

# Ecological Impacts of the North Atlantic Oscillation (NAO) in Mediterranean Ecosystems

Oscar Gordo, Carles Barriocanal, and David Robson

**Abstract** Large-scale climate indices have received much attention in recent years in ecology-climate research due to the advantages they have over typically used local weather variables, such as temperature or rainfall. In the Mediterranean, the North Atlantic Oscillation (NAO) is a major forcing of climate patterns, especially precipitation. More than 60 studies to date have demonstrated the effects of the NAO on both terrestrial and aquatic Mediterranean ecosystems. In terrestrial ecosystems, the NAO affects the phenology and growth of plants and crop yields. It also affects the condition and diet of mammals and disease-related mortality in amphibians. The effects of the NAO are probably better known in marine ecosystems, where the impact on the hydrodynamics of the water column and currents is felt in the dynamics of populations from plankton to fishes in both pelagic and benthonic environments. Additionally, birds are an especially well studied taxon when it comes to effects of the NAO. The NAO has been shown to affect the population dynamics of water birds by impacting the availability and extent of their habitat and by influencing dispersal decisions of individuals. The NAO plays an essential role in the migration of birds throughout the Mediterranean basin, and it is probably a reason for the observed advance of arrival dates during the spring in Europe. In spite of the notable number of studies carried out to date, we are far from knowing accurately the ecological impacts of the NAO on Mediterranean ecosystems. More efforts are needed to understand regional differences in the NAO effects within the Mediterranean basin and how they compare with more northern latitudes of Europe.

**Keywords** Birds · Climate · Ecosystem · Phenology · Review

## 1 Why Using Large Scale Climate Indices in Ecology?

We are all aware that environmental conditions, defined as the set of abiotic variables to which organisms are subjected, shape the distribution, abundance, behavior

---

O. Gordo (✉)

Departamento de Zoología y Antropología Física, Universidad Complutense de Madrid, Madrid, Spain  
e-mail: ogordo@bio.ucm.es

and ultimately the evolution of organisms (Begon et al., 2006). Among environmental drivers, climate is recognized as one of the most important abiotic factors. Therefore, one should not be surprised that organisms are responding to the ongoing climate change, even though observed changes in Earth's climate have so far been relatively small (e.g., the global mean annual temperature has increased only by about 0.7°C during the last century (Solomon et al., 2007)). Even though many other factors operate on a long-term temporal scale (e.g., density-dependent processes, land-use transformations, etc.) and may prevent us from establishing unambiguously a causal link between climate change and some responses of organisms (Sala et al., 2000; Forchhammer and Post, 2004), evidence of climate change impacts on organisms is abundant. The impacts are widespread, ranging from the equator to the poles in both terrestrial and aquatic ecosystems and suggesting a climate change imprint on the biosphere at a global scale (Parmesan and Yohe, 2003; Root et al., 2003). Climate-induced responses range from the plasticity of many traits to adapt to weather variability to persistent alterations in ecosystem functioning, community composition and functional interactions among species. Therefore, climate change signals are already apparent on all biological scales (Parmesan, 2006; Rosenzweig et al., 2008).

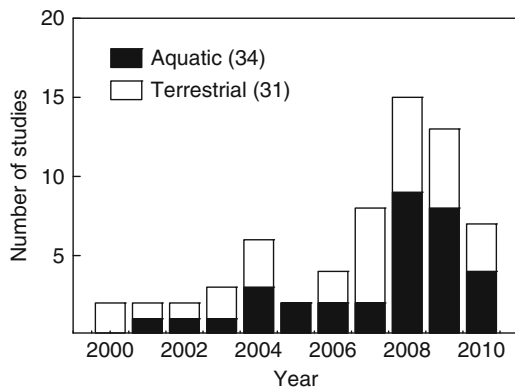
Given the current global climate change scenario, there is an urgent need to understand better how organisms are affected by climate. This understanding is essential to the accurate prediction of the biological consequences of the ongoing alterations of climate and from this to delineate the necessary actions to ensure conservation of natural populations, communities and ecosystems. One of the main challenges in the study of the effects of climate on organisms is to find the key climate parameter controlling a certain biological phenomenon and its temporal and spatial scales (Hallett et al., 2004; Stenseth and Mysterud, 2005; Gordo, 2007). Temperature is probably the most frequently used climate variable in ecological research. In fact, many biological processes are temperature-dependent (e.g., metabolism, development, activity, etc.), and thus, one may make sound predictions about its effect. In addition, temperature is the climate variable with the most homogeneous and coherent pattern of change across the globe during the last century (i.e., global warming; Solomon et al., 2007). However, temperature is not the only important variable. Other variables, such as precipitation (rainfall and snow), solar radiation, wind, etc., are also essential for individual survival and ecosystem functioning and are, in some cases, as in arid regions, more important than temperature. Therefore, the key climate variable may differ according to the species or the biological process under study. Moreover, the effect of a certain climate variable may vary in space, being more influential for some populations than for others (Forchhammer et al., 2002a, b; Stenseth et al., 2004; Doi and Takahashi, 2008). Such complex responses of organisms to climate are just a reflection of the fact that weather cannot be described simply by temperature or rainfall. Weather is complex to quantify because it results from a collection of physical features of the atmosphere at a certain moment along with their interactions. In addition, weather does not affect organisms in isolation. Climate fluctuations affect all organisms in a certain ecosystem, and it is essential to understand how climate influences organisms and their interactions

with other individuals. In summary, the influence of climate on the individual seems too complex to be described simply by one or a few climate variables.

Large-scale climate indices may help one to deal with these complexities resulting from the heterogeneous influence of climate across taxa and populations. It is obvious that organisms adapt to climate at a local scale by responding to temperature, amount of rainfall, intensity of winds, and so on. However, climate is a paradigm of spatial autocorrelation because sites that are close together resemble each other in their patterns of temporal variability of climate. This feature arises from the fact that local weather is controlled by atmospheric circulatory patterns, which work on a large scale. Climate indices are able to summarize in a single value the weather conditions for a large area. This synthetic nature has been demonstrated to be of great value and use in ecology-climate research, and the application of climatic indices has become increasingly frequent during the last decade (Fig. 1).

