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Review Paper

Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond

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Whereas the El Niño Southern Oscillation (ENSO) affects weather and climate variability worldwide, the North Atlantic Oscillation (NAO) represents the dominant climate pattern in the North Atlantic region. Both climate systems have been demonstrated to considerably influence ecological processes. Several other large-scale climate patterns also exist. Although less well known outside the field of climatology, these patterns are also likely to be of ecological interest. We provide an overview of these climate patterns within the context of the ecological effects of climate variability. The application of climate indices by definition reduces complex space and time variability into simple measures, 'packages of weather'. The disadvantages of using global climate indices are all related to the fact that another level of problems are added to the ecology–climate interface, namely the link between global climate indices and local climate. We identify issues related to: (i) spatial variation; (ii) seasonality; (iii) non-stationarity; (iv) nonlinearity; and (v) lack of correlation in the relationship between global and local climate. The main advantages of using global climate indices are: (i) biological effects may be related more strongly to global indices than to any single local climate variable; (ii) it helps to avoid problems of model selection; (iii) it opens the possibility for ecologists to make predictions; and (iv) they are typically readily available on Internet.

Keywords: climate; teleconnections; time-series analysis; nonlinearity; terrestrial; marine

1. INTRODUCTION

Ecologists know very well that weather and climate affect the performance of individuals and, as a result, both the abundance and distribution of species. While ecologists have historically focused on the effects of locally measured weather components, an interest in large-scale climate fluctuations has recently emerged (e.g. Brown 1995; Fromentin & Planque 1996; Gaston & Blackburn 2000). Large-scale climate patterns provide a conceptual framework and a broader understanding of observed changes in the local physical environment. Holmgren *et al.* (2001), Ottersen *et al.* (2001), Blenckner & Hillebrand (2002), Stenseth *et al.* (2002), Drinkwater *et al.* (2003), Straile *et al.* (2003), Walther *et al.* (2002) and Mysterud *et al.* (2003) have recently adopted this approach and comprehensively described the effects of large-scale climate variability on marine, terrestrial and limnic ecosystems. The main objective of this review is to help ecologists orient themselves among several of the more prominent large-scale climate patterns and their corresponding indices.

Quite obviously, climate does not affect populations through a single weather variable, but rather through a blend of weather features (see Remmert 1980). Proxies for the *overall* climate condition—representing a 'package of weather'—might, at least at an initial stage provide a robust assessment of the ecological effects of climate fluctuations, not least because of the more holistic account of the climate systems (Namias & Cayan 1981). By definition, such climate indices ought to reduce complex space and time variability into simple measures. Climate indices like those for the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) have been shown to be of great use to ecologists (Stenseth *et al.* 2002). The visibility of such climatic fluctuations (be it through weather variables or climate indices) in ecological patterns and processes, however, may be both unclear and difficult to discover (see Kaitala & Ranta 2001; Jonzén

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et al. 2002; Stenseth *et al.* 2002; see also electronic Appendix A available on The Royal Society's Publications Web site).

The climate literature is vast and not easy for ecologists to digest. Moreover, when climatologists disagree on the best ways to define climate phenomena (e.g. Trenberth 1997; Wallace 2000) or even their actual existence (e.g. Deser 2000; Ambaum *et al.* 2001), it is difficult for ecologists to assess their merit. We provide a tutorial-like review of some key issues relating to climate variation and ecological processes. Our review is, deliberately, biased toward the NAO and ENSO—just as is the literature on climate and ecology. Nevertheless, our discussion should be of general relevance for ecologists interested in the ecological effects of other large-scale climate patterns.

2. WEATHER, CLIMATE AND TELECONNECTIONS

Atmospheric phenomena are loosely divided into the realms of 'weather' and 'climate'. The pronounced atmospheric fluctuations occurring from hour to hour and day to day constitute the *weather*. Features such as local temperature, air pressure, humidity, cloudiness, precipitation and wind describe weather. *Climate* is usually defined to be the prevailing weather, describing both the average conditions and the variations (and distributions) of weather conditions for some particular geographical locality or region.

Profound undulations in the extratropical atmospheric flow (the so-called 'planetary-scale waves') are the result of atmospheric processes modulated by high mountains and land–sea boundaries. Planetary waves displace air north and south around our planet. These waves are geographically anchored but do change in time, either as heating patterns in the atmosphere vary or because of internal (chaotic) processes. The transient behaviour of the atmospheric planetary-scale waves generates anomalies in climate on seasonal and longer time-scales over large geographical regions. Thus, some regions may be cooler or drier than average, while thousands of kilometres away warmer and wetter conditions may prevail. These simultaneous physical variations in climate over distant parts of the globe are, within the meteorological literature, commonly referred to as 'teleconnections' (Wallace & Gutzler 1981; Esbensen 1984; Barnston & Livezey 1987; Kushnir & Wallace 1989; Trenberth *et al.* 1998).

