely independent, we calculated for each species a final model of the relative probability of presence by multiplying the three maps.

We evaluated the reliability of the models using independent points of presence collected mainly in Italy, Spain, UK, Sweden, and Norway. In particular, we calculated the Boyce index (and index of the calibration capacity of the models) for both the classical bioclimatic model and for the final model of relative probability of presence. Our results clearly demonstrate that our approach produces more accurate and better performing models compared to simple bioclimatic ones.

Combining our approach with future scenarios for land use and climate, it will be possible to build more robust models showing potential changes in species distribution. Furthermore, it will be possible to incorporate also models of species' biotic interactions and dispersal distances, providing a biologically richer outcome.

9. CLIMATE CHANGE AND TROPHIC NETWORKS:

Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe

João Braga, Laura J. Pollock, Ceres Barros, Núria Galiana, José Montoya, Dominique Gravel, Luigi Maiorano, Alessandro Montemaggiori, Gentile Francesco Ficetola, Stéphane Dray, Wilfried Thuiller (submitted) - *Glob. Ecol. Biogeogr.*
.

Male European kingfisher (*Alcedo atthis*) with prey (credits Lorcan Handler).

TITLE

Spatial analyses of multi-trophic terrestrial vertebrate assemblages in Europe

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ABSTRACT

Aim While much has been said on the spatial distribution of taxonomic and phylogenetic diversity of large animals, how the associated food-web properties are distributed through geographic and environmental space is largely unknown. Here, we analyze the spatial structure of terrestrial vertebrate food webs and revisit traditional diversity-environmental relationships in light of trophic interactions.
Location Europe.
Methods We combined an expert-based food web of all European terrestrial vertebrates (mammals, breeding birds, reptiles and amphibians) with their respective spatial distributions. We characterized local food webs using 16 different properties representing… that we mapped across Europe. We related these properties to a set of environmental layers representing different ecological hypotheses (e.g. climate and landscape properties) and tested their relative importance in explaining the spatial distribution of European terrestrial vertebrate food web structure/properties.
Results We found two major structural descriptors in European food web structure, the first being related to species diversity and trophic length (*size* structural descriptor), and the second dimension was related to connectance and proximity of species within a web (*web realization* structural descriptor). These two descriptors of food webs strongly varied across Europe, with a strong latitudinal gradient. Among our sets of climatic and landscape predictors, annual temperature was the most important driver of the food web *size*, while temperature seasonality and human footprint mostly drove *web realization*.
Main conclusions Similarly to taxonomic diversity, there are overwhelming effects of climate and disturbance in shaping the spatial structure of European terrestrial vertebrate food webs. Given the ever-increasing availability of such datasets, our analyses pave the way for a better integration of food-web properties in biogeography.

Key words: ecological network, spatial ecology, food webs, topological networks.

Documenting large-scale biodiversity distributions and understanding what drives these patterns between or within different regions of the world has long fascinated naturalists (Wallace, 1876). The recent and ever-increasing rise of large-scale distribution databases (e.g. IUCN, BirdLife, Map of Life) has led to new comprehensive analyses of biodiversity distribution. Thanks to available data on species traits and phylogenetic relatedness, global and regional patterns of species, trait and phylogenetic diversity are now well documented for terrestrial vertebrates (Jetz & Fine, 2012; Jetz et al., 2012; Mazel et al., 2014, 2017).

Niche-based theory of species distributions posits that environmental conditions determine where species occur geographically. Species assemblages that experience similar climatic conditions should, therefore, also exhibit similar diversity (Davies et al., 2011). However, assemblages are not only the mere sum of species co-occurring in a particular area, but also result from other processes such as biotic interactions (e.g. predation, competition, facilitation, etc.). While past biogeographic studies have investigated how species or trait diversity vary in space and the underlying role of environment (e.g. Davies et al., 2011; Safi et al., 2011; Mazel et al., 2017), we know little about the spatial distribution of ecological networks of terrestrial vertebrates and how they are influenced by environmental drivers. Food webs depict trophic interactions between species, and their interaction structure can be characterized by a number of topological metrics (e.g. connectance, link density). Food web structure is multidimensional, comprising food web complexity metrics (e.g., species richness, connectance, number of trophic interactions), taxa composition (e.g., proportion of basal, intermediate and top predator species), feeding strategy (e.g., generality, vulnerability), and length (trophic level, chain length). To summarize such a structure, some authors have used an ordination space, collapsing food web structure in two main orthogonal dimensions, one linked to species richness and the other to connectance (Vermaat, Dunne & Gilbert, 2009; Baiser, Ardeshiri & Ellison, 2011). However, to our knowledge, no study has explored the spatial distribution of such food web structural dimensions, especially in terrestrial systems.

Recent work from Albouy et al. (2014) mapped marine food web structure based on species climatic niche overlap and inferred trophic interactions from body-mass in the Mediterranean basin. They found that climate warming could lead species to shift their range, which could result in strong changes in food web structure across spatial gradients. Another example by Kortsch et al. (2015), showed how climate warming and ecological niches of species could affect the food web structure. The authors mapped marine food webs based on empirical data and related temporal and spatial food web? structural changes, especially the average degree (number of trophic interactions per species), to the range shift of more generalist species towards the North Pole. However, no explicit influence of climate or landscape descriptors on

food web topology was tested. Instead, microcosm and meta-analysis studies have shown that food web structure is influenced by climatic conditions (Romero et al., 2016), ecosystem productivity (Xiao et al., 2015), habitat fragmentation (Hagen et al., 2012) and human disturbance (Takemoto & Kajihara, 2016). Climatic conditions, such as temperature and precipitation gradients, are major driving forces on community assembly over large spatial scales, acting as filters to species with certain characteristics. In food webs, climatic conditions may affect the frequency of trophic interactions between species (Yee & Murray, 2004; Petchey, Brose & Rall, 2010), species dietary strategy (specialist vs. generalist under climatic variability; Vázquez & Stevens, 2004) and limit the persistence of top predators (Ledger et al., 2012). Primary productivity and ecosystem size may limit directly the length of food webs, especially in resource poor environments (Kaunzinger & Morin, 1998; Post, 2002). Habitat fragmentation also plays a role on shaping food webs. High levels of fragmentation may reduce the strength of interactions between species and lead to networks with lower link density (Hagen et al., 2012). These studies all have in common the analysis of discrete food webs and how isolated web properties are affected by a particular gradient. However, they are lacking the interaction between multiple topological properties over large and continuous landscapes.

Here, we build on the most complete species interaction database at European scale combined with distribution data to understand the spatial distribution of multi-trophic food webs, and how the environment, landscape, and anthropogenic pressure influence different topological network properties. We tackle these challenges by answering the following questions for tetrapod vertebrates in Europe:
 i) How are food web properties correlated in geographic space?
ii) What is the spatial distribution of vertebrate food web properties in Europe?
iii) How does climate and landscape configuration drive that spatial distribution?