Climatologists have defined over a dozen large-scale climate indices that govern most of the observable interannual variability of climate at the planetary scale. Among them, the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) are probably the most commonly used by ecologists and are those for which the ecological consequences are best known (Stenseth et al., 2002, 2003; Forchhammer and Post, 2004). As broadly described in other parts of this book, the NAO is a large-scale fluctuation in atmospheric pressure difference along a north-south gradient between the subtropical North Atlantic region (centered on the Azores) and the subpolar region (centered on Iceland). The differences in atmospheric pressure at sea level between the subtropical and the subpolar centers affect the speed and direction of the westerly surface winds across the North Atlantic from North America to Europe (40°N–60°N). As a consequence, the numbers and paths of storms and their associated weather are affected (Hurrell, 1995; Hurrell and van Loon, 1997). Furthermore, there are effects on ocean surface temperature and currents, which in turn have direct effects on heat transport in the North Atlantic and the sea ice coverage in the Arctic region (Ottersen et al., 2001; Stenseth et al., 2003). Although present throughout the year, the greatest interannual and decadal variability is seen during the boreal winter, when the atmosphere is most dynamically active

**Fig. 1** Number of published studies using the North Atlantic Oscillation as an explanatory variable of any biological phenomena in terrestrial or aquatic ecosystems of the Mediterranean region Source: Isi Web of Knowledge (access date 1-10-2010)



(Hurrell, 1995). The NAO is the most robust mode of recurrent atmospheric behavior in the North Atlantic and has been suggested as the most probable cause for the remarkable changes in the climate over the middle and high latitudes of the Northern Hemisphere during recent decades (Hurrell and van Loon, 1997; Hoerling et al., 2001; Visbeck et al., 2001).

Positive values of the NAO are associated with more frequent and stronger winter storms crossing the Atlantic Ocean on a more northerly track, leading to warmer and wetter conditions in northern Europe and in the eastern coastal areas of the United States (Ottersen et al., 2001; Visbeck et al., 2001; Mysterud et al., 2003; Stenseth et al., 2003; Forchhammer and Post, 2004). In contrast, during negative phases of the NAO, the westerlies are weakened and become less frequent, and the warm and wet winter weather remains over North America, leaving northern Europe cold and dry. The most important feature arising from a comparison between the positive and the negative phases of the NAO is that this large-scale atmospheric circulatory pattern has a geographically marked differential impact on local weather. Correlations between the NAO and other climate variables, such as temperature and rainfall, vary regionally (Hurrell and van Loon, 1997; Ottersen et al., 2001; Visbeck et al., 2001; López-Moreno and Vicente-Serrano, 2008), and thus, the value and interpretation of the NAO as a proxy of climate fluctuations is variable. A paradigmatic example of regional variability is found between northern and southern Europe. During a positive phase of the NAO, the northward track of storms leads to drought anomalies in the Mediterranean basin, while northern latitudes enjoy a wetter climate than average. Unfortunately, the heterogeneous effects of the NAO at the continental scale remain poorly studied in ecology (but see Sanz, 2002, 2003; Jonzén et al., 2006; Gouveia et al., 2008). Moreover, the overwhelming majority of studies about the ecological impact of the NAO have been focussed on central and northern Europe (Ottersen et al., 2001; Mysterud et al., 2003; Forchhammer and Post, 2004), where the intensity and sign of its effect are quite different from other areas.

## 2 Impacts of the NAO in Mediterranean Ecosystems

Although local climate is also driven by the NAO in the Mediterranean basin, especially precipitation patterns (Lamb and Pepler, 1987; Rodó et al., 1997; Quadrelli et al., 2001; Trigo et al., 2004; Rodrigo and Trigo, 2007; Vicente-Serrano and Cuadrat, 2007), there are few studies describing ecological impacts of the NAO in Mediterranean latitudes. A search in the Web of Science using the next chain “(NAO or North Atlantic Oscillation) and Mediterranean” provided only 65 studies in the fields of Ecology, Biodiversity and Conservation, Zoology, Forestry, Marine and Freshwater Biology, Fisheries, and Agriculture (Fig. 1). Terrestrial and aquatic (both marine and freshwater) ecosystems have received similar attention (31 vs. 34 articles, respectively). Most of the studies have been published in the last few years

in journals such as *Climate Research*, *Fisheries Oceanography*, *Global Change Biology*, *International Journal of Biometeorology*, *Journal of Animal Ecology*, *Journal of Marine Systems*, or *Progress in Oceanography*. Therefore, the study of ecological impacts of the NAO in Mediterranean ecosystems is recent and has occupied many pages in some of the top journals in ecology.

In terrestrial ecosystems, it has been demonstrated that positive NAO values are related to increased growth and advancement of spring phenological events, such as flowering, leaf unfolding or pollen release, of trees (Piovesan and Schirone, 2000; Avolio et al., 2008; Campelo et al., 2009; Rozas et al., 2009; Gordo and Sanz, 2010; Orlandi et al., 2010). Nonetheless, proposed mechanisms for the NAO effect in growth and phenology were different. In the case of plant growth, the main driver is soil moisture, which is dependent mainly on winter rainfalls, which are in turn strongly dependent on the NAO (Piovesan and Schirone, 2000; Campelo et al., 2009; Rozas et al., 2009). However, the effect of the NAO on spring plant phenology would be mediated by its effect on spring temperatures (Gouveia et al., 2008; Gordo and Sanz, 2010). From a more applied point of view, the NAO has been found to affect the yields of wheat and citrus in Spain (Gimeno et al., 2002; Rodríguez-Puebla et al., 2007). Interestingly, wine production and quality were not affected by the NAO in this country (Rodó and Comín, 2000), but they were affected in Portugal (Esteves and Orgaz, 2001). Such differences in crop effects may be due to differences in the regional influence of the NAO on local weather. Therefore, the NAO influence could vary even among areas close together within the Mediterranean basin.

Evidence of NAO effects in terrestrial animals is almost entirely limited to studies with birds. We still lack in depth knowledge on the NAO effect on invertebrate, amphibian, reptile or mammal distributions, abundances and behavior. In a recent study, Martínez-Jauregui et al. (2009) demonstrated that the NAO did not have an effect on seasonal variation of weight in females of red deer (*Cervus elaphus*) in a locality in central Spain. Interestingly, the NAO did play an important role in understanding changes in body weight of females of the same species in populations in Scotland and Norway. Geographical differences in the NAO effect are seen once more, suggesting that one needs to exercise caution in generalizing the NAO effect over broad areas because its effect shows marked regional differences, especially between the Mediterranean and more northern latitudes in Europe. However, the NAO has been an important predictor of the observed changes during the last 3 decades in the diet of the nearly extinct population of Iberian brown bears (*Ursus arctos*; Rodríguez et al., 2007). By altering the phenology and productivity of some plant species (Gordo and Sanz, 2010), the NAO may play an important role in the conservation of this iconic species. The NAO has also been demonstrated to be important to understanding amphibian declines in mountainous lakes of central Spain (Bosch et al., 2007). In this particular case, the NAO has driven increases in local temperatures, which have promoted the spread of a fungus disease that causes mass mortality among amphibians.