Indices for teleconnection patterns are derived from meteorological data in a variety of ways, most simply through one-point correlation maps of, for instance, sea-level pressure (SLP) (e.g. Wallace & Gutzler 1981), or more recently through a large array of statistical techniques that fall under the general heading of principal component (or eigenvalue) analysis (e.g. Barnston & Livezey 1987). Many distinct teleconnection patterns have been identified, including the Southern Oscillation (SO) in the tropics and a dozen or more patterns over the extratropical Northern Hemisphere. Though their precise nature and shape vary to some extent according to the statistical methodology and the dataset employed in the analysis, consistent regional characteristics that identify the most conspicuous patterns emerge.

Over the North Pacific sector these include (but are not limited to) the North Pacific (NP), West Pacific (WP), East Pacific (EP), Tropical/Northern Hemisphere (TNH) and Pacific–North American (PNA) patterns. Over the North Atlantic–European region these include the NAO, East Atlantic (EA), East Atlantic/Western Russia and Scandinavian (SCAN) patterns, among others (see Barnston & Livezey (1987) for detailed descriptions of the Northern Hemisphere patterns and a discussion of their seasonality). Similarly, various indices describe climate patterns over the Southern Hemisphere, including the Pacific–South American (PSA) pattern and the Antarctic Oscillation (AAO) (see § 5 for further discussion and table 1 for a list of all the climate indices and corresponding acronyms used here). Most of the aforementioned indices are available through the Web (e.g. http://www.cpc.ncep.noaa.gov/data/teledoc/telecontents.html, http://www.cgd.ucar.edu/cas/catalog/climind or http://tao.atmos.washington.edu/data_sets).

Table 1. An overview of large-scale climate patterns and the corresponding acronyms as used in this paper (alphabetically listed by acronym).

acronym	large-scale climate pattern
AAO	Antarctic Oscillation
AO	Arctic Oscillation
EA	East Atlantic pattern
EAWR	East Atlantic/Western Russia pattern
ENSO	El Niño Southern Oscillation
EP	East Pacific pattern
NAM	Northern Annular mode (identical to AO)
NAO	North Atlantic Oscillation
NP	North Pacific Oscillation
PDO	Pacific Decadal Oscillation
PNA	Pacific–North American
PSA	Pacific–South American
SAM	Southern Annular mode (as AAO, but opposite sign)
SCAN	Scandinavian pattern
SO	Southern Oscillation
TNH	Tropical/Northern Hemisphere pattern
WP	West Pacific pattern

3. THE NORTH ATLANTIC OSCILLATION—THE PHENOMENON AND ITS INDICES

The NAO refers to a north–south alternation in atmospheric mass between the subtropical Atlantic and the Arctic, and thus involves out-of-phase behaviour between the climatological low-pressure centre near Iceland and the high-pressure centre near the Azores (figure 1). It is the most robust pattern of recurrent atmospheric behaviour in the North Atlantic region (Barnston & Livezey 1987). Although present throughout the year, its fluctuations are of greatest amplitude during the cold season months (November–April) when the atmosphere is most dynamically active.

Swings from one extreme phase of the NAO to another produce large changes in the mean wind speed and direction over the Atlantic between 40° N and 60° N, the corresponding heat and moisture transport between the Atlantic and the neighbouring continents, as well as the intensity and number of storms, their paths and their associated weather (e.g. Hurrell 1995; Hurrell & van Loon

