Original article

Climate effects on the distribution of wetland habitats and connectivity in networks of migratory waterbirds

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ABSTRACT

The establishment and maintenance of conservation areas are among the most common measures to mitigate the loss of biodiversity. However, recent advances in conservation biology have challenged the reliability of such areas to cope with variation in climate conditions. Climate change can reshuffle the geographic distribution of species, but in many cases suitable habitats become scarce or unavailable, limiting the ability to migrate or adapt in response to modified environments. In this respect, the extent to which existing protected areas are able to compensate changes in habitat conditions to ensure the persistence of species still remains unclear. We used a spatially explicit model to measure the effects of climate change on the potential distribution of wetland habitats and connectivity of Natura 2000 sites in Italy. The effects of climate change were measured on the potential for water accumulation in a given site, as a surrogate measure for the persistence of aquatic ecosystems and their associated migratory waterbirds. Climate impacts followed a geographic trend, changing the distribution of suitable habitats for migrants and highlighting a latitudinal threshold beyond which the connectivity reaches a sudden collapse. Our findings show the relative poor reliability of most sites in dealing with changing habitat conditions and ensure the long-term connectivity, with possible consequences for the persistence of species. Although alterations of climate suitability and habitat destruction could impact critical areas for migratory waterbirds, more research is needed to evaluate all possible long-term effects on the connectivity of migratory networks.

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1. Introduction

Understanding the impacts of changing climate conditions and habitat loss across the multiple scales of biodiversity is one of the major challenges for the current century (Bellard et al., 2012). Although the effects of climate change are worldwide accepted, the biological responses vary widely across species and taxa, which can basically respond against the potential climate-related extinctions by moving or staying (Parmesan, 2006). Whilst moving implies the ability to disperse and colonize suitable habitats elsewhere (Schaefer et al., 2008), staying involves a series of mechanisms ranging from phenotypic acclimation (Bradshaw and Holzapfel, 2006) to evolutionary adaptation (Parmesan, 2006). However, available evidences point to the conclusion that many responses are mostly mediated by environmentally-induced plasticity rather than real microevolutionary adaptations (for more details about, see Gienapp et al., 2008 and references therein). Regardless of the responses, the availability of suitable habitats able to support such mechanisms and maintain minimum viable populations represents a further condition to counteract the effects of changing climate conditions.

Coupled with climate change, habitat destruction is considered another major threat on global biodiversity, able to influence the distribution of suitable areas for many species, thus limiting their ability to migrate or adapt in response to climate variability (Collingham and Huntley, 2000). To date, it is well known how the persistence of species in degraded landscapes is related to the combined role of climate change and habitat loss (Hill et al., 1999; Warren et al., 2001). Moreover, a strong influence on the persistence of local populations is given by the spatial configuration of habitats (i.e., the real spatial arrangement of habitats within the landscape), which was found to be related with pattern of habitat loss (Hill and Caswell, 1999).

The effects of climate variation on the distribution and availability of habitats are expected to be particularly severe on aquatic

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ecosystems (Sala et al., 2000; MEA, 2005), mainly related to changes in the quantity and quality of water supply due to the alterations in hydrological regimes and land-use change (Bates et al., 2008). This can result in a reduction of their functional capacity, or the shifting of their geographic location (Erwin, 2008) with significant impacts on the migratory fauna, especially birds (Robinson et al., 2009). Waterbirds include a large group of species whose distribution and persistence are intimately linked with the presence, availability and quality of water bodies, as well as by the seasonal conditions depending on the local resource peaks (Kreakie et al., 2012). Seasonal contraction and alteration of hydrological regimes can influence migrants, by reducing their migratory tendency or by expanding the range of resident species (Fiedler, 2003), thus increasing the mismatch between trophic levels (Both et al., 2006). Effects can be severe, especially on long-distance migrants, whose responses are limited by the amount of adaptive genetic variation (Pulido and Berthold, 2004) or by the strength of migratory connectivity (i.e., the seasonal movement of individuals between wintering and breeding sites, Webster et al., 2002). Indeed, the extent to which individuals share similar areas during the migration activity can influence the strength and direction of natural and sexual selection, as well as macro-evolutionary processes such as speciation (Ruegg, 2008), thus influencing the response of populations to selective pressures (Veen, 2013).