The NAO effects in marine ecosystems of the Mediterranean Sea are probably known with greater certainty than in terrestrial ecosystems. The NAO affects the water column hydrodynamics, which in turn affect vertical gradients of mixing, nutrient flow and irradiance, by its control of weather conditions (e.g., temperature, winds, or storms). Knowledge of water column hydrodynamics is essential to an understanding of plankton functioning, abundance, and diversity, so it is not surprising that plankton community dynamics are closely related to the NAO fluctuations in the Mediterranean Sea as well as in other areas (Katara et al., 2008; Kamburska and Fonda-Umani, 2009; Gladan et al., 2010; Pérez et al., 2010). For instance, in the northwestern Mediterranean, dominant zooplankton species vary under positive and negative phases of the NAO because each phase favors different species by imposing different hydrodynamic features (Molinero et al., 2005, 2008; de Puelles et al., 2007; de Puelles and Molinero, 2008). However, the NAO can also show regional differences in its effects in the sea. For instance, *Centropages typicus*, the commonest calanoid copepod in Mediterranean waters, showed a response to the NAO in its abundance in populations in the Gulf of Naples that was opposite to its response in the Bay of Villefranche (Mazzochi et al., 2007).

The NAO effect on hydrodynamics, and consequently on plankton, may have a cascade effect on higher trophic levels. Several studies have found significant associations between the NAO and fish and cephalopod abundances in the Mediterranean (Grbec et al., 2002; Relini et al., 2006, 2010; Bridges et al., 2009; Pérez et al., 2010; but see Ravier and Fromentin, 2004). In the northwestern region of the Mediterranean Sea, the collapse of the sardine *Sardina pilchardus* stocks in the 1990s has been related to the dominant positive phase of the NAO during recent decades (Guisande et al., 2004). Similarly, the collapse of the anchovy *Engraulis encrasicolus* population in 1987 in the Adriatic Sea has been attributed to low recruitment due to the extreme positive value of the NAO during the autumn of 1986 (Santojanni et al., 2006). Along with the cascade effect through hydrodynamics and plankton, fish abundances could also be indirectly affected by water discharge of Mediterranean rivers, which is closely related to the NAO due to precipitation patterns, because the rivers supply nutrients to the sea (Lloret et al., 2001; Cartes et al., 2009).

The NAO has also been related to the strength of some currents within the Mediterranean basin. This relationship has direct effects on the horizontal transport of nutrients from some regions to others of the sea, enhancing productivity and, as consequence, the richness of marine communities. For instance, population dynamics of the hake (*Merluccius merluccius*), an economically important fishery in the Mediterranean, have been linked to the NAO through its effect on currents in the Ligurian and Tyrrhenian Seas (Abella et al., 2008; Massutí et al., 2008).

It is not only the abundance and dynamics of marine organisms that are affected by the NAO. The NAO has also been suggested as the cause of the increase of thermophilic species in the Adriatic Sea as a result of its control over sea temperature (Dulcic et al., 2004; Grubelic et al., 2004).

The NAO fingerprint has also been detected in benthonic communities. For instance, periodical surveys of the benthic macrofauna (especially polychetes) in

the Bay of Banyuls-sur-Mer (France) since the 1960s have shown notable changes that have been partially attributed to NAO fluctuations (Lebrune et al., 2007). This fingerprint can reach even those benthic communities living at depths greater than 1000 m. Off the Catalan coast, it was found that changes in the abundance and composition of deep megabenthos were related to the contrasting values of the NAO between the surveys carried out at the end of the 1980s and the end of the 2000s (Cartes et al., 2009). Similarly, landings of the shrimp *Aristeus antennatus*, which lives at depths between 600 and 800 m, were higher following positive values of the winter NAO (Maynou, 2008a, b). In this case, there was a time lag in the response to the NAO, supporting the idea that the NAO effect may be carried by a population over a number of years following a particular NAO situation (Ottersen et al., 2001).

### 3 Effects of the NAO on Bird Populations

The NAO has a direct effect on demographic parameters, such as survival, dispersal or fecundity, of many animal species (Ottersen et al., 2001; Mysterud et al., 2003; Forchhammer and Post, 2004). Therefore, one expects to find effects of the NAO on abundances and dynamics of bird populations, and they have indeed been found (Sæther et al., 2004). For instance, a long-term study in a Norwegian population of dippers (*Cinclus cinclus*) demonstrated that year-to-year variations in the population size were positively related to the NAO index, i.e., the population increased under positive NAO values (Sæther et al., 2000). Positive NAO values were related to milder winters, which reduced the duration of the frozen surface of rivers where these individuals forage. These improved conditions for foraging enhanced survival, especially of the younger individuals, which recruited in larger numbers the next spring, leading to an increase in the breeding population.

In the Mediterranean region, the NAO effects on dynamics and demography of bird populations have been studied in a wide variety of species, such as water birds (Almaraz and Amat, 2004a, b; Figuerola, 2007; Bechet and Johnson, 2008; Jiguet et al., 2008), seabirds (Jenouvrier et al., 2009), raptors (Rodríguez and Bustamante, 2003; Costantini et al., 2010), and songbirds (Sanz, 2002, 2003; Grosbois et al., 2006; Rubolini et al., 2007; Balbontín et al., 2009). Such diversity of species demonstrates that NAO signals are apparent in the Mediterranean avifauna as a whole and supports the notion that the NAO effect can be found across all habitats of a large area like the Mediterranean.

Several studies have demonstrated effects of the NAO on water birds, a fact that is not surprising if we take into account the strong dependence of these species on lakes, ponds and marshlands. The occurrence and extent of wetlands in the Mediterranean region are strongly dependent on precipitation patterns, which in turn are driven by the NAO (see other chapters in this book). Almaraz and Amat (2004a, b) showed for the first time that large-scale indices, such as the NAO and the ENSO, were related to population dynamics of the white-headed duck (*Oxyura leucocephala*), a threatened water bird species. Low values of the winter NAO were

linked with increased rainfall, which led to a large expansion of the range of the species during the following breeding season as a result of an increase in wetland surface in Spain (Almaraz and Amat, 2004a). Furthermore, El Niño events (i.e., high ENSO values) were linked with increased rainfall during the summer in the Mediterranean, which reduced breeding densities and increased markedly the recruitment in the next year.

