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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.

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