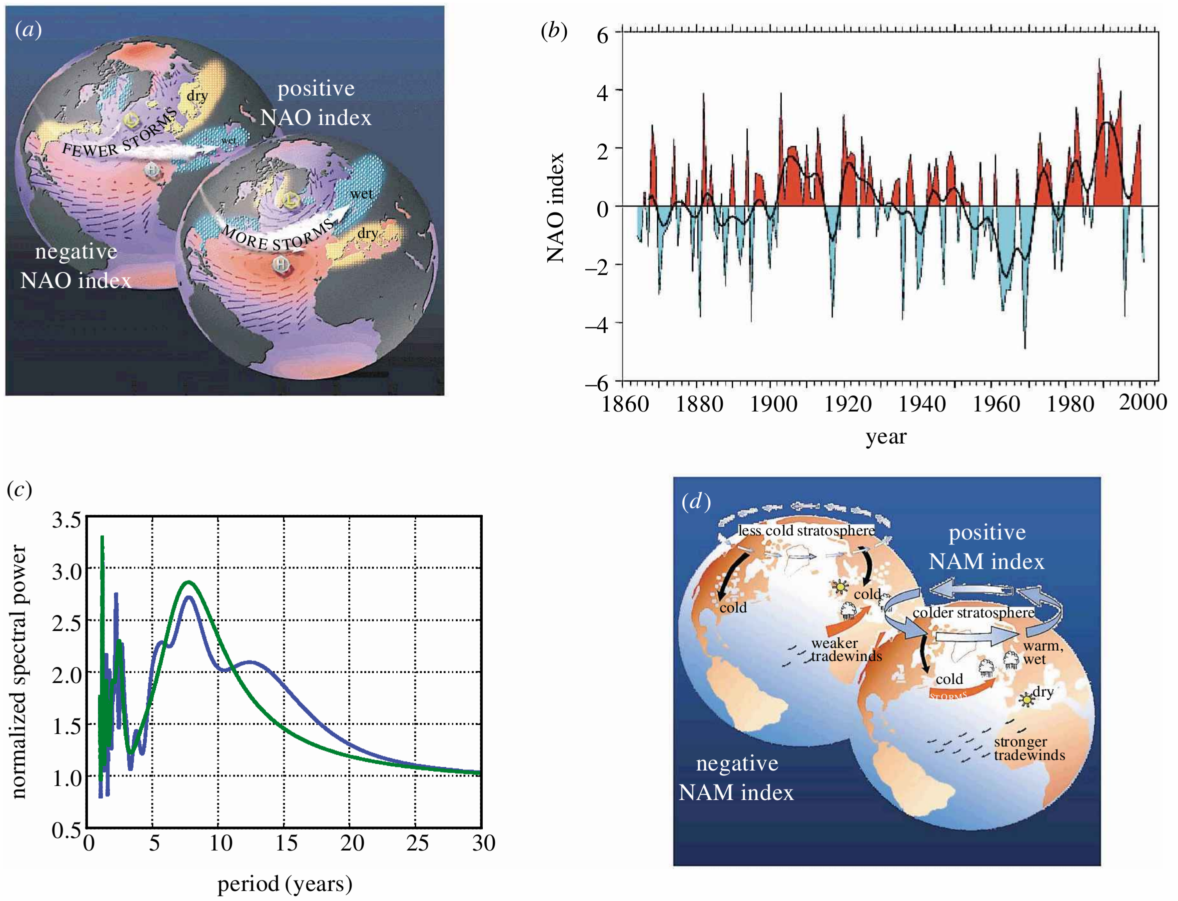

Figure 1. The North Atlantic Oscillation (NAO). (*a*) During positive (high) phases of the NAO index the prevailing westerly winds are strengthened and moved northwards causing increased precipitation and temperatures over northern Europe and southeastern USA and dry anomalies in the Mediterranean region (red and blue indicate warm and cold anomalies, respectively, and orange indicates dry conditions). Roughly opposite conditions occur during the negative (low) index phase (graph courtesy of Dr Martin Visbeck, http://www.ldeo.columbia.edu/~visbeck). (*b*) Temporal evolution of the NAO over the past 140 winters (index at http://www.cgd.ucar.edu/~jhurrell/nao.html). High (low) index winters are shown in red (blue) (Hurrell 1995). (*c*) Spectral decomposition. Periodogram (blue line) and maximum entropy (green line) for monthly values of the NAO index. Note the (weak) peak in the power spectrum at *ca.* 8 years (see also table 4 in electronic Appendix A and Pozo-Vazquez *et al.* (2000)). (*d*) The Northern Annular Mode (NAM)/Arctic Oscillation (AO). The left globe shows the positive phase with relatively low pressure over the polar region and high pressure at mid-latitudes, the right globe shows the negative phase (graph courtesy of Dr David Thompson, Colorado State University). Effects similar to those described in (*a*).

1997). Significant changes in ocean surface temperature and heat content, ocean currents and their related heat transport, and sea-ice cover in the Arctic and sub-Arctic regions are also induced by changes in the NAO.

During the so-called positive phase, there are higher than normal surface pressures south of 55° N combined with a broad region of anomalously low pressure throughout the Arctic and sub-Arctic. A positive NAO index (figure 1) is thus associated with a northward shift in the Atlantic storm activity, with enhanced storminess from southern Greenland across Iceland into northern Europe and a modest decrease in activity towards the south. Anomalous temperature variations include warming over Europe, Eurasia and over North America, with cooling over North Africa and the Middle East. Furthermore, drier-than-average conditions prevail over much of Greenland and the Canadian Arctic during high NAO-index winters, as well as over much of central and southern Europe, the Mediterranean and parts of the Middle East. By contrast, more precipitation than normal then falls from Iceland through Scandinavia. For a comprehensive overview of the NAO impacts, see Hurrell *et al.* (2003).

Because there is no unique way to define the spatial structure of the NAO (or any other climate pattern), it follows that there is no universally accepted index to describe the temporal pattern of the phenomenon. Most modern NAO indices are derived either from the simple difference in surface pressure anomalies between various northern (all on Iceland) and southern locations (table 2), or from the principal component (PC) time-series of the leading (usually regional) eigenvector of SLP. All of them are highly correlated, especially on seasonal and longer time-scales (Hurrell *et al.* 2003; Jones *et al.* 2003). Many examples of the former exist, usually based on instrumental records from individual stations near the NAO centres of action (e.g. Rogers 1984; Hurrell 1995; Jones *et al.* 1997), but sometimes from gridded SLP analyses (e.g. Portis *et al.* 2001). A major advantage of most of these NAO indices based on individual stations near the NAO centres is their extension back to the mid-nineteenth century or earlier, while a disadvantage is that they are fixed in space (i.e. they can only adequately capture NAO variability for parts of the year (Hurrell & van Loon 1997; Portis *et al.* 2001). An advantage of the PC time-series

Table 2. An overview of some of the most important indices on the NAO.
(Location of southern node of the dipole, period of time-series available at given Web site, temporal resolution, Web site address and reference for the index.)