In similar studies, some breeding populations of waders from the Mediterranean showed clear fluctuations in their numbers related to the NAO. In the Doñana National Park (southwestern Spain), the black-winged stilt (*Himantopus himantopus*) breeds in numbers from a dozen pairs up to more than 14,000 pairs (which represents about 30% of the European population). Such extreme variability was related to positive and negative phases of the NAO, respectively, which affect the extent of the Doñana marshlands and consequently the phylopatry and dispersal behavior of this species (Figuerola, 2007). The NAO also drives the hydrological conditions of another major wetland area of the Mediterranean, the Camargue (southern France). Interestingly, the NAO signal is even detected in those populations that use strongly human-managed habitats, such as the commercial salt pans, for breeding, as in the case of the greater flamingo (*Phoenicopterus roseus*; Bechet and Johnson, 2008). Even though the date of the start of salt production determines the potential number of breeding pairs of the species each year, the observed breeding population is also dependent on the water levels in the Camargue lagoons, which are under the NAO influence. A larger extent of marshlands increases the food availability and thus the opportunities for breeding.

Kestrels are small falcons that inhabit open landscapes in Europe and Asia. During the twentieth century, the lesser kestrel (*Falco naumanni*) has shown marked declines, which have led to a threatened status in most European countries and even to extinction in some. Rodríguez and Bustamante (2003) investigated whether recent climatic changes were related to declines in populations from southern Spain. They found significant influences of the winter NAO and annual precipitation patterns on kestrel demography. However, rainfall outperformed the predictive ability of the NAO in demographic models because rainfall probably captured better the environmental variability at the local scale, i.e., at the scale of the breeding colonies of the species. Nevertheless, the rainfall in southern Spain and the NAO showed strong correlations, and thus the NAO influence on bird demography could be shown for this terrestrial species via precipitation amount and seasonal distribution. However, in spite of the drier conditions recorded during recent decades in the kestrel colonies as a result of the prevailing positive phase of the NAO, the authors concluded that the effect was not sufficient to explain the population declines and that causes must be sought in other environmental factors. In Italy, reproductive decisions and reproductive success in a population of kestrels (*Falco tinnunculus*) were also closely related to rainfall, temperature and the NAO index during both the spring and the previous winter (Costantini et al., 2010). Contrary to predictions, this population laid smaller clutches after mild and dry winters (i.e., positive winter NAO index). The authors hypothesized as possible causes for this result a greater survival of low-quality individuals during the winter and/or a disruption in prey phenology.

Nevertheless, the mechanism is unclear, and this fact demonstrated the complexities of the NAO influence on animal population dynamics. The NAO effect can be mediated by conditions in previous seasons, and the balance between current and past weather determines environmental conditions and thus the observable reproductive success.

In a similar way, the NAO effect may be different among different populations (e.g., Sanz, 2002), and this fact may lead to divergent patterns of response to climate change. For instance, barn swallows (*Hirundo rustica*) from Spain are more likely to survive during their first year of life when the winter NAO is positive, while Danish swallows show increased mortality during positive phases of the winter NAO (Balbontín et al., 2009). Unlike the black-winged stilt recruitment (Figuerola, 2007), the recruitment probability of the barn swallows to their natal areas was not affected by the NAO. In these studied populations of swallows, dispersal was explained by another large-scale climate index, the Southern Oscillation Index (SOI), which also showed an opposite effect between the two populations (Balbontín et al., 2009).

## 4 Effects of the NAO on Bird Migration

Every year millions of individuals move between breeding and wintering areas in one of the most fascinating events of nature: bird migration. Bird migration has long been known to be influenced by weather (Newton, 2008). In fact, the arrival of some migratory species, such as swallows or cuckoos (*Cuculus canorus*), has been traditionally used as an unequivocal signal of spring onset. This sensitivity of bird migratory phenology to weather has led to a renewed interest in this phenomenon in light of the ongoing climate change. If bird migration is sensitive to climate fluctuations, we can use it as a bioindicator of climate change impacts. A plethora of studies has demonstrated shifts in the timing of migration for many species along with significant relationships between climate from departure, passage and arrival areas and bird phenology (see reviews in Gordo, 2007; Lehikoinen and Sparks, 2010). Although climate change seems to be the cause for the alteration of bird migration timing during recent decades, the precise ecological and evolutionary mechanisms by which birds are changing their migratory schedule in response to the new environmental conditions remain to be elucidated.

The arrival date of a migrant to a certain site depends on two factors: (1) the onset date of migration and (2) the speed of progression across the areas between the start and end points of its journey (Gordo, 2007). Experiments with captive birds have demonstrated that the onset of migration is controlled by inflexible endogenous rhythms with a genetic basis (Berthold, 2001; Newton, 2008). However, a growing number of correlative studies have recently suggested some plasticity in the onset of migration; i.e., birds may adjust their departure date according to the prevailing weather or to the ecological conditions found at their departure areas (Saino et al., 2004; Gordo et al., 2005; Saino et al., 2007; Gordo and Sanz, 2008). In addition, many other studies have demonstrated that temperature, precipitation, wind, or vegetation phenology in the passage areas affect bird progression (Gordo, 2007). Overall,

the evidence suggests that climate may influence bird migration both directly and indirectly at several times throughout the year and at several sites. Such complexities of climate effects are not surprising if one takes into account the fact that migrants spend much time moving across vast areas. In this situation, large-scale climate indices become ideal explanatory variables for bird migratory phenology because they are capable of summarizing these complexities of local weather in a single variable that is easy to interpret and obtain (see Section 1).

The NAO index was employed for the first time by Forchhammer et al. (2002a) to explain migratory phenology of some common migrants in Norway. Since then, more than 30 studies have used this variable to explain interannual variability in arrival dates of migrants (Gordo, 2007; Hubálek and Čapek, 2008; Donnelly et al., 2009; Balbontín et al., 2009; Tøttrup et al., 2010). As a norm, most of the time-series of arrival dates show a negative relationship with the NAO; i.e., birds arrive early when the NAO (especially the winter NAO index) is positive (Gienapp et al., 2007). Positive NAO values imply milder winters and thus an advance of the spring (e.g., earlier flowering and leafing of plants, Gordo and Sanz, 2010) and an enhancement of weather conditions during migratory flights (e.g., more tail winds, Hüppop and Hüppop, 2003; Sinelschikova et al., 2007). Therefore, the proposed mechanism for the effect of positive NAO values on migration is the improved environmental conditions for migratory progression across Europe in terms of both food availability and the weather.