Materials and Methods

Study area and environmental variables
We analyzed the entire extent of Europe (excluding Macaronesia region and Iceland). We used four uncorrelated climatic variables taken from the Wordclim database (Hijmans et al., 2005) resampled at 10 km^2 resolution to match the spatial distribution of terrestrial vertebrates (see below). Variables were annual mean temperature, temperature seasonality (standard deviation of monthly mean temperature), total annual precipitation and coefficient of variation of precipitation. These variables were chosen since they correlate with diversity across large spatial scales (REF). We also quantified landscape configuration using the richness of distinct habitats within a pixel using the GlobCover habitat classification at 300 m resolution. We finally quantified the available energy in each pixel through estimates of net primary productivity (grams of carbon per year at 0.25 decimal degrees spatial resolution;

Imhoff et al., 2004) and the influence of humans on natural landscape through the human footprint index (at 1 km spatial resolution; Sanderson et al., 2002) by averaging each variable at each 10 km^2 pixel.

Species distribution of all European tetrapod vertebrates

We extracted European species range maps for all terrestrial vertebrates (mammals, breeding birds, amphibians, squamates and testudines) from Maiorano *et al.*, (2013). Published data followed a regular grid of 300 m resolution (WGS84) where a pixel got a 0 value for unsuitable habitat or a value equal to 1 or 2 for secondary and primary habitat, respectively. For practical reasons, we up-scaled each species range map to a 10 km by 10 km equal-size area grid (ETRS89). This up-scaling procedure allowed us to make sure the energy and heterogeneity of the pixel were fully captured and to have equal area between low and high latitude. We did so by first projecting the original data (300 m resolution, WGS84) onto an equal-sized reference grid (300 m resolution, ETRS89) and then aggregated the distribution to a 10 km resolution grid. We considered the species as present in a cell when at least one 300m pixel coded either as 1 or 2 fell within a 10 km pixel. In total, we focused on 521 birds, 288 mammals, 251 squamates and testudines species and 104 amphibian species that naturally occur in Europe (see S1 for full species list).

Trophic interactions between all vertebrates

A metaweb compiles all potential predator-prey interactions between species for a given regional species pool. Here, we built the complete metaweb of European terrestrial vertebrates from expert knowledge and grey literature (e.g. field guides). We considered a trophic interaction feasible between any pair of species when one of the species potentially preys on any life stage of another species (e.g. egg and larval when applicable, juvenile or adult). To account for non-vertebrate interactions, for instance plant-herbivore interactions or insectivore-invertebrates, we also added 12 general diet categories, i.e. detritus, coprophagous, mushrooms, mosses and lichens, algae, fruits, grains, other plant parts, invertebrates, fish, domestic animals and carrion. These diet categories were used to determine local assemblages and species trophic level properties (see below).

Local assemblages and food web structure

Local realized food webs were built by intersecting the metaweb with co-occurrence matrix for each pixel. A species was considered present in a pixel if it met three criteria: 1) primary suitable habitat was available within that pixel (given that the pixel intersected species' geographical range), 2) non-primary consumers had at least one prey species in the same pixel (note that primary consumers are not constrained by resource availability), and 3) at least one habitat was shared with its prey (for non-primary consumers only). For each 10 km pixel, we then calculated sixteen food-web metrics that characterize type of taxa present, strategy, web complexity and chain

length of each local realized web (see Table 1 for details).

Since food web properties are known to strongly correlate with each other, we investigated their multi-dimensional structure through a limited number of composite descriptors. We did so by using a principal component analysis on the sixteen food web metrics across Europe (Table 1).

Food web properties and spatial drivers

To relate our set of food web composite descriptors to environmental layers (climate and landscape variables), we used a generalized additive model (GAM) for each of the selected composite descriptors. We used GAM instead of a generalized linear model since we had no *a priori* expectation regarding the shape of the relationships between the response variable and the predictor variables, and we assumed that non-linear relationships are possible. In our particular case, we built constrained GAMs to avoid over-flexible responses and better express ecologically meaningful relationships. We thus used a maximum degree of smoothing of 3, which somehow represents a polynomial of degree 2 maximum.

Both the environmental variables and the food web topological metrics inevitably show some spatial dependence. To account for spatial dependency, we built an autocovariate variable for each of the composite descriptors to estimate how much the response variable for any site reflects the values of the neighboring sites (Dorman et al. 2007) (function *autocov_dist* in *spdep* R package). However, since this autocovariate was unconditional to the environmental variation, we related each autocovariate variable (for each composite descriptor) to the set of environmental variables using a bootstrap aggregating model (random forest). We then extracted the residuals of the model and used them as a spatial variable independent of the environment (or at least of the environmental variables used here in the study). The importance of such a variable reflected the presence of an unmeasured spatial process not linked with environment that correlated with food web structure.

To estimate the importance of each predictor variable on the spatial distribution of realized food webs, we used a "permutation accuracy importance" method (Strobl et al. 2007, 2009). The predictor to test is randomized so that its original association to the response variable is broken. The permutated variable and the remaining unchanged predictors are then used to predict the response. A "variable importance" score is then measured as the Pearson correlation between the original prediction and the one after permutation of the selected predictor (Strobl et al. 2009). The more the Pearson correlation decreases when the variable is permutated, the more important the variable is. The whole procedure was repeated 100 times. To ease the interpretation of the results, we reported the average (1 − Pearson correlation). Values close to 1 reflected high importance, values close to 0, no importance.

Food web structure

The metaweb was composed in total of 1140 species, with around 66% of basal, 33% of intermediate and 0.1% of top predators' species. Link density and connectance were 61.93 and 0.05 respectively. The average and maximum trophic level within the metaweb was 2.36 and 3.78, respectively. Species within the metaweb were on average separated by 1.9 links. The full topological properties are presented in appendix S2.

We calculated and mapped realized food web topological properties (see Table 1 for a description of properties used) across the European continent. At the continental scale, food webs varied from 10 to 305 species and had on average 194 species; each species had on average 16.63 trophic interactions. Mountain ranges (e.g. the Alps, Carpathians) and northern latitudes were associated with food webs with fewer species and links. In contrast, food webs were richer and more link dense in lowlands and southern regions of Europe. Connectance was on average 0.09, and was higher towards northern regions of Europe, such as Scandinavia. For full maps of all individual topological properties see appendix Figure S.1.

Composite descriptors of the local realized food webs

We retained two composite descriptors out of the principal component analysis that together explained more than 60% of the total variation in food web structure. The first descriptor, that we hereafter called *size,* explained 43.77% of structural variation and was related to food web taxa composition (proportion of intermediate and basal species), vertical structure, diet specialization, and species diversity (Table 2). We observed a dichotomy between the proportion of basal and intermediate species, where richer communities had proportionally more intermediate species (i.e. species having both prey and predators in local food webs) and fewer basal species. Along this descriptor, we also observed a positive co-variation between the proportion of intermediate species and the number of species, which suggested that food webs get longer with species richness and diversity gets more concentrated in the middle. *Size* descriptor also showed that diet specialization increased with species diversity.