southern node	geographical location (latitude; longitude)	years	temporal resolution	Web site for time-series	reference
Ponta Delgada	37°44′ N; 25°40′ E	1874–present	monthly	http://www-bprc.mps.ohio-state.edu/NAO	Rogers (1984)
Lisbon	38°45′ N; 9°5′ W	1864–present	December–March	http://www.cgd.ucar.edu/~jhurrell/nao.html	Hurrell (1995)
Ponta Delgada	37°44′ N; 25°40′ E	1865–present	monthly	http://www.cgd.ucar.edu/~jhurrell/nao.html	Hurrell (1995)
Gibraltar	36°08′ N; 5°22′ W	1821–present	monthly	http://www.cru.uea.ac.uk/cru/data/nao.htm	Jones *et al.* (1997)
PC1	20°–70° N, 90° W–40° E	1899–present	December–February	http://www.cgd.ucar.edu/~jhurrell/nao.html	
mobile by month	20°–80° N, 70° W–0°	1873–1995/ 1948–1999	monthly		Portis *et al.* (2001)

approach is that such indices are more optimal representations of the full NAO spatial pattern; yet, as they are based on gridded SLP data, they can only be computed for parts of the twentieth century, depending on the data source.

Several highly resolved proxy records of North Atlantic climate variability have been used to reconstruct the winter NAO index for the past (Cook 2003). Many have been based on information on tree rings from Europe and North America (e.g. Cook *et al.* 1998) or ice-core data from Greenland (e.g. Appenzeller *et al.* 1998). Recently, several multi-proxy reconstructions extending as far back as the fifteenth century have been published (Glueck & Stockton 2001; Cook 2003).

Since the NAO is most pronounced during winter and fluctuations during this time of year leave long-lasting imprints on surface conditions, in particular over the oceans and in terms of spring snowmelt, a winter index is well suited for studying both contemporaneous and subsequent ecological effects (see Post *et al.* 1999; Esteves & Orgaz 2001; Mysterud *et al.* 2001). However, ecologists interested in non-winter climate mechanisms may benefit from applying NAO indices derived for other times of the year. Examples include the seasonally and geographically varying 'mobile' NAO index of Portis *et al.* (2001) (see table 2), or the principal component time-series of the leading eigenvectors of seasonal SLP variability (see http://www.cgd.ucar.edu/~jhurrell/nao.html). Furthermore, indices of atmospheric variability can be obtained through nonlinear approaches, such as cluster analysis or nonlinear PCA (Monahan *et al.* 2000, 2001). Such approaches yield spatial patterns and time-series that differ from the more traditional (linear) approaches (see Hurrell *et al.* (2003) for an example related to the NAO), and these differences could be important for some studies.

4. EL NIÑO SOUTHERN OSCILLATION—THE PHENOMENON AND ITS INDICES

Fluctuations in tropical Pacific sea surface temperature (SST) are related to the occurrence of El Niño, during which the equatorial surface waters warm considerably from the International Date Line to the western coast of South America. The atmospheric phenomenon linked to El Niño is termed the SO, which involves exchanges of air between the eastern and western hemispheres centred in tropical and subtropical latitudes (figure 2). Whereas changes in tropical Pacific SSTs may occur without a swing in the SO, El Niño (EN) and the SO are linked so closely that the term ENSO is used to describe the atmosphere–ocean interactions throughout the tropical Pacific. Much of our understanding of the underlying physics of this coupled ocean–atmosphere phenomenon has evolved over the past several decades, beginning with the pioneering work of the late Jacob Bjerknes (1966, 1969).

The term 'El Niño' was used for centuries in reference to the annual occurrence of warm, southward-flowing oceanic current off the coast of Ecuador and Peru around the time of Christmas (Aceituno 1992; Trenberth 1997). More recently, this term has been associated with the large-scale warming that occurs every few years and changes the local and regional ecological conditions. It is this Pacific basin-wide phenomenon that forms the link with the anomalous global climate patterns, including the PNA (note that a list of large-scale climate patterns with acronyms is given in table 1) in the Northern Hemisphere and the PSA teleconnection pattern in the Southern Hemisphere (Kidson 1988; Kiladis & Mo 1998). 'El Niño', then, corresponds to the warm phase, while 'La Niña' refers to the cold phase of ENSO.

Quinn *et al.* (1978) provide a listing of El Niño events back to 1726, but only qualitatively based on the coastal phenomenon. Quantitative ENSO indices are based on SSTs averaged within defined areas (see table 3) spanning the equatorial Pacific. More recently, an ENSO index has been defined as the difference in normalized SST anomalies between various regions (the so-called Trans-Niño Index (TNI); Trenberth & Stepaniak (2001); see table 3). More complex instrumental indices, either based on statistical analyses of SST or SLP fields, or multivariate indices (Wolter & Timlin 1998) are also available (see table 4 in electronic Appendix A). Furthermore, reconstructions based on proxy variables such as tree rings extend the time-series substantially back into the past (e.g. Stahle *et al.* 1998; Allan & D'Arrigo 1999).