However, this picture may be less clear than it seems because most of the studies have been conducted in northern and western Europe, where the NAO effect is stronger and bird populations are subjected along their entire migratory route to the NAO influence. If we focus on the particular case of Mediterranean populations, there are few studied cases, and those studies that do exist usually suggest no effect of the NAO. In Spain, the arrival dates of five common migrants, the white stork (*Ciconia ciconia*), the cuckoo, the swift (*Apus apus*), the barn swallow or the nightingale (*Luscinia megarhynchos*), were not related to the NAO, either for earlier individuals or for later ones (Gordo and Sanz, 2008). In a locality of central Italy, the arrival dates of the first swifts, swallows and nightingales were not related to either the winter NAO (December–March) or the spring NAO (March–May) (Rubolini et al., 2007). Here, only one species, the house martin (*Delichon urbicum*), advanced significantly their arrival in response to positive winter NAO. In a long-term monitoring study of the arrival dates of nightingales in Croatia (Kralj and Dolenc, 2008), the winter NAO did not show any effect. Although the number of studies of Mediterranean bird populations is still small, the evidence suggests that the NAO has little influence on their arrival dates. This fact supports the idea that the NAO effect would be felt mainly from the Mediterranean latitudes northwards and thus, that only those populations breeding in the northernmost regions of the continent, and consequently with extensive migratory routes over Europe, would be significantly influenced by the NAO (Forchhammer et al., 2002a; Hüppop and Hüppop, 2003). Moreover, some studies have demonstrated that the negative

relationship with the winter NAO is stronger in short-distance migrants (i.e., those species overwintering in the Mediterranean basin) than in long-distance ones (i.e., those species overwintering to the south of the Sahara) (Rainio et al., 2006; Tøttrup et al., 2010). If it is considered that positive NAO values are related to drought in the Mediterranean and thus to harsh ecological conditions, it follows that short-distance migrants must benefit from a positive NAO *en route* but not during their wintering stay in the Mediterranean. Unfortunately, the environmental factors operating on the dynamics of wintering populations in the Mediterranean are poorly known, as is the effect of the NAO.

Finally, the Mediterranean basin is an obligatory passage area for all long-distance migrants coming from Africa and moving into Europe for breeding (Newton, 2008). In spite of this key role in the European-African migratory system, only two studies have analyzed the NAO effect on passing migratory bird populations. The *Istituto Nazionale per la Fauna Selvatica* from Italy has been promoting since 1988 the monitoring scheme *Progetto Piccole Isole*. This is a network of ringing sites located in islands and coastal sites, mainly in the central and western parts of the Mediterranean Sea (Italy, Spain, France and Malta), that uses standardized protocols for trapping birds (Spina et al., 1993). One of the pioneering and most active ringing stations is located on the Italian island of Capri. There, the passage dates of nine trans-Saharan species were positively correlated to the winter NAO both in early and in late individuals, in opposition to the relationship found between the NAO and passage dates for the same species in ringing sites in Scandinavia (Jonzén et al., 2006). While a positive NAO would enhance migration across Europe (see above), it would impair ecological conditions in northern Africa by droughts in the Mediterranean basin and rainfall deficits during the monsoon season in West Africa (Lamb and Pepler, 1987; Hurrell, 1995; McHugh and Rogers, 2001; Oba et al., 2001; Stige et al., 2006). Therefore, the contrasting effect of the NAO in passage dates of the same species between Mediterranean and Scandinavian latitudes reinforces the idea of the heterogeneous effect of this variable among regions and thus their populations. Populations in Scandinavia have traveled for weeks across Europe and have benefited from enhanced conditions for migratory progression due to positive phases of the NAO. However, in Italy, just after the birds leave Africa, the positive phase of the NAO has the opposite consequences in the environment, and this is reflected in a delayed passage date. However, this is just one study in a single locality. A recent study with 11 migratory species on 3 Spanish islands demonstrated that the NAO did not have any effect on passage dates (Robson and Barriocanal, 2011). Moreover, it was the worst explanatory variable of the timing of migration compared to other predictors, such as temperature, vegetation productivity or the SOI. This extreme contrast in the results of different studies highlights the urgent need to develop more studies in the Mediterranean region to elucidate the true effects of the NAO on migratory bird phenology and the potential regional variability in the effects in relation to each migratory route across the Mediterranean.

## 5 Conclusions

There is already a notable number of studies that have assessed the effect of NAO fluctuations on a wide variety of species and biological phenomena in the Mediterranean region (Fig. 1). However, after a comprehensive review of the available evidence, we conclude that the impacts of the NAO on Mediterranean ecosystems are still poorly understood, especially on terrestrial ecosystems. We have identified three major non-excluding possible causes for the present state of the art:

- (i) There is a considerable heterogeneity in the species and biological phenomena studied, and consequently, there are only one or a few populations studied in each case and usually from a single site. This fact hinders seriously our capacity to make generalizations because the NAO effect on local weather (the relevant scale for organisms) varies among regions (even within the Mediterranean), and we must be very cautious about extrapolating results from one site to others. In addition, many studies, especially in aquatic ecosystems, just report significant associations between the NAO and biological phenomena without providing a mechanistic interpretation of these results. We are firmly convinced that without a biological interpretation, results are of limited use.
- (ii) Most of the studies have assessed only the effect of the winter NAO index (December–March), probably imitating the pioneering studies carried out in northern latitudes. Indeed, this phase shows the greater variability (Hurrell, 1995), but the potential influence of the NAO in organisms through climate patterns of other seasons has been completely neglected (but see Gordo and Sanz, 2010). The NAO effect on climate over the whole annual cycle is well-known by the climatologists (e.g., this book), but this is another point where considerably additional progress needs to be made. The climatologic literature is extensive, but unfortunately it is difficult to understand for most ecologists. In addition, the method of studying and defining climate patterns by climatologists is not necessarily the most relevant for organisms (e.g., see Doi et al., 2008). It seems obvious that there is an urgent need to establish multidisciplinary collaborations between climatologists and ecologists to deal accurately with the complex interactions between climate and biosphere.
- (iii) Despite the NAO influence on the variability of Mediterranean climate, the NAO may indeed have little effect on Mediterranean ecosystems, especially on terrestrial ecosystems, as the remarkable number of studies reporting non-significant results may demonstrate (e.g., Ravier and Fromentin, 2004; Grosbois et al., 2006; Gordo and Sanz, 2008; Jiguet et al., 2008; Kralj and Dolenc, 2008; Jenouvrier et al., 2009; Robson and Barriocanal, 2011). Moreover, some studies have shown that the NAO effect is overridden by local weather (e.g., Rodríguez and Bustamante, 2003; Gordo and Sanz, 2010). The extremely variable nature of the Mediterranean climate among years as well as the complex balances between temperature and rainfall could be the cause for the poor correlations with the NAO. However, a larger sample of studies would be needed to distinguish unambiguously between a real absence of an effect and a simple lack of evidence.

In view of the current climate change, we need to improve our knowledge about climate effects on organisms. The NAO, as a major driver of climate in the Mediterranean region, may become a keystone to the understanding of past, present and future impacts of climate change on Mediterranean ecosystems. However, the mechanisms by which the NAO influences organisms in Mediterranean ecosystems are different and to some extent more complex than they are in more northern latitudes. These facts demand of the Mediterranean ecologists more original thought and more effort to start long-term monitoring programs of biodiversity and to enhance and maintain those already in progress.