A common worldwide response to the threat on biodiversity is to provide sustainable management of habitats and ecosystems through conservation strategies. To address this specific task, the European Union (EU) established the Natura 2000 network to guarantee the long-term connectivity of valuable areas for biodiversity (http://ec.europa.eu/environment/nature/natura2000). This network of conservation areas comprises two different typologies of sites: i) Special Areas of Conservation (SACs, Habitats Directive 92/43/EEC), to ensure the safeguard of vulnerable fauna (with the exclusion of birds), flora and habitats and, ii) Special Protection Areas (SPAs, Birds Directive 09/147/EC), to ensure the conservation of sites for vulnerable birds species. About 17% of the EU surface is covered by more than 27,000 Natura 2000 sites, of which 2,585 within the Italian boundaries, covering more than 21% of the national territory (http://www.minambiente.it/pagina/rete-natura-2000).

Despite the efforts made for the identification, establishment and maintenance of protected areas, recent studies have shown the poor reliability of such areas to cope with climate change (Hannah et al., 2007; Araújo et al., 2011; Rubio-Salcedo et al., 2013), suggesting a renewed prioritization in conservation policies to protect networks of sites able to maintain the long-term connectivity (Hole et al., 2009). Although these studies have identified limits in the current system of protected areas, the influence of changing habitat conditions on the potential connectivity is not yet clear (but see Mazaris et al., 2013; Saura et al., 2014). Indeed, threshold limits have been observed for some critical levels of habitat availability and rate of climate change, suggesting a 'deathly mix' for the persistence of species (Travis, 2003).

Here, we investigate the effects of changing climate conditions on the potential distribution of suitable habitats for migratory waterbirds and the connectivity of Natura 2000 sites in Italy. To answer this question we focused on sites with predominance of aquatic habitats, where information about the presence of waterbirds identified as such by the African Eurasian Waterbird Agreement (AEWA, http://www.unep-aewa.org) were available. We used a network approach based on a spatially explicit model to quantify the extent to which modifications in habitat conditions might influence the ability of existing areas to ensure the presence of migratory waterbirds within the network.

2. Materials and methods

2.1. Methodological outline

We followed a methodological framework focused on a patch-based perspective in modelling the effects of climate change on the potential connectivity of conservation areas, which we assumed as a proxy to analyse the likelihood of species persistence. The general framework can be summarized as follows: i) measuring the potential for water accumulation for each patch (see Appendix A.1), ii) building up the potential connectivity matrix and, iii) measuring the contribution of each patch to the connectivity of surrounding network. The starting dataset included 84 georeferenced areas (downloaded from ftp://ftp.dpn.minambiente.it/Natura2000/TrasmissioneCE_2013/) representing sites with a predominance of aquatic habitats within the Natura 2000 network in Italy, where information about the presence of waterbirds identified as such by the African Eurasian Waterbird Agreement (AEWA, http://www.unep-aewa.org) were available (Fig. 1).

2.2. Building up the connectivity matrix

In a spatial context, some basic features of the patches, such as the surface or inter-patch distance, can be considered useful proxies for identifying the connectivity threshold in landscapes represented by suitable habitats for a given species (Bunn et al., 2000; van Langevelde, 2000). In this case, the knowledge of some specific characteristics, such as the maximum dispersal distance or the home range, can help us construct a network of interconnected patches and subsequently remove improbable links (Bunn et al., 2000). However, the scale of investigation, coupled with the widespread distribution and distance covered during migration by most of waterbirds did not allow identifying an exact threshold for connectivity. We therefore simplified our analytical approach by considering species that can freely move between patches, and the resulting connectivity matrix produces an adjacency matrix with no zeros.

The connectivity matrix was calculated by using a gravity model, which allows a better estimation of long-distance dispersal between discrete points in heterogeneous landscape (Bossenbroek et al., 2001). A gravity model incorporates two different types of landscape data potentially influencing the connectivity: nodes features and spatial distance. Inferred from Newton's law of gravitation, the gravity equation form predicts flow based on 'mass' or potential flow from a site and is typically used for predicting transportation flow and trade of economic goods (Bhattacharya et al., 2008), human migration (Levy, 2010) or infectious disease (Xia et al., 2004). Gravity models focus on the intensity of interactions between nodes separated by a certain physical distance, starting from the assumption that in networks where nodes occupy positions in Euclidean space, spatial constraints may have strong effect on the connectivity pattern. A general gravity model takes the form of:

$$T_{nm} = N_n N_m f(d_{nm}) \tag{1}$$

where N_n and N_m measure the importance of locations n and m, respectively, which can be given by any measure of interest (e.g., population size, area), whilst the deterrence function f describes the influence of space (d_{nm}). Therefore, the strength of interaction between two locations is proportional to the number of possible 'contacts', $N_n N_m$, as a function of specific constraints based on distance costs, here given by the potential for water accumulation, WPA (see Appendix A.1 for an extensive explanation about the derivation of WPA). To derive a measure able to encapsulate an
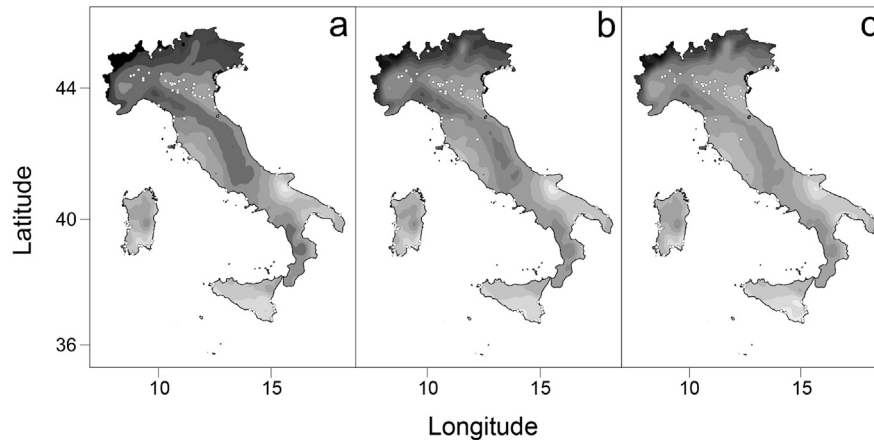
Fig. 1. Spatial distribution of the water potential accumulation (*WPA*) under current climate conditions (a), and the A1B (b) and A2 climate scenario (c) based on the CSIRO-Mk3.0 model (http://www.ipcc.ch). Data were rescaled in a 0-1 scale with darker colours corresponding to the highest *WPA* values (i.e., higher probability of water accumulation). White circles are for sampled locations.

estimate of the dimension of a patch, the *WPA* for each location was averaged over the number of cells inside the polygon, which we considered as a surrogate measure of the surface of a patch. We further evaluated the possible dependence between the surface of the patches and the *WPA*s calculated under current and projected climate scenarios by means of an overall MANOVA test of multivariate regression, where the significance of the regression was given by the Rao's *F* statistic computed from the Wilks lambda with one-tailed *F*-test.

To scale the effect of distance on connectivity, *f* was expressed by a power law, $(d_{nm})^{-\alpha}$, with α the scaling parameter of distance (here $\alpha = 1$). Therefore, Eq. (1) equates the strength of connectivity between two patches as a function of the relative potential for water accumulation. In a nutshell, the likelihood of patches occupancy by waterbirds increases with water availability (i.e., a proxy for suitable habitats) and diminishes proportionally for increasing distances.

2.3. Patches contribution to connectivity

Patches contribution to connectivity was measured by means of the eigenvector centrality (λ_C), which was found to have advantages over other graph-theoretical measures of nodes centrality (Bonacich, 2007). Centrality encloses a wide range of measures able to identify the role of a node with respect to its neighbours or the entire network (Estrada and Bodin, 2008; Opsahl et al., 2010). Among others, λ_C can be used with signed, fully-connected and valued graphs and did not distinctively differ from other measures of centrality (e.g., degree) when positions are all equal in degree (regular graphs), or in core-periphery structures in which high degree positions tend to be connected to each other (Bonacich, 2007). This metric was previously used to identify keystone species in food webs (Allesina and Pascual, 2009) and has also been generalized in a metapopulation context as the metapopulation capacity of fragments in a landscape (Hanski and Ovaskainen, 2000), where the eigenvector identifies the contribution of a single patch to the growth rate and persistence of entire metapopulation.

