

The North Atlantic Oscillation and ecology: links between historical time-series, and lessons regarding future climate warming

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ABSTRACT: Indices of the North Atlantic Oscillation (NAO) have been very useful for explaining interannual variability in many ecological time series. We suggest that this is based on a combination of 3 factors: (1) the strong relationship between NAO and meteorological conditions in winter; (2) qualitative changes in environmental conditions in response to winter conditions, especially temperatures; and (3) the central importance of those conditions for the distribution and population dynamics of species in temperate and boreal regions. The increase in winter temperatures associated with a shift of NAO towards its positive phase in recent years has resulted in a relief from winter stress for many species and populations. This has reduced mortality rates during winter, thereby influencing local population dynamics and allowing, for example, the northward expansion of many species. In contrast to winter warming, the recent increase in summer temperature has had fewer ecological consequences, as it has not been large enough to cause an increase in heat stress to critical levels during summer. The difference in the ecological consequences of winter and summer warming also explains why reductions in the ranges of species have been observed less often than expansions during the past few decades. However, with further warming, summer heat stress might become an increasingly important determinant of the response of species to climate warming. This suggests that studies analysing the effects of the winter NAO on species dynamics and distributions will give us only a limited perspective on the further consequences of climate warming.

KEY WORDS: NAO · Winter ecology · Range expansion · Heat stress · Climate indices · Climate change

Indices of the North Atlantic Oscillation (NAO) have been used as climate proxies in ecological studies (Drinkwater et al. 2003, Mysterud et al. 2003, Straile et al. 2003). Several NAO indices have been established, all of which represent a normalised air pressure difference between the Icelandic Low and the Azores High (Hurrell 1995, Hurrell et al. 2003). Surprisingly, the use of these very simple climate indices is able to shed much light on the interannual variability of ecological descriptors, even in the best-studied freshwater, marine

and terrestrial systems. Variability in the winter NAO has been linked to the population dynamics of species differing in size by several orders of magnitude, e.g. algae and whales (Drinkwater et al. 2003, Straile et al. 2003). It has been linked e.g. to the growth (Piovesan & Schirone 2000) and phenology (Post & Stenseth 1999) of plants, and the phenology of butterflies (Sparks et al. 2005), amphibians and birds (Forchhammer et al. 1998). The sex ratio and body size of deer (Post et al. 1999a, Mysterud et al. 2003) and predator–prey inter-

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actions between crustaceans and algae (Straile 2002), and between wolves and moose (Post et al. 1999b) have also been linked to NAO. The ability of NAO indices to explain the interannual variability of ecological state variables cries out for an explanation.

Paradoxically, in some case studies, indices of NAO predict ecological processes even better than local meteorological variables (Hallett et al. 2004). This has been attributed to the fact that NAO indices average out meteorological conditions across time and space in a useful way (Hallett et al. 2004), and integrate different aspects of climate such as air temperature, wind speed and precipitation (Stenseth & Mysterud 2005).

However, these are rather technical aspects of the reasons for the utility of NAO as an ecological predictor. We maintain that there is a deeper meaning, which conveys important messages to ecology and climate impact research (Straile 2005). NAO is a good predictor of interannual ecological variability, because it is most strongly related to the climate of the Northern Hemisphere during winter and early spring (Hurrell 1995)—a period of the year that is of critical importance for ecological dynamics, at least in temperate, boreal and arctic regions (Campbell et al. 2005, Sturm et al. 2005). The sensitivity of ecological dynamics in winter (as compared to other seasons) has several reasons.

- (1) Gradual changes in winter meteorology not only affect environmental conditions directly (e.g. air temperatures); they can also result in changes of phase (e.g. from snow to rain in terrestrial systems, or from water to ice in aquatic systems), and influence the transition from mixing to non-mixing regimes in aquatic ecosystems (Straile 2005). Ecosystems will be influenced more strongly by such shifts in abiotic environmental conditions than by gradual changes in temperature.
- (2) Temperature differences, of e.g. a few °C, may be more important during winter than during summer, because in summer biotic interactions usually increase in importance, resulting in a reduction in the relative importance of abiotic variables for population dynamics. For example, the population dynamics of key herbivores (*Daphnia* spp.) in lakes are strongly influenced by water temperature in spring (Straile 2002), whereas during summer, factors such as predation and food quantity and quality are paramount (Sommer et al. 1986).
- (3) More importantly, differences in the severity of winter (i.e. in the extent and duration of freezing) not only affect metabolic rates, but also directly influence the survival of plants, invertebrates (Crozier 2004, Thielges et al. 2004, Battisti et al. 2005) and vertebrates (Tonn & Paszkowski 1986, Tonn et al. 2004, Altwegg et al. 2005, Chan et al. 2005, Korlund & Steen 2006).