The second descriptor, hereafter named *web realization,* explained 20.01% of the total variance and was mainly related to the amount of realized interactions (i.e. connectance) and the proximity between species (characteristic path length) (Table 2). Food webs associated with higher connectance were more clustered and had more trophically similar species (same prey and predators), while food webs with lower connectance had proportionally more top predators, species were more distant and higher standard deviations in vulnerability and generality.

Spatial distribution of the composite descriptors of the European food webs

The *Size* descriptor showed strong latitude and altitude gradients. In high elevations

and in northern latitudes, assemblages have shorter food chains with fewer species and more trophic generalists than south and central European assemblages (Fig. 1a). *Web realization* descriptor showed highest values in the Northeast of the Scandinavian Peninsula and artic coast of Russia, which suggested that food webs have high connectance and are composed by more trophically similar species. Lowest *web realization* values were located in United Kingdom, south of Sweden and in southwestern Mediterranean islands, where food webs had more top predators, lower connectance and generality and vulnerability were more variable (Fig. 1b).

Relationships between climate, energy and human presence and composite food web descriptors

The introduction of autocovariate variables in our GAM models increased the goodness of fit for all models. This suggested that an unmeasured spatial process was affecting the spatial distribution of networks and the importance of this variable was higher in the *web realization* descriptor model than *size* descriptor (Fig. 3).

The GAM model relating our first composite descriptor of local realized food webs (namely *size* descriptor) reached a high goodness of fit (R^2 = 0.69) showing the importance of environmental predictors to explain this particular descriptor of the food web. The most important variables explaining food web *size* were average annual temperature and temperature seasonality, followed by primary productivity (Fig. 3). Both temperature variables related positively and linearly with food-web *size*, while primary productivity showed a unimodal relationship (Fig. 4). In other words, high temperatures and high seasonality sites support more complex food webs than do areas with colder climates and low seasonality. However, this relationship depends on productivity, where complex food webs were found in intermediatly productive areas.

Concerning *web realization*, the GAM model was slightly less explanatory (R^2 = 0.47). In these, human footprint was the most important variable, followed by the autocovariate variable, temperature seasonality and annual average, and productivity (Fig. 3). Interestingly, human footprint showed a parabolic behavior, where low and high values of this index contributed positively to *web realization*, and intermediate values contributed negatively (Fig. 4). Similar to the *size* descriptor, temperature seasonality and annual temperature were positively correlated with *web realization* descriptor, however at extreme values of temperature seasonality the contribution to *web realization* was negative. Primary productivity was also an important variable in this model, and its contribution to *web realization* was mostly positive.

DISCUSSION

The variation of food web structure over broad spatial scales is largely unknown in terrestrial systems. Thanks to the compilation of a large dataset comprising pairwise

trophic interactions between European tetrapods, their geographical distributions and habitat preferences, we standardized the construction of local food webs, allowing the analysis of food web structure across broad and continuous spatial scales. By doing so, we were able to explore how food web structure varies across Europe.

Food web topological properties have been demonstrated to vary in function of number of nodes and/or connectance (Martinez, 1994; Riede et al., 2010). Indeed, food web structure had already been collapsed into fewer structural dimensions in an ordination space, which coincided with food web richness and connectance (Vermaat et al., 2009; Baiser et al., 2012). Here, we observed a similar decomposition of food web structural variation for European tetrapod vertebrate food webs. The size descriptor related diversity, food web vertical structure, and diet specialization, while the web realization descriptor related connectance, topological proximity of species, and species trophic similarity. In others words, the structural decomposition of food webs into these two descriptors suggested that food webs with more or less species can independently be more or less connected (Martinez, 1992).

The spatial distribution of *size* and *web realization* revealed how diverse terrestrial vertebrate food web structure was across the European. The study of such distribution may aid the identification of more sensitive food web areas. For instance, the British Isles and Scandinavian peninsula revealed species poor and less connected food webs with less trophically unique species. Robustness, i.e. propensity to suffer secondary extinctions, has been related to lower species richness and connectance (Saint-Béat et al., 2015). Hence, disturbances in these areas, such as climate change or changes in land-use practices, that affect species richness may have a disruptive effect on these already fragile food webs. Therefore, the spatialization of food webs may provide the means to measure structural diversity and link it to food web theory.

The broad scale of our approach allowed to investigate the impacts of climate and landscape variables on food web structure. Climatic gradients, in particular temperature and precipitation, have long been associated as drivers of biodiversity at both local and global scales (Currie, 1991). Climate variables may affect food web structure at several fronts. First, climate acts as an abiotic filter on the assembly of species (Keddy, 1992), which may affect the functional composition of communities and impact food web structure (Lurgi, Lopez & Montoya, 2012; Blanchard, 2015). Second, it has been suggested that climate variability may directly affect the vertical structure of the food web, where climate stability allows for longer food web chains and narrower diet niches (Menge & Sutherland, 1987; Vázquez & Stevens, 2004; Cirtwill, Stouffer & Romanuk, 2015). Third, climate may affect food web structural properties, where interannual temperature variability can be negatively correlated with modularity (Welti & Joern, 2015). Our study showed that European food web

structure, compressed into two descriptors, was highly affected by annual average temperature and its seasonality. Higher temperature and its respective seasonality contributed to more speciose, longer and more diet specialized food webs. Interestingly, the effect of temperature seasonality on food web structure was counter-intuitive, where more climate instability was associated with more complex food webs. To explain the mechanism.

The work from Vermaat et al. (2009) contributed to the understanding of how food web structure co-varied with primary productivity, where trophic level, omnivory, proportion of top species co-varied with primary productivity. In here, we raised a similar question, how resource availability may affect European food web structure in space. Our results showed that there is indeed an effect of resource availability on food web structure; primary productivity explained food web structure (both descriptors). In particular, we showed that the effect of productivity depends on the amount of resources available. Resource availability is one of the hypotheses that relates food web structure with energy, where more resources available to basal species lead to more species in the network and thus increasing food chain length, especially in low productive environments (Jenkins, Kitching & Pimm, 1992; Post, 2002). Here, we observed an intermediate threshold, above which the effect of primary productivity on food web structure did not change. Therefore, the importance of this variable may differ across the European landscape, acting as a filter to food web structure in some regions (e.g. northern latitudes) but not in others.

Human presence may lead to changes in land-use, habitat fragmentation and pollution, which in turn can negatively affect biodiversity (Barnosky et al., 2011) and food web structure (Evans, Pocock & Memmott, 2013). Here, we used the human footprint index as a measure of anthropogenic pressure to understand its correlation with vertebrate food web structure. We did find a negative relationship between human footprint and the web realization structural descriptor (Fig. 4). However, we cannot assume this to be a cause-effect relationship, and it is more likely that it comes from a spatial coincidence between human footprint, species richness and connectance. On the one hand, climatic conditions and resource availability may affect the spatial distribution of human densities and species diversity alike, which would explain why the two are positively correlated with human population densities (Araújo, 2003). Indeed, despite the weak importance of human footprint on the size descriptor (Fig. 3), its effect peaked at intermediate levels of human disturbance, where we also found food webs with more species and higher trophic levels (Fig. 4). On the other hand, even though the two major complexity food web topological properties, species richness and connectance, were nearly orthogonal in our ordination space (Fig. 1), they were negatively correlated at extreme low values of richness. In general, very small food webs had high values of connectance (note in Fig. S1 that areas with low species richness coincide with areas with high

connectance). Therefore, areas with low human footprint also had high *web realization,* via low values of connectance.