Table 3. An overview of some of the most important ENSO indices.
(Period of time-series available at given Web site, temporal resolution, description of index, Web site address and reference for the index.)

name	years	temporal resolution	definition	Web site for time series	reference
Southern Oscillation Index	1882–present	monthly	standardized difference of SLP between Tahiti (17°33′ S; 149°37′ W) and Darwin (12°28′ S; 130°51′ E)	http://www.cgd.ucar.edu/cas/catalog/climind/	Trenberth (1984)
Japan Meteorological Agency (JMA) index	1868–present	monthly	five month running mean of spatially averaged SST anomalies over the tropical Pacific between 4° S – 4° N; 150° W – 90° W	http://www.coaps.fsu.edu/~legler/jma_index1.shtml	Japan Meteorological Agency
Niño regions 1+2	1950–present	monthly	SST anomalies relative to a base period climatology (0–10° S; 90° W – 80° W)	http://www.cpc.ncep.noaa.gov/data/indices/index.html	
Niño region 3	1950–present	monthly	SST anomalies relative to a base period climatology (5° S – 5° N; 90° W – 150° W)		Trenberth (1997)
Niño region 3.4	1950–present	monthly	SST anomalies relative to a base period climatology (5°S – 5° N; 120° W – 170° W)		Trenberth (1997)
Niño region 4	1950–present	monthly	SST anomalies relative to a base period climatology (5° N – 5° S; 160° E – 150° W)		
trans-Niño index	1871–present	monthly	difference in normalized anomalies of SST between Niño-1 + 2 and Niño-4 regions	http://www.cgd.ucar.edu/cas/catalog/climind/	Trenberth & Stepaniak (2001)
multivariate ENSO index (MEI)	1950–present	sliding bimonthly	calculated from sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky, all observed over the tropical Pacific	http://www.cdc.noaa.gov/~kew/MEI/table.html	Wolter & Timlin (1998)

Various SO indices also exist, mostly based on SLP time-series data. The most common one is defined by the normalized SLP anomalies of Tahiti (17°33′ S; 149°37′ W) minus those of Darwin (12°28′ S; 130°51′ E; see table 3). During an EN event, SLP tends to be higher than usual at Darwin and lower than usual at Tahiti, making the SO index negative.

5. SOME OTHER CLIMATE PATTERNS AND INDICES

A somewhat confusing debate in the meteorological literature relates to the difference between the NAO and the Northern Hemisphere Annular Mode (NAM; Thompson *et al.* 2000; see figure 1)—earlier called the Arctic Oscillation (AO; Thompson & Wallace 1998). The NAM is defined as the first PC time-series of the mean SLP field over the Northern Hemisphere, north of 20° N. Its spatial expression, however, is dominated by the NAO structure over the Arctic and Atlantic sectors, and thus its index is highly correlated with indices of the NAO (generally 0.9 or higher for monthly and seasonal anomalies; see Deser (2000); Hurrell *et al.* (2003)). Whereas the debate over the NAO versus the NAM paradigm is of some interest to ecologists (see Aanes *et al.* 2002), it should be recognized that the distinction primarily has implications for interpreting the underlying dynamical mechanisms that give rise to NAO/NAM fluctuations (Wallace 2000).

One argument in favour of the NAM paradigm is its strong similarity to the spatial pattern of the AAO (Antarctic Oscillation), also referred to as the Southern Annular Mode (SAM), the leading mode of atmospheric circulation variability in the Southern Hemisphere (Gong & Wang 1998, 1999; Thompson & Wallace 1998, 2000; Wallace 2000). The AAO has by definition the opposite sign to the SAM. The AAO/SAM dominates the extratropical Southern Hemisphere circulation on weekly and monthly time-scales, and its high-index polarity is characterized by cold polar temperatures, low pressure over the polar cap, and strong circumpolar westerly flow approximately along a latitude of 60° S. Months corresponding to the low-index polarity are marked by anomalies roughly opposite in sign. The AAO index has shown a decreasing trend and a clear periodic component of 4–5 years since 1960 (figure 3*b*), and it seems to relate to the rainfall inter-annual variability in southern Chile (figure 3*c*,*d*).

On inter-annual time-scales, it is well recognized that large atmospheric circulation anomalies (especially over