The eigenvector centrality was derived from the left eigenvector associated with the leading eigenvalue of the connectivity matrix (T_{nm}) and identifies patches that are hubs for the potential connectivity of surrounding network. Connectivity matrices were developed for current climate conditions (1961–1990, 30 years centred on 1975) and the A1B and A2 scenarios (IPCC, 2007) based

on the CSIRO-Mk3.0 model. These scenarios describe a world with a very rapid economic growth, global population that peaks in mid-century and declines thereafter together with the rapid introduction of new and more efficient technologies (IPCC, 2007). The evidence for a constant increase in greenhouse gas emissions, coupled with the continued failures to agree on legally binding global reductions, make the "A" family the less conservative and, therefore, the most probable climate scenarios (see Kriticos et al., 2012 for details). Matrices for each scenario were derived by averaging all future projections, from 2030 to 2100 (see Appendix A.1 for further clarification).

2.4. Variability in patches contribution to connectivity and spatial constraints

To assess the effect of changing climate conditions on the contribution of the patches to the overall network connectivity, the degree of λ_C variation between different scenarios was measured by fitting its cumulative distribution to different models. Model fitting allowed us to measure the degree of asymmetry/symmetry in the distribution of λ_C within the network, or to find critical values of λ_C over which the distribution exhibits patterns that might indicate a sudden collapse of the system. A power law model, $P(\lambda_C) \sim \lambda_C^{-\gamma}$, indicates asymmetry in the frequency distribution of the eigenvector centrality, with the bulk of nodes having low values of λ_C and only few nodes having high λ_C. By contrast, an exponential model, $P(\lambda_C) \sim \exp(-\gamma\lambda_C)$, indicates a more homogeneous distribution of the λ_C values within the network, whilst a truncated power law (i.e., a power law with exponential cut-off), $P(\lambda_C) \sim \lambda_C^{-\gamma} \exp(-\lambda_C/\lambda_{C[x]})$, typically exhibits a faster exponential decay at some critical level (i.e., the cut-off point, $\lambda_{C[x]}$). Fitting models were compared by using the Akaike's information criterion (*AIC*, Burnham and Anderson, 1998). Results were expressed as *AIC* differences, $\Delta AIC = AIC - \min(AIC)$, with the best model having $\Delta AIC = 0$.

Finally, we searched for a latitudinal dependence between the effects of different climate scenarios and the distribution of λ_C values. Eigenvector centrality for current climate conditions were compared with those of projected scenarios by means of their differences, $\Delta\lambda_C = C_c(\lambda_C) - P_R(\lambda_C)$, with $C_c(\lambda_C)$ and $P_R(\lambda_C)$ the eigenvector centrality for current climate conditions and projected scenarios, respectively. To test for a latitudinal correlation and the presence of a latitudinal breakpoint, a piecewise regression between $\Delta\lambda_C$ and the absolute latitude was performed. We compared the goodness of fit of the piecewise regressions with the equivalent

linear regressions by ANOVA, measuring the reduction in residual standard error. All computations were performed with R (R Development Core Team, 2011).

3. Results

The *WPA* distribution within the selected sites (Fig. 1) showed a significant difference between current climate conditions and both the A1B (Student's *t*-test, $t = 68.804$, $p < 0.001$) and A2 climate scenarios (Student's *t*-test, $t = 22.817$, $p < 0.001$), whilst non-significant differences were found between A1B and A2 (Student's *t*-test, $t = -0.859$, $p = 0.391$). The *WPA* values measured under different climate conditions were independent of the size of the patches (overall MANOVA, $F = 2.753$, $p = 0.06$), observing a negative trend where a drastic reduction of the *WPA* within the conservation areas emerged for future scenarios (Fig. 2). The effect of estimated *WPA*s on connectivity led to a quasi-normal distribution in the frequency values of T_{nm} for current climate conditions (Fig. 3a and a less symmetric distribution for the A1B and A2 scenarios (Figs. 3b and c). The shift from a symmetric to an asymmetric distribution might indicates a decrease in the potential connectivity and, therefore, the probability of two areas to be linked becomes gradually less likely to occur.