**Acknowledgements** Oscar Gordo was supported by a Juan de la Cierva contract (ref. JCI-2009-05274).

## References

- Abella A, Fiorentino F, Mannini A, Relini LO (2008) Exploring relationships between recruitment of European hake (*Merluccius merluccius* L. 1758) and environmental factors in the Ligurian Sea and the Strait of Sicily (Central Mediterranean). *J Mar Syst* 71:279–293
- Almaraz P, Amat JA (2004a) Complex structural effects of two hemispheric climatic oscillators on the regional spatio-temporal expansion of a threatened bird. *Ecol Lett* 7:547–556
- Almaraz P, Amat JA (2004b) Multi-annual spatial and numeric dynamics of the white-headed duck *Oxyura leucocephala* in southern Europe: seasonality, density dependence and climatic variability. *J Anim Ecol* 73:1013–1023
- Avolio E, Pasqualoni L, Federico S, Fornaciari M, Bonofiglio T, Orlandi F, Bellecci C, Romano B (2008) Correlation between large-scale atmospheric fields and the olive pollen season in Central Italy. *Int J Biometeorol* 52:787–796
- Balbontín J, Møller AP, Hermosell IG, Marzal E, Reviriego M, de Lope F (2009) Divergent patterns of impact of environmental conditions on life history traits in two populations of a long-distance migratory bird. *Oecologia* 159:859–872
- Bechet A, Johnson AR (2008) Anthropogenic and environmental determinants of Greater Flamingo *Phoenicopterus roseus* breeding numbers and productivity in the Camargue (Rhône delta, southern France). *Ibis* 150:69–79
- Begon M, Townsend CR, Harper JL (2006) *Ecology: from individuals to ecosystems*, 4th edn. Blackwell Publishing, Oxford
- Berthold P (2001) *Bird migration: a general survey*. Oxford University Press, Oxford
- Bosch J, Carrascal LM, Durán L, Walker S, Fisher MC (2007) Climate change and outbreaks of amphibian chytridiomycosis in a montane area of Central Spain: is there a link? *Proc Roy Soc Lond B* 274:253–260
- Bridges CR, Krohn O, Deflorio M, de Metrio G (2009) Possible NAO and SST influences on the eastern bluefin tuna stock – the in-exfish approach. *Collect Vol Sci Papers ICCAT* 63: 138–152
- Campelo F, Nabais C, García-González I, Cherubini P, Gutiérrez E, Freitas H (2009) Dendrochronology of *Quercus ilex* L. and its potential use for climate reconstruction in the Mediterranean region. *Can J For Res* 39:2486–2493
- Cartes JE, Maynou F, Fanelli E, Papiol V, Lloris D (2009) Long-term changes in the composition and diversity of deep-slope megabenthos and trophic webs off Catalonia (western Mediterranean): Are trends related to climatic oscillations? *Prog Oceanogr* 82:32–46
- Costantini D, Carello L, Dell’Omo G (2010) Patterns of covariation among weather conditions, winter North Atlantic Oscillation index and reproductive traits in Mediterranean kestrels. *J Zoology* 280:177–184

- de Puellas MLF, Alemany F, Jansa J (2007) Zooplankton time-series in the Balearic Sea (western Mediterranean): Variability during the decade 1994–2003. *Prog Oceanogr* 74:329–354
- de Puellas MLF, Molinero JC (2008) Decadal changes in hydrographic and ecological time-series in the Balearic Sea (western Mediterranean), identifying links between climate and zooplankton. *ICES J Mar Sci* 65:311–317
- Doi H, Gordo O, Katano I (2008) Heterogeneous intra-annual climatic changes drive different phenological responses at two trophic levels. *Clim Res* 36:181–190
- Doi H, Takahashi M (2008) Latitudinal patterns in the phenological responses of leaf colouring and leaf fall to climate change in Japan. *Glob Ecol Biogeogr* 17:556–561
- Donnelly A, Cooney T, Jennings E, Buscardo E, Jones M (2009) Response of birds to climatic variability: evidence from the western fringe of Europe. *Int J Biometeorol* 53:211–220
- Dulcic J, Grbec B, Lipej L, Paklar GB, Supic N, Smircic A (2004) The effect of the hemispheric climatic oscillations on the Adriatic ichthyofauna. *Fresenius Environ Bull* 13:293–298
- Esteves MA, Orgaz MDM (2001) The influence of climatic variability on the quality of wine. *Int J Biometeorol* 45:13–21
- Figuerola J (2007) Climate and dispersal: Black-winged stilts disperse further in dry springs. *PLoS ONE* 2:e539
- Forchhammer MC, Post E (2004) Using large-scale climate indices in climate change ecology studies. *Popul Ecol* 46:1–12
- Forchhammer MC, Post E, Stenseth NC (2002a) North Atlantic Oscillation timing of long- and short-distance migration. *J Anim Ecol* 71:1002–1014
- Forchhammer MC, Post E, Stenseth NC, Boertmann DM (2002b) Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. *Popul Ecol* 44:113–120
- Gienapp P, Leimu R, Merilä J (2007) Responses to climate change in avian migration time – microevolution or phenotypic plasticity? *Clim Res* 35:25–35
- Gimeno L, Ribera P, Iglesias R, de la Torre L, García R, Hernández E (2002) Identification of empirical relationships between indices of ENSO and NAO and agricultural yields in Spain. *Clim Res* 21:165–172
- Gladan ZN, Marasovic I, Grbec B, Skejic S, Buzancic M, Kuspilic G, Matijevic S, Matic F (2010) Inter-decadal variability in phytoplankton community in the Middle Adriatic (Katela Bay) in relation to the North Atlantic Oscillation. *Estuaries Coasts* 33:376–383
- Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58
- Gordo O, Brotons L, Ferrer X, Comas P (2005) Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Glob Change Biol* 11:12–21
- Gordo O, Sanz JJ (2008) The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *J Ornithol* 149:199–210
- Gordo O, Sanz JJ (2010) Impact of climate change on plant phenology in Mediterranean ecosystems. *Glob Change Biol* 16:1082–1106
- Gouveia C, Trigo RM, DaCamara CC, Libonati R, Pereira JMC (2008) The North Atlantic Oscillation and European vegetation dynamics. *Int J Climatol* 28:1835–1847
- Grbec B, Dulcic J, Morovic M (2002) Long-term changes in landings of small pelagic fish in the eastern Adriatic – possible influence of climate oscillations over the Northern Hemisphere. *Clim Res* 20:241–252
- Grosbois V, Henry PY, Blondel J, Perret P, Lebreton JD, Thomas DW, Lambrechts MM (2006) Climate impacts on Mediterranean blue tit survival: an investigation across seasons and spatial scales. *Glob Change Biol* 12:2235–2249
- Grubelic I, Antolic B, Despalatovic M, Grbec B, Paklar GB (2004) Effect of climatic fluctuations on the distribution of warm-water coral *Astroides calycularis* in the Adriatic Sea: new records and review. *J Mar Biol Assoc UK* 85:599–602
- Guisande C, Vergara AR, Riveiro I, Cabanas JM (2004) Climate change and abundance of the Atlantic-Iberian sardine (*Sardina pilchardus*). *Fish Oceanogr* 13:91–101

- Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* 430:71–75
- Hoerling MP, Hurrell JW, Xu T (2001) Tropical origins for recent North Atlantic climate change. *Science* 292:90–92
- Hubálek Z, Čapek M (2008) Migration distance and the effect of North Atlantic Oscillation on the spring arrival of birds in Central Europe. *Folia Zoologica* 57:212–220
- Hüppop O, Hüppop K (2003) North Atlantic Oscillation and timing of spring migration in birds. *Proc Roy Soc Lond B* 270:233–240
- Hurrell JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269:676–679
- Hurrell JW, Van Loon H (1997) Decadal variations in climate associated with North Atlantic Oscillation. *Clim Change* 36:301–326
- Jenouvrier S, Thibault JC, Viallefont A, Vidal P, Ristow D, Mougin JL, Brichetti P, Borg JJ, Bretagnolle V (2009) Global climate patterns explain range-wide synchronicity in survival of a migratory seabird. *Glob Change Biol* 15:268–279
- Jiguet F, Doxa A, Robert A (2008) The origin of out-of-range pelicans in Europe: wild bird dispersal or zoo escapes? *Ibis* 150:606–618
- Jonzén N, Lindén A, Ergon T, Knudsen E, Vik JO, Rubolini D, Piacentini D, Brinch C, Spina F, Karlsson L, Stervander M, Andersson A, Waldenström J, Lehikoinen A, Edvardsen E, Solvang R, Stenseth NC (2006) Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312:1959–1961
- Kamburska L, Fonda-Umani S (2009) From seasonal to decadal inter-annual variability of mesozooplankton biomass in the Northern Adriatic Sea (Gulf of Trieste). *J Mar Syst* 78:490–504
- Katara I, Illian J, Pierce GJ, Scott B, Wang JJ (2008) Atmospheric forcing on chlorophyll concentration in the Mediterranean. *Hydrobiologia* 612:33–48
- Kralj J, Dolenec Z (2008) First arrival dates of the Nightingale (*Luscinia megarhynchos*) to Central Croatia in the early 20th century and at the turn of the 21st century. *Cent Eur J Biol* 3:295–298
- Lamb PJ, Pepler RA (1987) North Atlantic Oscillation: concept and application. *Bull Am Meteorol Soc* 68:1218–1225
- Lebrune C, Gremare A, Guizien K, Amouroux JM (2007) Long-term comparison of soft bottom macrobenthos in the Bay of Banyuls-sur-Mer (north-western Mediterranean Sea): a reappraisal. *J Sea Res* 58:125–143
- Lehikoinen E, Sparks TH (2010) Bird migration. In: Møller AP, Fiedler W, Berthold P (eds) *Effects of climate change on birds*. Oxford University Press, Oxford, pp 89–112
- Lloret J, Leonart J, Solé I, Fromentin JM (2001) Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. *Fish Oceanogr* 10:33–50
- López-Moreno JJ, Vicente-Serrano SM (2008) Positive and negative phases of the winter-time North Atlantic Oscillation and drought occurrence over Europe: a multitemporal-scale approach. *J Clim* 21:1220–1243
- Martínez-Jauregui M, San Miguel-Ayaz A, Mysterud A, Rodríguez-Vigal C, Clutton-Brock TH, Langvatn R, Coulson T (2009) Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries? *Glob Change Biol* 15:1727–1738
- Massutí E, Monserrat S, Oliver P, Moranta J, López-Jurado JL, Marcos M, Hidalgo M, Guijarro B, Carbonell A, Pereda P (2008) The influence of oceanographic scenarios on the population dynamics of demersal resources in the western Mediterranean: hypothesis for hake and red shrimp off Balearic Islands. *J Mar Syst* 71:421–438
- Maynou F (2008a) Environmental causes of the fluctuations of red shrimp (*Aristeus antennatus*) landings in the Catalan Sea. *J Mar Syst* 71:294–302
- Maynou F (2008b) Influence of the North Atlantic Oscillation on Mediterranean deep-sea shrimp landings. *Clim Res* 36:253–257

- Mazzochi MG, Christou ED, Di Capua I, de Puelles MLF, Fonda-Umani S, Molinero JC, Nival P, Siokou-Frangou I (2007) Temporal variability of *Centropages typicus* in the Mediterranean Sea over seasonal-to-decadal scales. *Prog Oceanogr* 72:214–232
- McHugh MJ, Rogers JC (2001) North Atlantic Oscillation influence on precipitation variability around the Southeast African convergence zone. *J Clim* 14:3631–3642
- Molinero JC, Ibañez F, Souissi S, Buecher E, Dallot S, Nival P (2008) Climate control on the long-term anomalous changes of zooplankton communities in the northwestern Mediterranean. *Glob Change Biol* 14:11–26
- Molinero JC, Ibañez F, Souissi S, Chifflet M, Nival P (2005) Phenological changes in the northwestern Mediterranean copepods *Centropages typicus* and *Temora stylifera* linked to climate forcing. *Oecologia* 145:640–649
- Mysterud A, Stenseth NC, Yoccoz NG, Ottersen G, Langvatn R (2003) The response of terrestrial ecosystems to climate variability associated with the North Atlantic Oscillation. In: Hurrell JW, Kushnir Y, Ottersen G, Visbeck MH (eds) *The North Atlantic Oscillation: climatic significance and environmental impact*. American Geophysical Union, Washington, pp 235–262
- Newton I (2008) *The migration ecology of birds*. Academic Press, London
- Oba G, Post E, Stenseth NC (2001) Sub-Saharan desertification and productivity are linked to hemispheric climate variability. *Glob Change Biol* 7:241–246
- Orlandi F, García-Mozo H, Galán C, Romano B, Díaz de la Guardia C, Ruiz L, del Mar Trigo M, Domínguez-Vilches E, Fornaciari M (2010) Olive flowering trends in a large Mediterranean area (Italy and Spain). *Int J Biometeorol* 54:151–163
- Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia* 128:1–14
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Syst* 37:637–669
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Piovesan G, Schirone B (2000) Winter North Atlantic Oscillation effects on the tree rings of the Italian beech (*Fagus sylvatica* L.). *Int J Biometeorol* 44:121–127
- Pérez FF, Padín XA, Pazos Y, Gilcoto M, Cabanas M, Pardo PC, Doval MD, Farina-Busto L (2010) Plankton response to weakening of the Iberian coastal upwelling. *Glob Change Biol* 16:1258–1267
- Quadrelli R, Pavan V, Molteni F (2001) Wintertime variability of Mediterranean precipitation and its links with large-scale circulation anomalies. *Clim Dyn* 17:457–466
- Rainio K, Laaksonen T, Ahola M, Vähätalo AV, Lehikoinen E (2006) Climatic responses in spring migration of boreal and arctic birds in relation to wintering area and taxonomy. *J Avian Biol* 37:507–515
- Ravier C, Fromentin JM (2004) Are the long-term fluctuations in Atlantic bluefin tuna (*Thunnus thynnus*) population related to environmental changes? *Fish Oceanogr* 13:145–160
- Relini LO, Mannini A, Fiorentino F, Palandri G, Relini G (2006) Biology and fishery of *Eledone cirrhosa* in the Ligurian Sea. *Fish Res* 78:72–88
- Relini LO, Palandri G, Garibaldi F, Relini M, Cima C, Lanteri L (2010) Large pelagic fish, swordfish, bluefin and small tunas, in the Ligurian Sea: biological characteristics and fishery trends. *Chem Ecol* 26:341–357
- Robson D, Barriocanal C (2011) Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds. *J Anim Ecol* 80:320–331
- Rodó X, Baert E, Comín FA (1997) Variations in seasonal rainfall in Southern Europe during the present century: relationships with the North Atlantic Oscillation and the El Niño-Southern Oscillation. *Clim Dyn* 13:275–284
- Rodó X, Comín FA (2000) Links between large-scale anomalies, rainfall and wine quality in the Iberian Peninsula during the last three decades. *Glob Change Biol* 6: 267–273