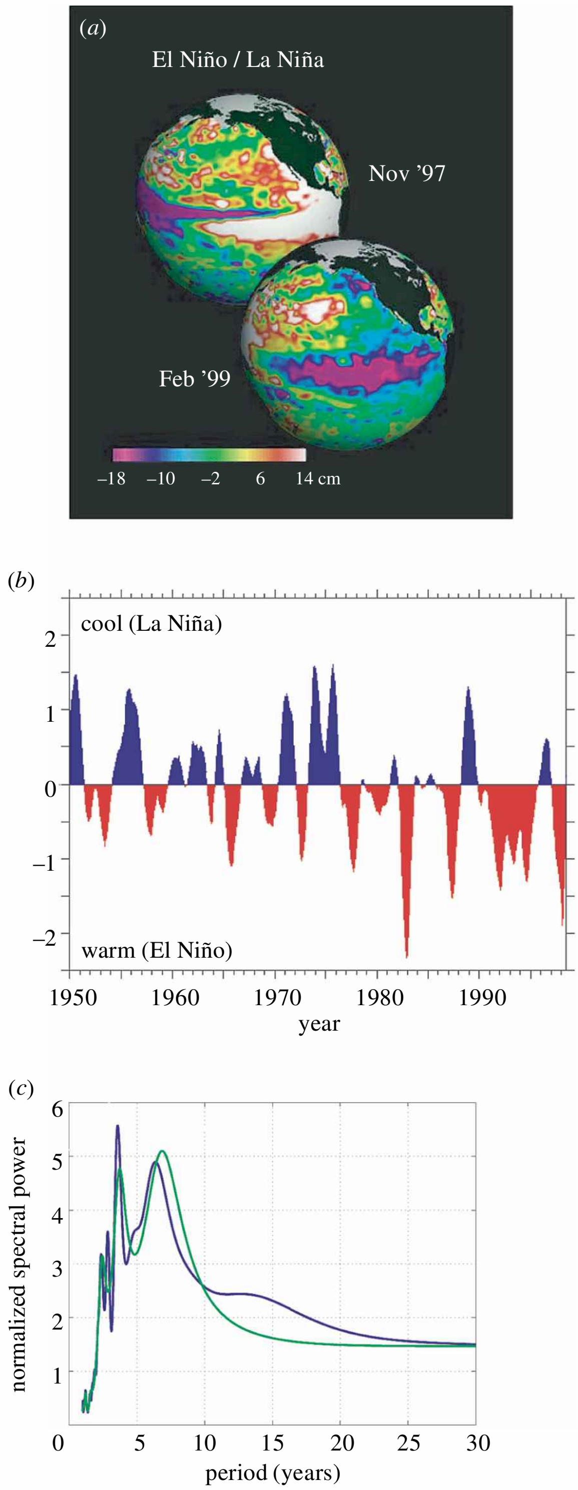

Figure 2. The El Niño Southern Oscillation (ENSO). (*a*) El Niño (upper left globe) and La Niña conditions. Red and blue indicate warm and cold anomalies, respectively, and orange indicates dry conditions (from Jet Propulsion Laboratory at http://topex-www.jpl.nasa.gov/science/el-nino.html, with permission). (*b*) Normalized Tahiti minus Darwin SLP anomalies (from http://www.cgd.ucar.edu/cas/catalog/climind/soi.html). (*c*) Spectral decomposition. Periodogram (blue line) and maximum entropy (green line) for monthly values of the Southern Oscillation index. See table 4 in electronic Appendix A for information on the spectral analysis.

the Pacific) are associated with ENSO (e.g. Trenberth *et al.* 1998). The PSA pattern in the Southern Hemisphere and the PNA pattern in the Northern Hemisphere can both be viewed as the extratropical arms of ENSO. Over the extratropics of the Northern Hemisphere, the NAO and PNA patterns are the most prominent and, like the NAO, the PNA is most pronounced during boreal winter. The PNA teleconnection pattern has four centres of action. Over the North Pacific Ocean, geopotential height (or pressure) fluctuations near the Aleutian Islands vary out-of-phase with those over the subtropical Pacific, forming an alternating atmospheric mass movement pivoted along the mean position of the Pacific subtropical jet stream. Variations in air pressure over western Canada and the northwestern USA are negatively correlated with those over the southeastern USA, but are positively correlated with the Aleutian centre. The significance of the locations and the respective phases of the four centres of the PNA are in their relation to the mean atmospheric circulation. Fluctuations in the PNA pattern 'represent variations in the waviness of the atmospheric flow in the western half-hemisphere and thus the changes in the north–south migration of the large-scale Pacific and North American air masses and their associated weather' (Kushnir 2001).

On inter-decadal time-scales, two benchmark indices of wintertime climate fluctuations over the North Pacific are the North Pacific (or Aleutian Low) index (Trenberth & Hurrell 1994) and the Pacific Decadal Oscillation (PDO) of Mantua *et al.* (1997). The former is defined by SLP anomalies averaged between 30° and 65° N over the Pacific, while the latter is defined as the leading principal component of SST anomalies north of 20° N. These two indices are, however, not independent of each other: the relationship is such that cooler than average SSTs occur during periods of lower than average SLP over the central North Pacific, and vice versa. A striking feature of the NP or PDO indices is the occurrence of extended periods (two to three decades in duration) of predominantly positive or negative departures from the long-term mean. Very little is known about the mechanisms producing these nominal 50 year variations.

6. THE CLIMATE–LOCAL WEATHER INTERFACE

To fully understand how climate influences ecology, we ought to understand the link(s) between climate (as picked up by indices discussed above) and local weather parameters, as well as the relationships between weather/climate and ecological processes and patterns. Unfortunately, the use of climate indices therefore adds another level of problems to an ecologist interested in elucidating the role of climate in ecological systems—the not always straightforward relationship between climate indices and local weather patterns. Among the important drawbacks, which all relate to the fact that climate operates mechanistically on ecological systems through local weather variations, are the following.