The importance of the autocovariate variable in *web realization* descriptor model suggested the presence of other spatial processes. Since we use species co-occurrences to design European tetrapod assemblages, biogeographical processes, such as barriers to species dispersal or even other biotic factors could lead to spatial similarities and/or dissimilarities in food web structure not explained solely by climate nor resource availability. Further work is needed to include such processes, which could be done by including the assemblages' composition (restricted to the variance not explained by the climate and landscape configuration) in the spatial analysis of food web structure.

A limitation to our design was the even contribution of each prey to the predator's diet and every trophic interaction was constant in space (i.e. if two species interacted in the metaweb, they always interacted across their intercepted spatial range). The former implied that we did not account for biomass relations or metabolic requirements (in contrast, weighted food webs interactions may be defined by biomass relationships) and as consequence we may have inflated omnivory and connectance. The latter implied no species diet or behavioral adaptability (e.g. prey behavioral changes in function of predator presence or predator diet shift due to presence of competitors; Preisser et al., 2009; Van Dijk et al., 2008) and as a consequence our webs may have an inflated number of trophic interactions. We are aware of such issues and more work is necessary to quantify the level of uncertainty of our method, for instance, by using highly resolved empirical food webs and quantify the difference in topological properties obtained with the two methods. Nevertheless, this work is a good example of how biogeography may help comprehend terrestrial food webs spatial patterns.

CONCLUSION

The rise of more resolved food web data, the construction of metawebs allows standardization of effort and opens the avenue to broad-scale food web structure studies (Morales-Castilla et al., 2015). Our study represents one attempt to map food web structure spatial variation at a continental scale. In this study, we found two major aspects of food web structure that are strongly tied to the underlying environment, one linking species diversity and structure and the other how much connected they are.
We aimed at investigating the effect of broad-scale climate gradients, resource availability and human disturbance on food webs structure. We showed that climate was correlated food web structure, especially annual average temperature and temperature seasonality. Resource availability, measured as net primary productivity,

had a limitative effect on food web structure and anthropogenic disturbance showed to be strongly associated with the realization of trophic interactions.

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Table 1. Definitions of food web topological properties used in our study.

Topological property	Definition
Species richness	Number of species
Connectance	Proportion of realized links that occur in a web.
Link density	Average number of links per species.
Clustering coefficient	Probability of linkage of two species, given that both are linked to a third species.
Characteristic path length	The mean shortest food chain length between species pairs
Vulnerability	Mean and standard deviation of number of predators per species.
SD of Vulnerability	
Generality	Mean and standard deviation of number of prey per species.
SD of Generality	
Maximum trophic similarity	Mean maximum number of links (in- and outward) shared between all pairs of species.
Proportion of basal	Proportion of species without any (vertebrate) prey.
Proportion of intermediate	Proportion of species with prey and predators.
Proportion of top predator species	Proportion of species without any predators.
Proportion of omnivores	Proportion of species that feed on more than one trophic level.
Mean trophic level	Mean prey average trophic level
Maximum trophic level	Maximum prey average trophic level

Table 2. Correlation between European food web properties and the major principal components axes of the PCA (Size and web realization).

Topological metric	Size descriptor	Web realization descriptor
Species richness	0.31	-0.08
Connectance	-0.05	0.51
Link density	0.32	0.15
Clustering coefficient	0.07	0.32
Characteristic path length	0.13	-0.42
Vulnerability	-0.12	-0.23
SD of Vulnerability	0.28	-0.19
Generality	-0.32	0.06
SD of Generality	-0.20	-0.39
Maximum trophic similarity	-0.10	0.33
Proportion of basal	-0.32	0.04
Proportion of intermediate	-0.13	-0.28
Proportion of top predator species	0.33	0.03
Proportion of omnivores	0.31	-0.05
Mean trophic level	0.35	0.02
Maximum trophic level	0.31	0.03
Variance explained (%)	43.7	20.1