The contribution of individual patches to the network connectivity, measured by the eigenvector scores of the potential connectivity matrix T_{nm}, showed different trends among the explored scenarios. Eigenvectors centrality calculated for current climate conditions showed a more uniform spatial distribution throughout the landscape (Fig. 4a), as indicated by the exponential cumulative distribution of λ_C (Table 1). On the other hand, a less uniform spatial distribution has been observed for the A1B and A2 scenarios (Figs. 4b and c), where the contribution of the northernmost areas to the potential connectivity was greater and the cumulative distribution of λ_C showed a truncated power law (i.e., a power law with exponential cut-off, Table 1). The asymmetric distribution of the eigenvector scores, together with the presence of a cut-off point in the cumulative distribution of λ_C suggested the existence of a geographic threshold beyond which the system might show a sudden collapse in the distribution of centralities.

The piecewise regression of $\Delta\lambda_C$ against the absolute latitude revealed similar breakpoints in the relationship of the λ_C differences between C_C and A1B and between C_C and A2 scenarios with

latitude (around 44 degrees of latitude, Figs. 5a and b, respectively). In both cases, the piecewise regressions improved the fit of the model compared to the simple linear regressions: adjusted r^2 increased from 0.658 to 0.723 for $\Delta\lambda_C$ calculated under the A1B scenario ($F = 11.21$, $p < 0.001$) and from 0.606 to 0.742 for $\Delta\lambda_C$ calculated under the A2 scenario ($F = 13.43$, $p < 0.001$). Data followed the same trend above and below the breakpoints. $\Delta\lambda_C$ decreased for increasing latitude, whilst the slope of the relationship increased below the breakpoints, from -0.005 to -0.01 for $\Delta\lambda_C$ calculated under the A1B scenario and from 0.009 to -0.02 for $\Delta\lambda_C$ calculated under the A2 scenario. Under both scenarios patches always had $\Delta\lambda_C > 0$, meaning that under future climate projections all the sites exhibited a decrease in the eigenvector scores.

4. Discussion

In this work, we evaluated the impact of changing climate conditions on the functional connectivity of aquatic habitats within sites of the Natura 2000 network in Italy, which we considered as proxies for the potential persistence of waterbirds. Our results show the geographic displacement of the relative contribution of the patches for network connectivity, identifying a latitudinal threshold beyond which a sudden collapse of the system is possible. The implications for conservation might be serious, in view of the high dependence of migratory waterbirds on aquatic habitats (Kreakie et al., 2012).

To date, many studies provided indirect estimates of the impact of changing climate conditions on species distribution, highlighting the global poor reliability of protected areas to cope with such changes (Hannah et al., 2007; Araújo et al., 2011; Rubio-Salcedo et al., 2013). Ultimately, these studies suggest the need of a joint effort in contrasting climate change and increase the number of protected areas, to set up conservation strategies able to avoid climate-related extinctions (Hannah et al., 2007). However, not all protected areas retain an equal climatic suitability for all species, although studies have shown their ability to provide a buffer against climate variations for specific groups of species, even under the worst scenarios (Araújo et al., 2011).

By using existing conservation areas as a proxy for the potential species distribution, we showed a consistent reduction of the potential for water accumulation that might limit the amount of suitable habitat for migratory waterbirds. Both projections used in our analyses are based on the most probable climate scenarios (Kriticos et al., 2012), with a very rapid economic growth, global population that peaks in mid-century and declines thereafter and the rapid introduction of new and more efficient technologies (IPCC, 2007). Under the A1B scenario (fossil CO_2 emissions that peak in the 2050 and then decline, global mean temperature increasing between 2 and 4 °C and low land-use change), the potential for water accumulation is significantly different from current climate conditions. The same trend has been observed under the A2 scenario (fossil CO_2 emissions constantly increasing until 2100, global mean temperature increasing between 3 and 5 °C and medium land-use change). These results agree with future previsions about the role of climate change on aquatic ecosystems (Sala et al., 2000; MEA, 2005), highlighting the steady depletion of the amount of potential aquatic habitats within the conservation areas. The impacts of such scenarios on the potential connectivity of selected sites were very similar.