(i) *Spatial variation.* The weather response to a given value (or range of values) of a climate index typically depends on the geographical location.
(ii) *Seasonality.* Climate indices, by definition, reduce complex space and time variability into simple meas-

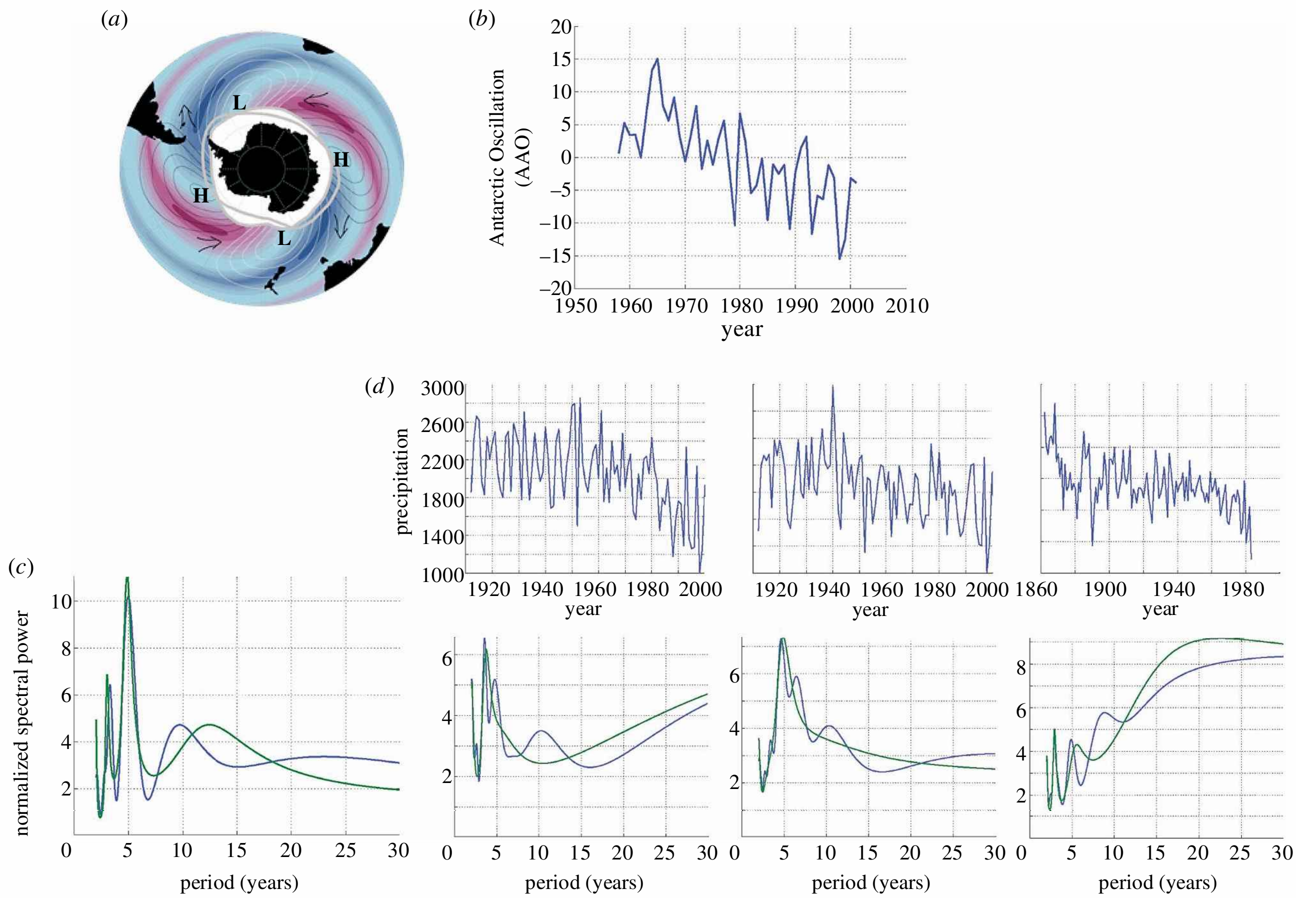

Figure 3. The Antarctic Oscillation (AAO). (*a*) The Antarctic circumpolar wave. Simplified schematic summary of interannual variations in sea surface temperature (red: warm, blue: cold), atmospheric sea-level pressure (H and L), meridional wind stress (denoted by the arrows) and sea-ice extent (grey lines). Sea-ice extent is based on an overall 13 year average. Downloaded from the CLIVAR Web pages (www.clivar.org). (*b*) Time-series of the AAO index; (c) Periodogram (blue line) and maximum entropy (green line) for yearly values of the AAOI. (*d*) Rainfall (yearly values) in three southern Chilean cities (Valdivia, Temuco and Puerto Montt in this order). Time-series in first row, last row the corresponding spectral densities. See table 4 in electronic Appendix A for information on the spectral analysis.

ures. It is important to realize that most months or seasons are not dominated by any particular climate regime in the extratropics.

(iii) *Non-stationarity*. The relationship between climate indices and local weather may vary over time (and therefore also the ecological responses), which is called non-stationarity (Hamilton 1994). There is little evidence for truly stationary periodic behaviour in the atmosphere, and the influence of climate patterns vary, sometimes significantly, over time. For example, in Flatanger (central Norway), Norway spruce (*Picea abies*) tree rings were not related to the NAO for the full period 1873–1997, but showed a negative relationship between growth and the NAO between the shorter period from 1920 to 1940 (Solberg *et al.* 2002). Furthermore, Barents Sea temperature (and thus ecological processes) was strongly linked to the NAO early in the previous century and from 1970 onwards, but in-between the connection was weak (Ottersen *et al.* 2003).