Figure 1. Principal components analysis (PCA) of European food web metrics. The first two axes explained a total of 63.8% of all of the structure of European food webs. The first PCA axis, named *size* structural descriptor, was mainly related to species richness, trophic level and nodes vertical position. The second PCA axis, named *web realization* structural descriptor, was related mostly with connectance and characteristic path length. Red arrows represent the direction and value of correlations between individual topological metrics and each structural food web descriptors. The four food webs were drawn from the closest point to the centroid at each quadrant.
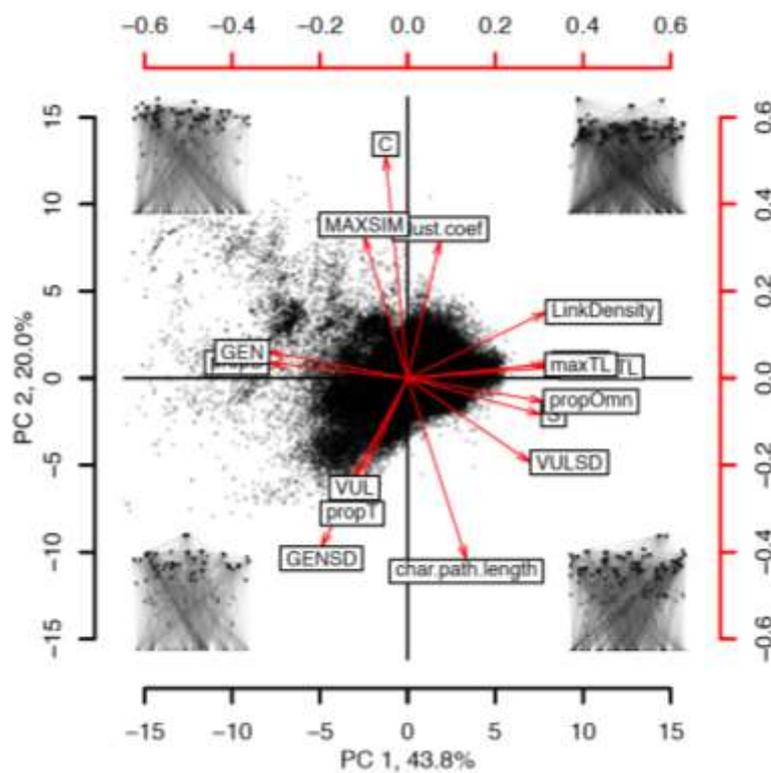
Figure 2. Spatial distribution of the two composite descriptors of the European tetrapod vertebrate food webs. a) *Size* descriptor linked to species diversity, trophic length and nodes vertical distribution. b) *Web realization* linked to connectance, trophic similarity and species proximity in the web.