A shift from a quasi-symmetric to a left-skewed distribution in the connectivity values was observed for both scenarios, suggesting a uneven distribution of climate impacts, which is consistent with the observed geographic trend (IPCC, 2007). As a consequence, under both scenarios the patches lose their contribution to connectivity in a non-random way. The exponential cumulative
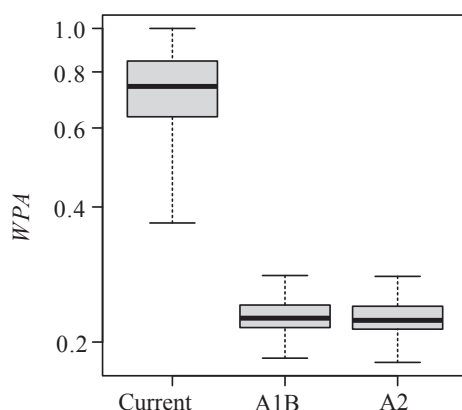
Fig. 2. Distribution of the *WPA* (Water Potential Accumulation) values within the selected areas for current climate conditions and the A1B and A2 future scenarios. The horizontal line dividing boxes in two indicates the median, box limits are the first and third quartiles of the distribution, and whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range from the box. *Y*-axis is given in logarithmic scale.
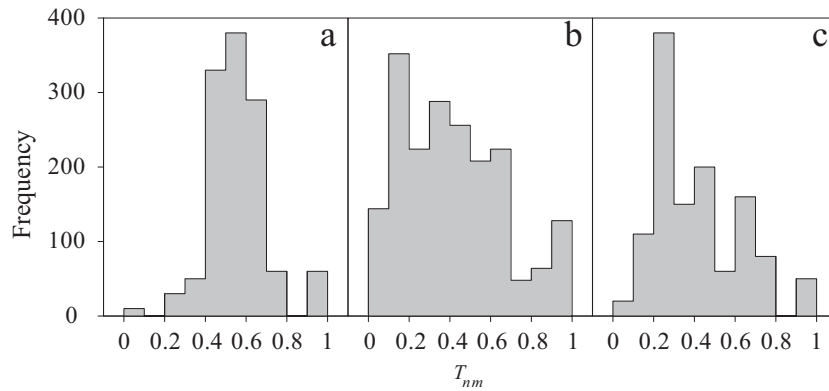
Fig. 3. Frequency distribution of the connectivity values (T_{nm}) under current climate conditions (a), and the A1B (b) and A2 climate scenario (c).
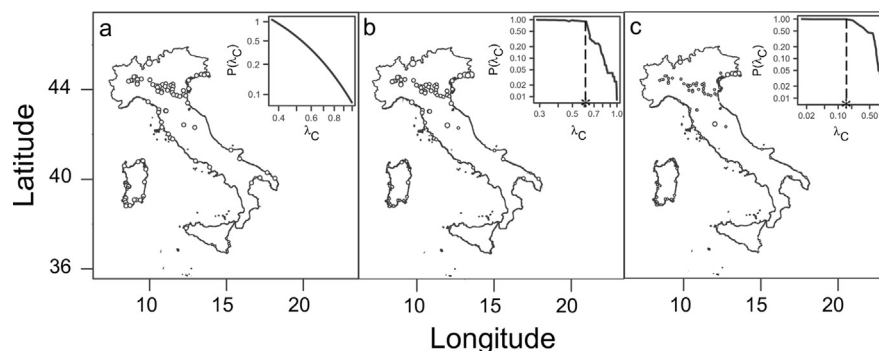
distribution of the eigenvector centrality under current climate conditions showed the ability of most of sites in ensuring the connectivity of the system, with geographically localized areas that contribute more to the robustness of the system. However, the projected climate scenarios emphasized the presence of a cut-off point in the distribution of λ_C, meaning that the frequency of sites with extremely high values of λ_C is lower than under a pure power-law distribution and, therefore, only few sites in the tail of the distribution are important for the cohesion of the network. This leads to a phase transition in the distribution of centrality, observing a critical value above which the systems loses its connectivity.

From a geographic point of view, the effects of changing climate conditions on network connectivity showed a latitudinal break-point for both scenarios. As the climate factors are spatially clustered (Loarie et al., 2009), changes in temperatures, as well as in precipitation regimes will affect disproportionally the hydroperiod of aquatic systems, influencing the spatial distribution of the amount and quality of suitable habitats for a wide array of species. Accordingly, the contribution of individual sites to the overall network connectivity is expected to follow such gradient and we found similar latitudinal breakpoints under both scenarios, observing a sudden increase in the relative contribution of the patches for increasing latitude. The magnitude of $\Delta\lambda_C$ remains high, with the bulk of areas exhibiting a sudden decrease of the eigenvector centrality and no site showing an increase in its potential for connectivity. Recent studies have shown the effects climate change on the northward displacement of the potential range of most of European breeding birds (Huntley et al., 2008). However, this

potential displacement can be sustained as long as the connectivity between areas along the flyways is guaranteed by the presence of suitable habitats. Our results show that the southern areas will be more affected by changing climate conditions and this might indicate the risks to cut off the flyway, at least for those species migrating across the Mediterranean and breeding in northern Italy (e.g., Collared Pratincole, *Glareola pratincola,* Brichetti and Fracasso, 2004).