(iv) *Nonlinearity*. A nonlinear (and even non-monotonic) relationship between large-scale climate and local weather may alone be sufficient to produce a nonlinear (and even non-monotonic) relationship between performance of individuals and large-scale climate (Mysterud *et al.* 2001). Realizing that ecological processes may also respond nonlinearly to local weather, changes in climate may indeed give rise to unexpected effects due to either of the two nonlinear relationships. Which of the two is operating can unfortunately not be established without data on local weather patterns.

(v) *Lack of correlation*. Any single climate index may possibly explain only a relatively small part of the local climate variability. For some areas, it may be difficult to recommend the 'best' climate index for a particular study in advance. The performance of an index depends on the ecological question under consideration. For example, if the interest lies in fish populations off the Pacific coast of South America, then the most suitable index could be the Niño 1 + 2 SST time-series, even though the largest ocean signal could possibly be further west. One should use the climate index (or indices) 'picking up' most of the relevant climatic–weather variation for the specific ecological system under study.

Some precautionary remarks on the danger of spurious relations between climatic indices and ecological variables are in order. It is well known that strong temporal dependence in two independent time-series may induce spurious relations between the two series according to standard inference in an ordinary regression model (see Granger *et al.* (2001) and the references therein). This problem is further exacerbated in the setting of nonlinear models. One approach to avoid this pitfall is to pre-whiten the series before studying their relationship. More importantly, a statistically significant relationship is less likely to be spurious if the found relationship is consistent with some mechanistic link between the variables under study.

7. THE CLIMATE–ECOLOGY INTERFACE

Ecologists are faced with a difficult choice between two main approaches when studying the effects of climate on a particular ecological system; the traditional approach using local weather measures or the more recent approach using large-scale climatic indices such as those reviewed above. While local weather obviously has the advantage of being directly linked to mechanisms actually affecting the particular system, the use of (also) large-scale climate indices has the following advantages:

(i) *Spatial variation*. Climate indices point to a large-scale spatial correlation in weather patterns, which may be ecologically important by themselves, particularly so for marine ecosystems (Rodionov 1995; Schwartzlose *et al.* 1999). In terrestrial systems, it has helped to understand the spatial pattern of snow cover with respect to altitude. For example, on the west coast of Norway, temperature is a main determinant of whether precipitation falls as rain or snow. Because temperatures in coastal, low land regions are often *ca*. 0 °C during winter, and since temperature declines with altitude, altitude is a key factor determining whether precipitation falls as rain or snow (Mysterud *et al.* 2000).

(ii) *Model selection issues*. Climate indices provide an easy solution to the problem of how to select weather parameters. For example, common approaches in terrestrial ecosystems when using local weather is to use monthly (or seasonal) averages of at least temperature and precipitation (and snow depth for winter season), which may result in up to 10–20 weather variables. Many weather parameters are likely to have some relatively low and uniform correlations with the ecological phenomenon—a situation leading to the model being selected being highly stochastic (Mallows 1995). In that sense, using a large-scale index is similar to the use of principal components Regression (Hastie *et al.* 2001), where a PC analysis is first used to reduce the number of predictor variables. Furthermore, the fact that different weather variables are used among studies makes difficult any comparison of the importance of climate, but of course the fact that large-scale indices show spatial variation in their relationships to weather parameters may also hinder comparisons among studies. This is further complicated by the fact that climate effects may interact with other factors such as population density. In such cases, a proper understanding of a population system often requires an integration of knowledge about both the feedback structure (given by density dependencies; Royama (1992); Bjørnstad *et al.* (2001)) and the climatic variability (Stenseth *et al.* 2002).

(iii) *Predictability*. Ecologists have often been very interested in explaining what has happened, with a low rate of success in predicting the future. As some climate systems, to some degree, are predictable (see Allan *et al.* 1996; Hurrell *et al.* 2003), the use of climate indices may help biologists to be more successful in predicting ecological effects.

(iv) *Biological effects*. In many situations, the most important effects of the climate on individuals are the result of interacting weather variables. In such cases, a given large-scale climatic index may be a better representation of climatic effects than any single local weather variable.

(v) *Availability*. Last, but not least, most indices are easily obtained from the web or even long-time frames. For many areas, local weather station data are either not available or only available for a short period of time.

8. CONCLUSION

The application of climate indices, which by definition reduce complex space and time variability into simple measures, has helped ecologists appreciate the global nature of climate systems, and it has provided statistically tractable climate factors. Difficulties with this approach are related to the not always straightforward relationship between climate indices and local weather patterns. In addition, there have been too many examples in the literature of ecologists using climate indices not expected to correlate with local climate, and a lack of an ecological effect is therefore not surprising. In both cases, ecologists need a deeper understanding of climatology rather than simply using some arbitrary or much-used climate index. This review has been written in an effort to help further develop such an insight among ecologists.

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