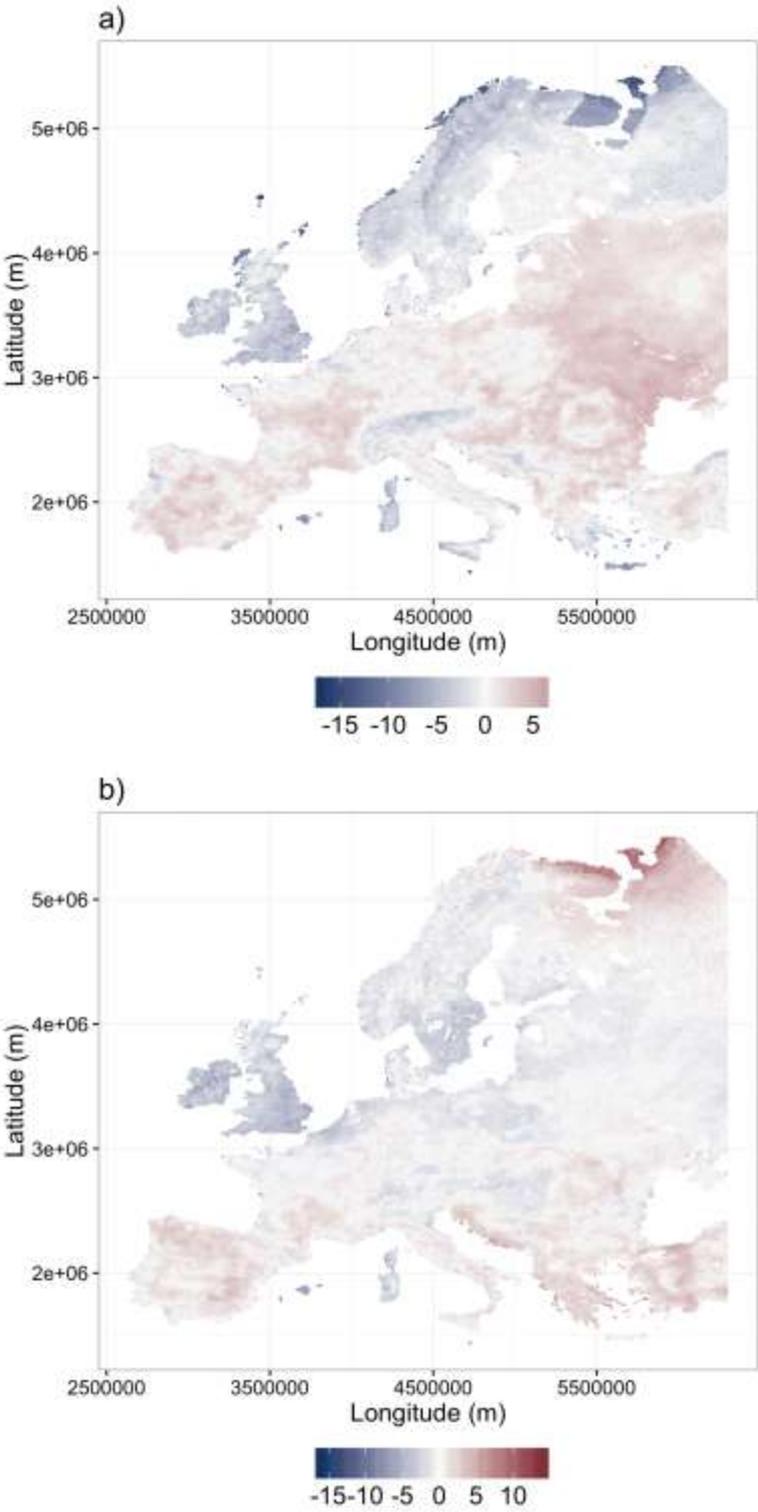
Figure 3. Variable importance for each structural composite descriptor model. Climatic variables are depicted in light gray. Landscape variables are depicted in dark gray. In both models, temperature variables (annual average and seasonality) were among the most important variables. *Size* descriptor model explained 69.7% of the variance, while *web realization* models explain 47.5%.
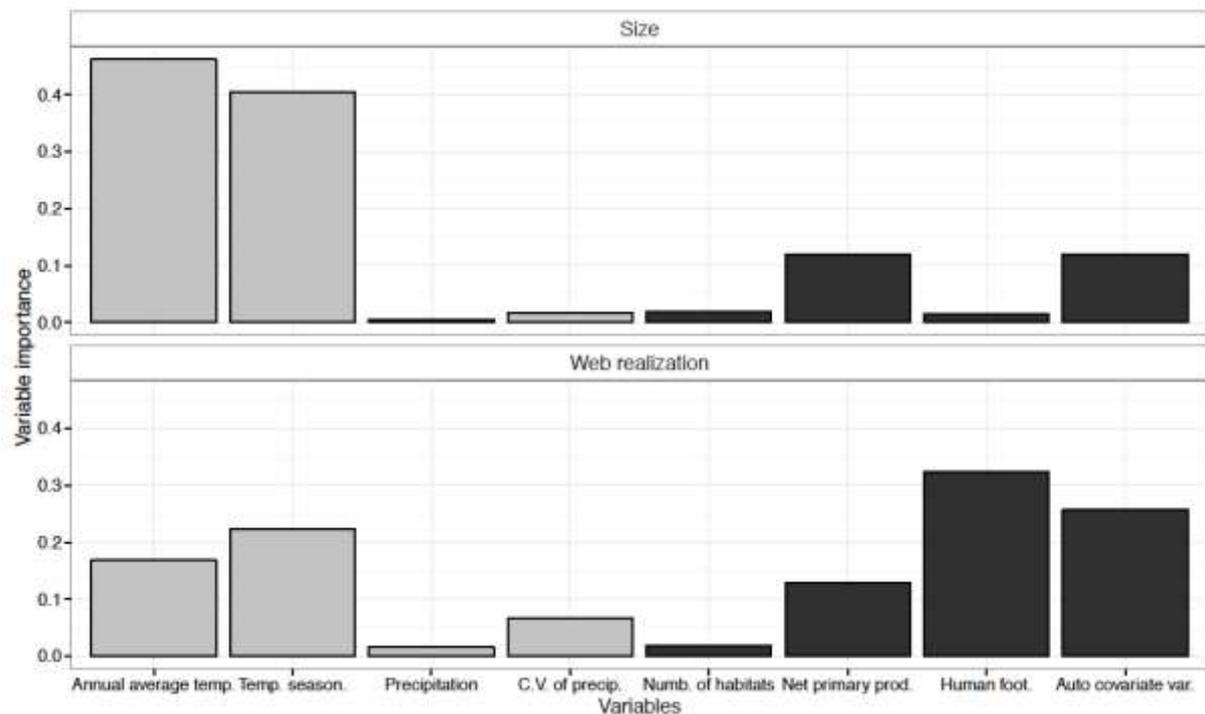
Figure 4. Partial response plots of a) Food web *size* and b) *Web realization* descriptors of the European food web in function of the climatic and landscape predictors. a) Food web *size* descriptor linked to species diversity, trophic length and nodes vertical position. Lines are the estimated effects of each predictor with the respective 95 % confidence intervals shaded in grey. Note that these intervals are very narrow.
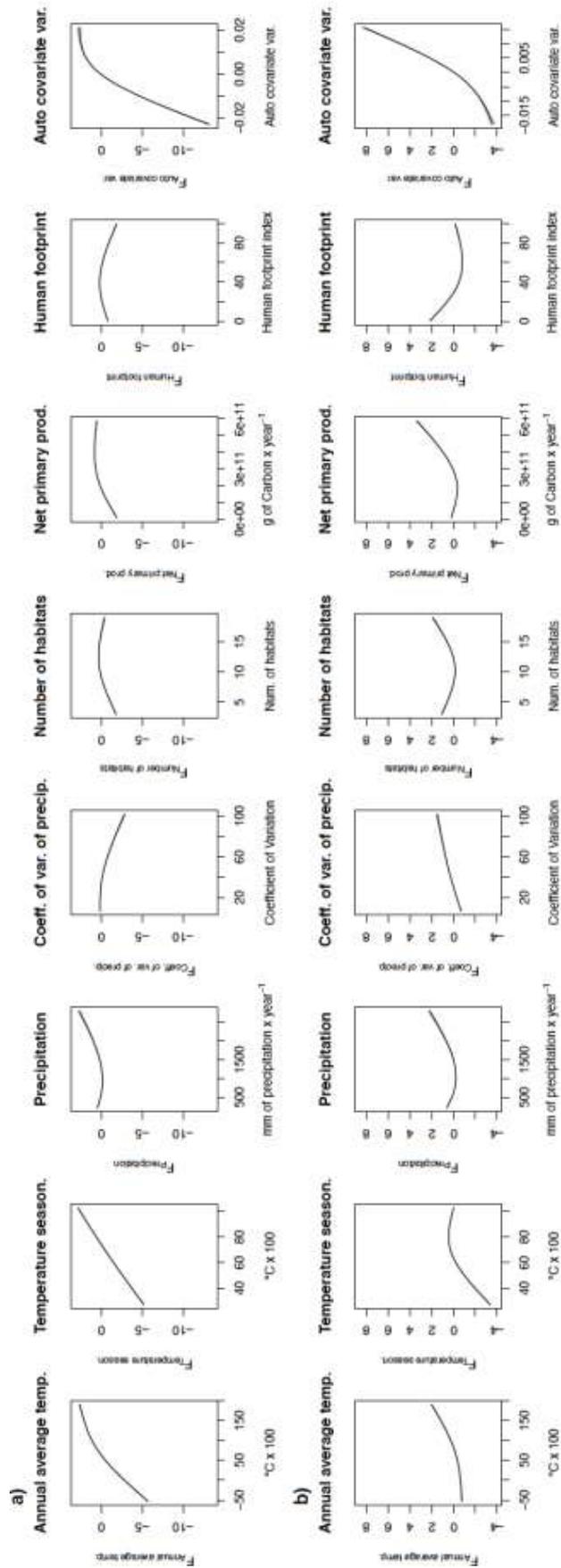
Figure S1. Spatial distribution of individual metrics.