- Rodrigo FS, Trigo RM (2007) Trends in daily rainfall in the Iberian Peninsula from 1951 to 2002. *Int J Climatol* 27:513–529
- Rodríguez C, Bustamante J (2003) The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? *J Anim Ecol* 72:793–810
- Rodríguez C, Naves J, Fernández-Gil A, Obeso JR, Delibes M (2007) Long-term trends in food habits of a relict brown bear population in northern Spain: the influence of climate and local factors. *Environ Conserv* 34:36–44
- Rodríguez-Puebla C, Ayuso SM, Frías MD, García-Casado LA (2007) Effects of climate variation on winter cereal production in Spain. *Clim Res* 34:223–232
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60
- Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B, Tryjanowski P, Liu C, Rawlins S, Imeson A (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature* 435:353–357
- Rozas V, Lamas S, García-González I (2009) Differential tree-growth responses to local and large-scale climatic variation in two *Pinus* and two *Quercus* species in northwest Spain. *Ecoscience* 16:299–310
- Rubolini D, Ambrosini R, Caffi M, Bricchetti P, Armiraglio S, Saino N (2007) Long-term trends in first arrival and first egg laying dates of some migrant and resident bird species in northern Italy. *Int J Biometeorol* 51:553–563
- Saino N, Rubolini D, Jónzén N, Ergon T, Montemaggiori A, Stenseth NC, Spina F (2007) Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. *Clim Res* 35:123–134
- Saino N, Szep T, Romano M, Rubolini D, Spina F, Møller AP (2004) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7:21–25
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy Poff N, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Santojanni A, Arneri E, Bernardini V, Cingolani N, Di Marco M, Russo A (2006) Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. *Clim Res* 31:181–193
- Sanz JJ (2002) Climate change and breeding parameters of great and blue tits throughout the western Palaearctic. *Glob Change Biol* 8:408–422
- Sanz JJ (2003) Large-scale effect of climate change on breeding parameters of pied flycatchers in Western Europe. *Ecography* 26:45–50
- Sæther BE, Sutherland WJ, Engen S (2004) Climate influences on avian population dynamics. *Adv Ecol Res* 35:185–209
- Sæther BE, Tufto J, Engen S, Jerstad K, Rostad OW, Skåtan JE (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science* 287:855–856
- Sinelschikova A, Kosarev V, Panov I, Baushev AN (2007) The influence of wind conditions in Europe on the advance in timing of the spring migration of the song thrush (*Turdus philomelos*) in the south-east Baltic region. *Int J Biometeorol* 51:431–440
- Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the 4th assessment report of the Intergovernmental panel on climate change. Cambridge University Press, Cambridge
- Spina F, Massi A, Montemaggiori A, Baccetti N (1993) Spring migration across central Mediterranean: general results from the ‘Progetto Piccole Isole’. *Die Vogelwarte* 37:1–94
- Stenseth NC, Ehrlich D, Rueness EK, Lingjærde OC, Chan KS, Boutin S, O’Donoghue M, Robinson DA, Viljugrein H, Jakobsen KS (2004) The effect of climatic forcing on population synchrony and genetic structuring of the Canadian lynx. *Proc Natl Acad Sci USA* 101:6056–6061

- Stenseth NC, Mysterud A (2005) Weather packages: finding the right scale and composition of climate in ecology. *J Anim Ecol* 74:1195–1198
- Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science* 297:1292–1296
- Stenseth NC, Ottersen G, Hurrell JW, Mysterud A, Lima M, Chan KS, Yoccoz NG, Ådlandsvik B (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc Roy Soc Lond B* 270:2087–2096
- Stige LC, Stave J, Chan KS, Ciannelli L, Pettorelli N, Glantz M, Herren HR, Stenseth NC (2006) The effect of climate variation on agro-pastoral production in Africa. *Proc Natl Acad Sci USA* 103:3049–3053
- Tøttrup AP, Rainio K, Coppack T, Lehtikoinen E, Rahbek C, Thorup K (2010) Local temperature fine-tunes the timing of spring migration in birds. *Integr Comp Biol* 50:293–304
- Trigo RM, Pozo-Vázquez D, Osborn TJ, Castro-Díez Y, Gámiz-Fortis S, Esteban-Parra MJ (2004) North Atlantic oscillation influence on precipitation, river flow and water resources in the Iberian Peninsula. *Int J Climatol* 24:925–944
- Vicente-Serrano SM, Cuadrat JM (2007) North Atlantic Oscillation control of droughts in north-east Spain: evaluation since 1600 A.D. *Clim Change* 85:357–379
- Visbeck MH, Hurrell JW, Polvani L, Cullen HM (2001) The North Atlantic Oscillation: past, present, and future. *Proc Natl Acad Sci USA* 98:12876–12877