The loss of potential connectivity among conservation areas can have important consequences for migratory waterbirds, due to a contraction of suitable habitats related to all phases of migration. Indeed, climate change may influence migratory birds that spend different parts of the annual cycle in different geographic locations (van Noordwijk, 2003), modifying the availability of suitable habitats in different ways and in multiple locations (e.g., in breeding, wintering or stop-over areas), with deleterious impacts at some point in the annual migration cycles. Besides the responses of different species to the endogenous rhythms that control their migration (Both and Visser, 2001; Cotton, 2003), the presence of suitable habitats for breeding, wintering and staging periods represents a key element in determining their reproductive success and overall fitness.

Habitat fragmentation is considered one of the major issues concerning the loss of biodiversity, having important effects on dispersal, metapopulation dynamics and species persistence (Ovaskainen and Hanski, 2003). Our analysis shows the steady decrease in the contribution of existing conservation areas on network connectivity, mostly related to the geographic differences of the climate impacts on the distribution of aquatic habitats. The

Fig. 4. Spatial distribution of the eigenvector scores of selected sites (white circles, given in logarithmic scale). a) current climate conditions, b) A1B scenario, c) A2 scenario. Graphs on top-right corners show the cumulative distribution of λ_C under each scenario. The vertical dashed lines indicate the threshold values of λ_C beyond which the distribution exhibits a sudden collapse. Fitting parameters are shown in Table 1.

Table 1
Model fitting of the eigenvector centrality distribution for current climate conditions and future scenarios based on the CSIRO-Mk3.0 model. Bolded ΔAICs indicate better models. Exp, exponential; Pow, power law; Tru, truncated power law (i.e., power law with exponential cut-off). k is the degrees of freedom, γ the scaling exponent ($\gamma > 0$) and $\lambda_{C[x]}$ the critical eigenvector score for a truncated power law distribution (i.e., the value beyond which the distribution change from a power to an exponential law).

Scenario	Model		k	γ	$\lambda_{C[x]}$	AIC	ΔAIC	Log-likelihood
Current	Exp	$P(\lambda_C) \sim \exp(-\gamma\lambda_C)$	2	1.26		−352.515	**0**	165.851
	Pow	$P(\lambda_C) \sim \lambda_C^{-\gamma}$	3	0.186		−260.282	65.233	133.235
	Tru	$P(\lambda_C) \sim \lambda_C^{-\gamma}\exp(-\lambda_C/\lambda_{C[x]})$	3	0.751	0.628	−52.786	272.728	28.434
A1B	Exp	$P(\lambda_C) \sim \exp(-\gamma\lambda_C)$	2	1.096		−103.109	247.507	53.595
	Pow	$P(\lambda_C) \sim \lambda_C^{-\gamma}$	3	0.274		−255.469	95.147	130.817
	Tru	$P(\lambda_C) \sim \lambda_C^{-\gamma}\exp(-\lambda_C/\lambda_{C[x]})$	3	0.401	0.667	−350.616	**0**	178.39
A2	Exp	$P(\lambda_C) \sim \exp(-\gamma\lambda_C)$	2	2.687		−132.769	413.3781	68.423
	Pow	$P(\lambda_C) \sim \lambda_C^{-\gamma}$	3	0.052		−377.231	168.916	191.691
	Tru	$P(\lambda_C) \sim \lambda_C^{-\gamma}\exp(-\lambda_C/\lambda_{C[x]})$	3	0.549	0.244	−546.148	**0**	276.149

alteration of hydrological periods poses specific problems related to the availability and quality of suitable habitats for migratory waterbirds, especially if species need to cross ecological barriers during migration (Bairlein and Hüppop, 2004). The identification of a geographic threshold below which the impacts of changing climatic conditions seem to be more severe for the maintenance of potential connectivity raises serious questions about the role of conservation areas to act as a buffer against such changes. Although recent studies proved that areas within the Natura 2000 network should retain the climatic suitability for many species of birds (Araújo et al., 2011), it is not clear whether they can compensate the impacts of changing habitat conditions for migratory waterbirds. Our indirect estimates suggest that, if one considers the main ecological characteristic of the sites (i.e., the potential availability and distribution of aquatic habitats), most of them cannot compensate the climate uncertainty under future scenarios. Critical sites for the African-Eurasian flyway (e.g., wetlands located on the main islands) could be drastically impacted, becoming less attractive and, therefore, losing their potential for the whole network connectivity.