Increased survival rates during winter may result in range extensions, as exemplified by lepidopteran species (Crozier 2004, Battisti et al. 2005). On the other hand, winter mortality can limit the northward expansion of invasive species (Thielges et al. 2004). If key species are affected by winter temperatures, indirect, food-web mediated effects of winter severity may change community composition and ecosystem dynamics (Straile et al. 2003, Tonn et al. 2004, Eaton et al. 2005). For example, winter fish-kills in small boreal lakes during severe winters will allow increases in the abundance of amphibians and benthic invertebrates (Tonn et al. 2004, Eaton et al. 2005). Likewise, winter conditions are suggested to play a key role in the possible conversion of tundra into shrubland in arctic regions (Sturm et al. 2005), with obvious consequences for the local biota.

Winter severity has long been recognised to be a major determinant of the distribution of plants and animals (Lomolino et al. 2006). The ability to tolerate harsh winters and freezing conditions is a major evolutionary step, which a large number of clades failed to make (niche conservatism; see Peterson et al. 1999, Wiens & Donoghue 2004). The lack in many clades of evolved adaptations that would have allowed them to tolerate freezing temperatures has been suggested to contribute to the observed latitudinal trend in species richness (Wiens & Donoghue 2004).

Consequently, the reduction in winter severity associated with the shift of NAO towards its positive phase is expected to have—and indeed does have—a strong effect on population dynamics and species distribution (Stenseth et al. 2002, Walther et al. 2002).

Climate indices developed for other regions around the globe, e.g. the indices of the El Niño Southern Oscillation (ENSO, SOI) and of the Pacific Decadal Oscillation (PDO), have also been linked to ecological time series (Stenseth et al. 2003). The utility of PDO is also partly due to its influence on winter meteorological conditions (Fagre et al. 2003, Winder & Schindler 2004, Schindler et al. 2005). However, both the ENSO and PDO also have a strong impact on ecological dynamics via their influence on precipitation patterns, which in turn influence the occurrence and frequency of major droughts and wild fires (Fagre et al. 2003), or alternatively of unusually wet conditions in more arid regions (Lima et al. 1999). Hence, in arid regions, the utility of climate indices might be more strongly linked to summer conditions (i.e. the duration, occurrence and intensity of drought). Consequently, the ecological influence of the NAO in Mediterranean Europe may also operate via its influence on precipitation patterns (Cullen & deMenocal 2000).

However, in temperate regions of the Northern Hemisphere, winter warming during recent decades—

which is partly associated with NAO and for which variability in NAO is a good model system—had a stronger effect on ecological dynamics than summer warming, because the relief from winter stress was not accompanied by a strong increase in summer heat stress. Consequently, the number of studies reporting range expansions far exceeds the number reporting retractions and local extinctions at southern or low-elevation species boundaries (Thomas et al. 2006). While Thomas et al. (2006) suggest differences in detection and attribution probabilities to account for the discrepancy between expansion and extinction, seasonally specific consequences of warming (Crozier 2004, Battisti et al. 2005) will at least contribute to the observed patterns.

However, things may change. The European summer of 2003 was an example of summer temperatures that did indeed result in widespread drought and heat stress (Belmin 2003, Ciais et al. 2005, Mouthon & Daufresne 2006). Heat waves comparable to 2003 are expected to become common in temperate regions as the climate warms (Meehl & Tebaldi 2004). This suggests that the climate response of species and populations in temperate regions during the past few decades, which was strongly linked to the phase shift and variability of NAO, may not be a good model for predicting the ecological effects of further warming. Species and populations might suffer increasingly from heat stress in future, thus increasing the relative importance of range reductions and other adverse effects of global warming in temperate regions.

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