Figure S1. Spatial distribution of individual metrics (continued).

113
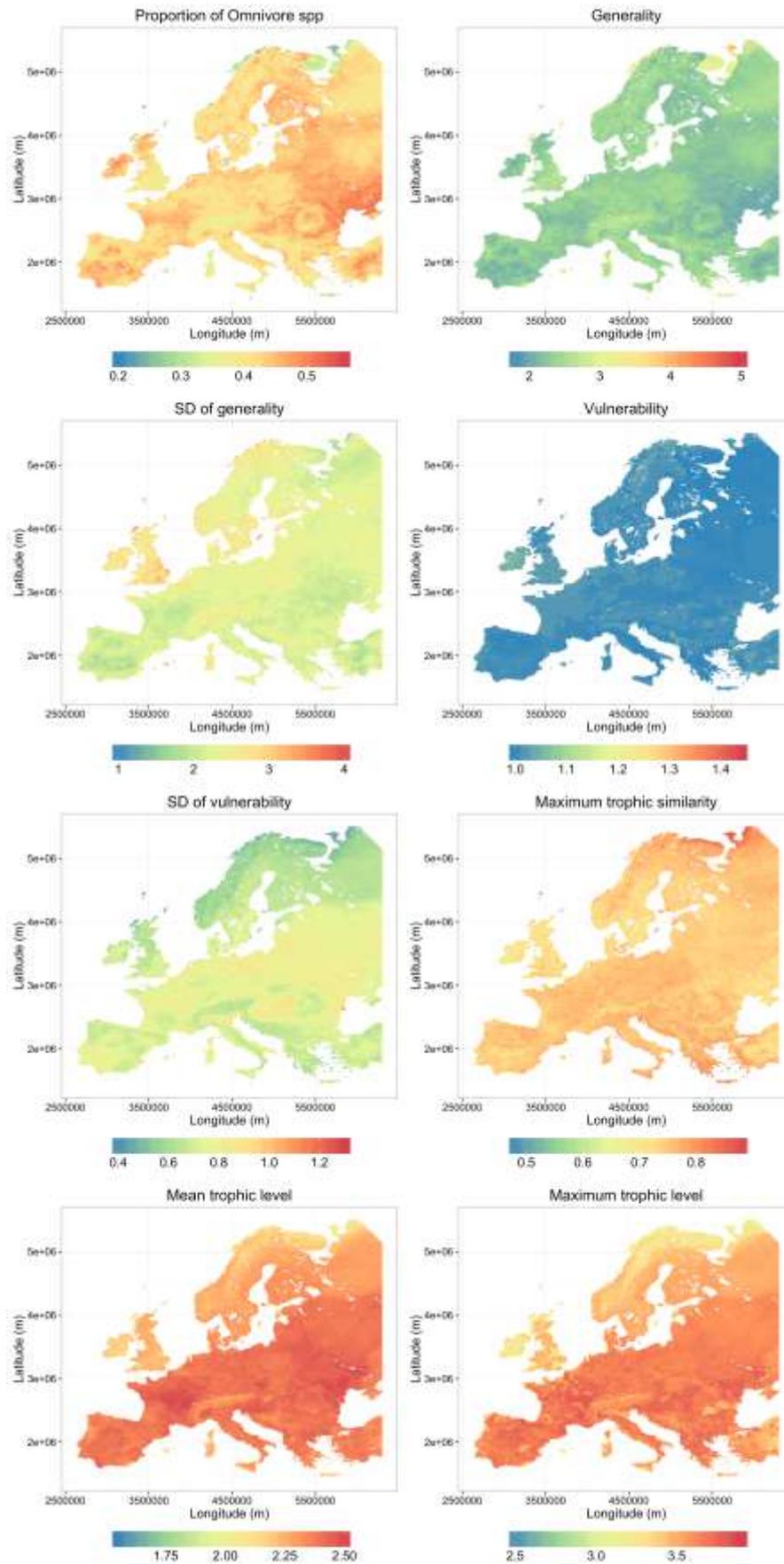
Figure S2 Spatial distribution of explanatory variables.
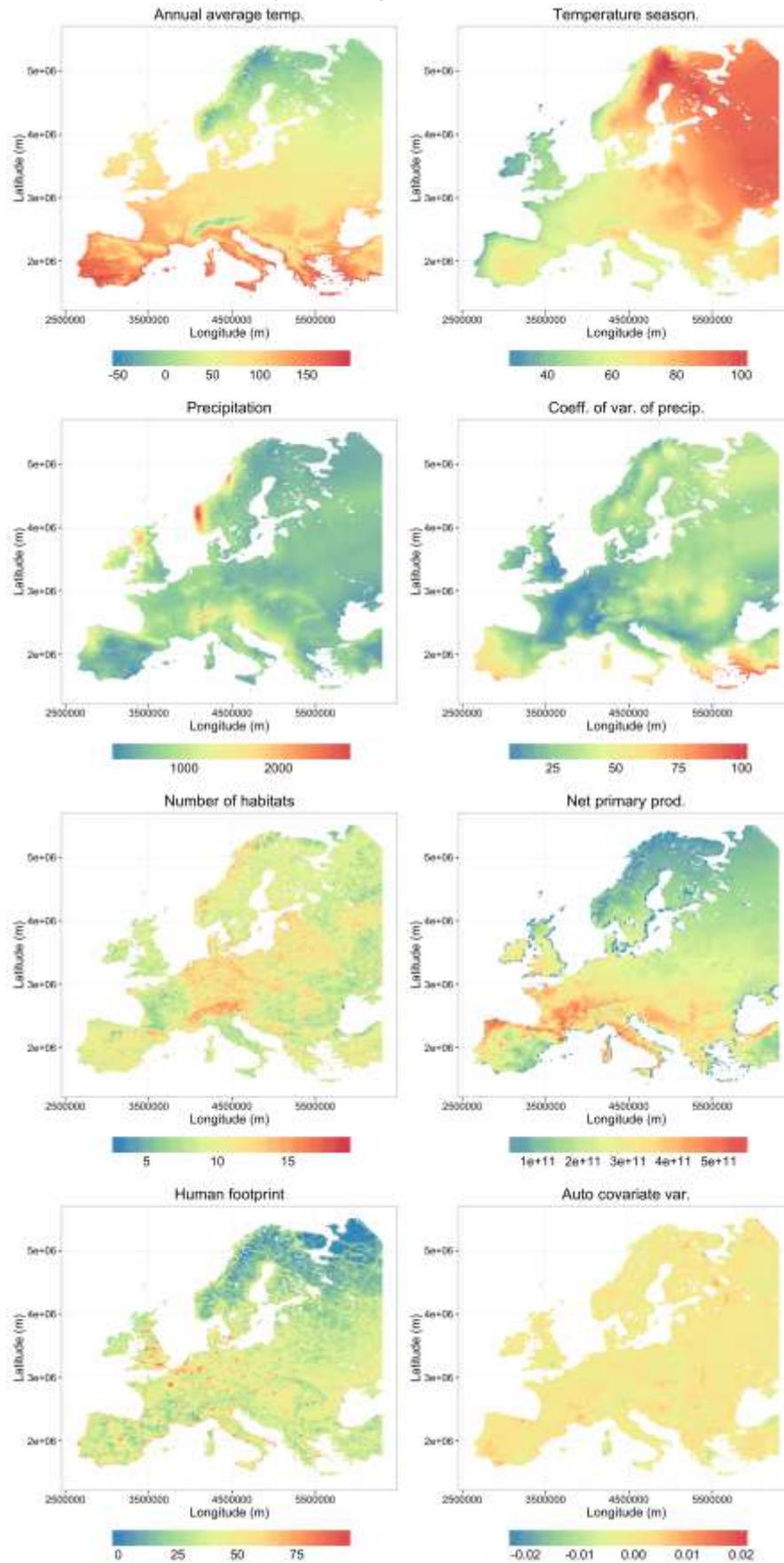
10. CONCLUSIONS

Climate change affects birds in different ways; it can alter distribution, abundance, behavior, even genetic composition. It can also affect the timing of events like migration or breeding.

Some migratory birds have advanced their spring arrival to Northern Europe, possibly by increasing the speed of migration through Europe in response to increased temperature *en route*. To prove it I compared the phenology of spring arrival of seven trans-Saharan migrants along their migration route and tested for patterns indicating that migration speed varied over the season using long-term data collected on the Italian island of Capri and at Ottenby Bird Observatory, Sweden (Jonzén *et al.,* 2006b). I found a linear relationship between median arrival dates on Capri and at Ottenby. The slope was not significantly different from one. On average, the seven species arrived 15 days later at Ottenby compared to Capri. There was a (non-significant) negative relationship between the species-specific arrival dates at Capri and the differences in median arrival dates between Capri and Ottenby, possibly indicating a tendency towards faster migration through Europe later in the season.

In order to better understand the extent to which changes in bird phenology reflect responses to weather conditions in the wintering or breeding areas, or during migration, I analyzed the relationships between the timing of spring migration of 9 species of trans-Saharan migratory birds across the Mediterranean, and thermal and precipitation anomalies in the main wintering areas south of the Sahara Desert and in North African stopover areas (Saino *et al.,* 2007). Median migration dates were collected on Capri by standardized mist-netting during 1981 to 2004 (data collected directly by me). High temperatures in sub-Saharan Africa (Sahel and Gulf of Guinea) prior to northward migration (February and March) were associated with advanced migration. Moreover, birds migrated earlier when winter rainfall in North Africa was more abundant. The relationships between relevant meteorological variables and timing of migration were remarkably consistent among species, suggesting a coherent response to the same extrinsic stimuli. In conclusion, the results suggest that thermal conditions in the wintering quarters, as well as rainfall in North African stopover areas, can influence interannual variation in migration phenology of trans-Saharan migratory birds.

European breeding birds are not equally distributed within continental Europe. I identified richness hotspots of European breeding birds in Europe and adjacent islands. Moreover, I assessed the extent to which by the end of the 21st century such hotspots will be exposed to average monthly temperature and precipitation patterns which can be regarded as extreme if compared to the climate experienced during 1950-2000. In particular, I considered the entire European sub-continent plus Turkey and a total of 542 species. For each species, I developed species-specific expert-based distribution models (validated against field data) which I used to calculate species richness maps. Considering four global circulation model outputs and three emission scenarios, I generated an index of risk of exposure to extreme climates, and I used a bivariate local Moran's / to identify the areas with a significant association between hotspots of diversity and high risk of exposure to extreme climates. The obtained results outline that richness hotspots for all species together are within northern central Europe and western Russia; species of conservation concern concentrate in the eastern-central part of Europe, while species whose distribution is mainly European are more represented in northern central Europe, Greece, Alps and Iberian Peninsula. A major result suggest that the main hotspots of European birds richness may be extensively influenced by the climate change projected to occur over the coming decades, especially in the Mediterranean bioregion, posing serious concerns for biodiversity conservation (Maiorano *et al.*, 2013).