Although our results attempt to shed light on the role of existing conservation areas in maintaining the connectivity for migratory waterbirds under climate scenarios, not all uncertainty were accounted for. First, we have expressly discarded information about population dynamics, the interdependencies between species or the plasticity of migratory behaviour, which can cause non-linear responses to climate change (Jonzén et al., 2006; Anderson et al., 2009). Second, we considered all sites equally important for

migration, although specific differences could exist among them. Together with spatial location, the subdivision of sites into breeding, wintering or stop-over areas, could drastically influence the impacts resulting from changing climate conditions for migratory connectivity (Taylor and Norris, 2010). Lastly, other sources of uncertainty in modelling the impacts of climate change on aquatic systems should be considered, as the role of rising sea level on coastal wetland habitats, which might require further investigation. However, our approach does not preclude the possibility of using a larger number of information to measure the relative importance of the patches, including for example information related to some specific aspect to investigate for the network coherence at species level.

Modelling approaches in conservation biology must necessarily be used with caution. The ability of birds to migrate at a sufficient rate to keep up with changing climate conditions depends not only on the dispersal characteristics of single species, but also on the structure of the surrounding landscape over which its migration occurs (Pearson and Dawson, 2003). This includes the presence of natural barriers or the contraction of suitable habitats due to anthropogenic fragmentation (e.g., deforestation, urbanization), which might limit the ability of species to fill the potential future climate spaces (Pearson and Dawson, 2003). Evidences show that models can predict the tendency of increasing/decreasing species range with reasonable accuracy, limiting the uncertainty by interpreting model projections conservatively (Araújo et al., 2011). Our results agree with other studies that showed the poor reliability of protected areas to cope with climate variations (Hannah et al., 2007; Araújo et al., 2011; Rubio-Salcedo et al., 2013), highlighting the impact of climate change on the potential distribution and availability of suitable habitats able to support the persistence of migratory birds during the entire annuity of migration.

A mixed approach between bioclimatic models based on species−environment relationship with features of landscape structure could be the key to improve our understanding on specific priorities in conservation policies. Furthermore, it should be taken in account the role of the sites for the potential connectivity, by prioritizing the patches on the basis of their contribution to the cohesion of entire network (e.g., the identification of connectivity hot-spots). Such approach could therefore help us to better understand the coupled impacts of climate change and habitat loss for the long-term conservation of biodiversity, reinforcing the need to protect in a more efficient way critical networks of areas.
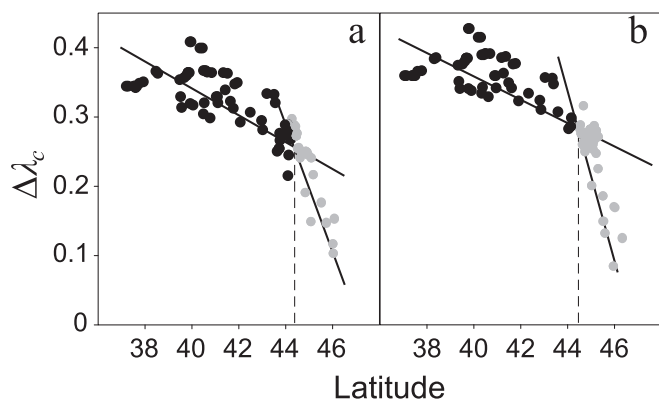
Fig. 5. Piecewise regression of the eigenvectors differences, $\Delta\lambda_C$, between the current climate conditions and A1B (a) and A2 scenario (b) against the absolute latitude. Trends in regressions for both scenarios show a decrease of λ_C values for increasing latitude, meaning that the northernmost sites should be less affected by changing climate conditions. Black and grey circles are for sites below and above the latitudinal breakpoint (vertical dashed lines), respectively.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2014.04.002.

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