In order to build more realistic scenarios for changes in the distribution of species breeding in continental Europe, I presented a proposal of a modelling approach based on the combination of state-of-the-art bioclimatic models, with expert based habitat suitability and distance to current distribution (Montemaggiori et al., 2015). Thus, for each species, I developed three layers: a) a bioclimatic model calibrated with an ensemble forecasting approach, considering six climatic variables and species' occurrences according to existing distribution data; b) the expert-based habitat suitability model (*sensu* Maiorano *et al.* 2013) and c) the distance from present distribution of the species. Assuming that the three layers are largely independent, I calculated for each species a final model of the relative probability of presence by multiplying the three maps.
I evaluated the reliability of the models using independent points of presence and calculated and index of the calibration capacity of the models for both the classical bioclimatic model and for the final model of relative probability of presence. The results clearly demonstrate that this approach produces more accurate and better performing models compared to simple bioclimatic ones (79% of cases). Combining this approach with future scenarios for land use and climate, it will be possible to build more robust models showing potential changes in species distribution. Furthermore, it will be possible to

incorporate also models of species' biotic interactions and dispersal distances, providing a biologically richer outcome.

After assessing where European birds are distributed in Europe, I wanted to investigate on their conservation level, also because many of their richness hotspots seem to be undergoing an extensively influence by the projected climate change.

The European Union has made extensive biodiversity conservation efforts with the Habitats and Birds Directives and with the establishment of the Natura 2000 network of protected areas, one of the largest networks of conservation areas worldwide. A gap analysis was performed of the entire Natura 2000 system plus national protected areas and all terrestrial vertebrates, including all European breeding birds (freshwater fish excluded).

For each species the representativeness in terms of the suitable area falling within the protected areas network (Protected areas and Nature 2000) and in Europe was calculated, and the IUCN conservation status and the presence in the annexes of the European Bird Directive were recorded. Furthermore, for each species I considered the threat status and, using the global distribution range obtained as described in Maiorano *et al.* (2013), I calculated the percentage of the distribution included in the EU and defined as endemics all species with distributions totally encompassed in the EU.

The results of this analysis were comforting: *a)* of the 31 species with a strictly European extent of occurrence ('endemic'), 90.3% (28 species) is covered by the network of protected areas (Protected areas + Nature 2000); *b)* all threatened species result protected by the network; *c)* a minimum of 74% of species reaches the representative target in the Protected areas and a maximum of 93% falls within the total coverage (Protected areas + Nature 2000) (Maiorano et al., 2015).

Because the gap analysis was performed for all species of European terrestrial vertebrates (freshwater fish excluded), I could also compare the results obtained for the birds with the ones obtained for the other classes. If the umbrella of protected areas in Europe is valid for birds, the same cannot be assessed for other European terrestrial vertebrates. In reptiles, for example, 60.9% of threatened species are not covered by the European protection network, and even 80.4% of endemic species live outside of it. This raises serious questions, especially concerning the criteria by which a higher level of protection is granted to the territory or by which the species are annexed to conservation directives. The European Commission initiated in 2014 a process aimed at assessing the importance of the Birds and Habitats Directives for biodiversity conservation. The presented results contribute to this assessment and suggest the system is largely effective for terrestrial vertebrates, especially birds, but would benefit from further updating of the species lists and field management.

To move beyond the simple projections of likely impacts of global change I finally decided to identify the most vulnerable species within the study area (Montemaggiori & Maiorano in prep.).

The adopted approach was to build a vulnerability index (Vi) for the European birds that integrates estimations of projected range change and different proxies of species resilience in a quantitative way. The index is completely quantitative, and it allows ranking species so as to prioritize conservation actions. According to the algorithm, five indicators are defined to compose the vulnerability index, expressing three operational aspects of vulnerability: the projected change in the distribution, the reservoirs for the species and the population trend. Two indicators capture the change in the species' future distribution within Europe, two measure the species resilience and one quantify the historical trend of the species over the past decades. I used one stressor, climate change, and one spatially explicit scenario, to represent the magnitude of the future change and to assess its impact on species distribution using MaxEnt species distribution model. The vulnerability index was developed for 499 breeding species in Europe.

The five base indicators contribute differently to the vulnerability of a species. The analysis of the single components of the index Vi for each species allows to highlight the relative weight of the different indicators, and a first exploration of the obtained results highlights the highest number of species with a high Vi value in the north-eastern part of the area study, mainly because of the strong reduction of habitat suitability for the future in that area. The average weight of each taxon, its diet, its habitat suitability, some behavioral aspects and its conservation status were also collected and used to understand if there are ecological indications linked to the calculated indices, in order to highlight specific management indications. From the analysis it seems to emerge that the most specialized species in terms of habitat seem to be those with higher Vi indices; aquatic species are more vulnerable, as well as those nesting on the ground. The degree of vulnerability increases for the larger species and finally, the proposed vulnerability index complements the assessment of extinction risk based on the IUCN European Red List. In particular, the vulnerability index points at species which are currently not threatened (LC), but are likely to become so, as for 50%, under climate change scenario. Their persistence in Europe is at risk over the next 80 years.

Very recently I wanted to start to explore a new territory: the impact of CC on ecological connections within the natural populations. So, I contributed, together with a group of ecologists coordinated by W. Thuiller (CNRS – Grenoble), to analyze the spatial structure

of terrestrial vertebrate food webs and revisit traditional diversity-environmental relationships in light of trophic interactions.

I therefore produced a web of trophic relationships between all European bird species and each single species of European terrestrial vertebrates (mammals, birds, reptiles and amphibians). This ecological web, together with the others built for all the other classes examined, has been combined with the spatial distributions of all the species projected into the future. The results of this analysis, which flowed into a contribution recently submitted (Braga et al., n.d.), show an evident effect of CC in modeling the spatial structure of trophic networks among all European terrestrial vertebrates. Similarly to taxonomic diversity, there are then overwhelming effects of climate and disturbance in shaping the spatial structure of European terrestrial vertebrate food webs. Another problem for the future.

In the end, I can not help but confirm the strong impact climate change has on the future of European birds. Climate change will play an import role on future species distribution by modifying habitat suitability and/or shrinking and displacing species extent of occurrences, but it will also affect the systemic and ecological traits of the species, seriously endangering one of the most important animal classes not only ecologically speaking, but also as a fundamental source of inspiration and beauty for mankind.

Chicks of Boreal owl (*Aegolius funereus*) (credits Nick Saunders).

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