Ecological processes and large-scale climate relationships in northern coniferous forests

Marc Macias Fauria

Academic dissertation

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Abstract

Ecological processes are controlled to varying degrees by climate. Large-scale climatic patterns (teleconnections) control the frequency of local weather phenomena over large regions (continents to hemispheres) and at different timescales (days to decades). This Ph.D. aims to explain how large-scale climate patterns synchronize a set of ecological processes northern coniferous forests (tree-ring growth, large area burnt by wildfire, and tree-mortality caused by mountain pine beetle) through controlling the frequency, duration, and spatial correlation of key local weather variables over large areas. Methodology was based on obtaining long complete ecological and climatic records and applying a variety of timeseries analyses in order to find out if climate and populations were related, and the nature and extent of such relationships, within a framework defined by knowledge on both the biological and the physical characteristics of the studied interactions. The description of the mechanisms through which such teleconnections control population traits is essential in these studies. Research on timeseries allowed the development of new methods to deal with highly autocorrelated data.

Overall, the studied processes were strongly related with and synchronized by large-scale climate. Mountain ranges played a major role in creating regional climatic gradients and thus strongly influenced relationships between climate and the ecological processes. Moreover, land use (grazing in this case) strongly affected the relationships between ecological processes (tree-growth) and climate. Relationships between climate and ecological processes were found to be highly dynamic and to have changed during the 20th century, driven in part by long-term climatic changes and by internal variability of large-scale climate patterns. Finally, an environmental multi-proxy reconstruction is presented using regional relationships between climate and proxy records.

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List of publications

This is an article dissertation based on the material and results presented originally in the following papers referred to in the text with Roman numerals I-VII:

I Macias, M., Timonen, M., Kirchhefer, A.J., Lindholm, M., Eronen, M. and Gutiérrez, E. 2004. Growth variability of Scots pine (*Pinus sylvestris*) along a west-east gradient across northern Fennoscandia: a dendroclimatic approach. Arctic, Antarctic, and Alpine Research 36(4): 565-574.

II Macias, M., Andreu, L., Bosch, O., Camarero, J.J. and Gutiérrez, E. 2006. Increasing aridity is enhancing Silver fir (*Abies alba* Mill.) water stress in its south-western distribution limit. Climatic Change 79: 289-313.

III Macias Fauria, M. and Johnson, E. 2007. Climate and wildfires in the North American boreal forest. Philosophical Transactions of the Royal Society B, doi: 10.1098/rstb.2007.2202.

IV Macias Fauria, M. and Johnson, E. 2008. Large-scale climatic patterns control area affected by mountain pine beetle in British Columbia, Canada. Submitted to Journal of Geophysical Research - Biogeosciences.

V Macias Fauria, M., Grinsted, A., Helama, S., Moore, J., Timonen, M., Martma, T., Isaksson, E. and Eronen, M. 2008. Reconstruction of winter maximum sea ice extent in the western Nordic Seas since AD 1200. Submitted to Journal of Climate.

VI Macias Fauria, M. and Grinsted, A., Helama, S., Holopainen, J. and Timonen, M. 2008. Estimation of the statistical significance of paleoclimatic and dendroclimatic calibration-verification statistics from autocorrelated time-series using Monte-Carlo methods. Submitted to Mathematical Geosciences (formerly Mathematical Geology).

VII Macias Fauria, M., Helle, T., Niva, A., Timonen, M. and Posio, H. 2008. Removal of lichen mat by reindeer enhances the growth of Scots pine. Submitted to Canadian Journal of Forest Research.

The author is responsible for data analysis, interpretation of results, and writing of the manuscripts. Co-authors provided the original data and reviewed the papers. In **Paper II**, Laia Andreu is responsible for much of the measurements (as well as the author), Oriol Bosch greatly helped in developing the chronology-level SNR analysis at varying spline lengths, and J. Julio Camarero is responsible for growth release analyses and Figure 7b. In **Paper VI**, Aslak Grinsted is responsible for most of the software development using Matlab, and Aslak Grinsted, Samuli Helama and the author are responsible for data analysis and interpretation.

1 Introduction: Large-scale climatic patterns and ecological processes

This Ph.D. aims to explain how large-scale climatic patterns synchronize a set of ecological processes — tree-growth, forest fires, and area affected by tree mortality caused by mountain pine beetle — in the northern coniferous forests, through the control of local weather variability over large areas.

1.1 Large-scale climatic patterns and ecological processes

Historically (up to the 1990s), the study of the relationships between ecological processes and climate was largely restricted to the assessment of the co-variability between a given index representing measurements of one of these processes and local weather parameters, such as precipitation (P), temperature (T), or snow depth (Stenseth et al. 2002). However, the coupling between climate and ecological processes is not restricted to the stand or study site level. Numerous studies report on long-distance synchrony in measurements of ecological processes and suggest that such synchrony might be due to some large-scale agent like climate, which causes spatially correlated environmental variability over large areas (Moran effect; Moran 1953). Examples of this are studies on tree-growth (e.g. Briffa et al. 2002; Andreu et al. 2007), plant phenology (e.g. Koenig and Knops 1998; Piovesan and Adams 2001; Schauber et al. 2002), or animal populations (e.g. Royama 1992; Ranta et al. 1997; Grenfell et al. 1998; Post 2003).

Moreover, climate research has identified and described over the last decades the mechanisms (or at least the patterns) behind large spatio-temporal correlation in local weather variations, such as the Arctic Oscillation (AO), the North Atlantic Oscillation (NAO), El Niño-Southern Oscillation (ENSO) or the Pacific Decadal Oscillation (PDO), among others (e.g. Van Loon and Rogers 1978; Trenberth and Paolino 1981; Wallace and Gutzler 1981; Hurrell 1995; Hare 1996; Mantua et al. 1997; Thompson and Wallace 1998, 2000). Internal atmosphere — and sometimes atmosphere-ocean — dynamics control the atmospheric wave and jet stream and produce recurrent spatial patterns of pressure, temperature, rainfall, storm tracks, wind speed, and/or jet stream location and intensity over vast areas (i.e. ocean basins and continents). These large-scale climatic patterns are called modes (e.g. Wallace and Thompson 2002) or teleconnections. Teleconnections operate at timescales that range from weeks to months, and are sometimes prominent for several years, representing an important part of the interannual to interdecadal variability of the atmospheric circulation. They are a naturally occurring aspect of our climate system, although it has been suggested that they might be the vehicle through which anthropogenic forcing of climate change operates (e.g. Corti et al. 1999; Visbeck et al. 2001).

Identification and description of teleconnections has enabled the calculation of indices that integrate a wide range of climatic variability over large areas and that can be tested against records of ecological processes. Increasing awareness among and interactions between biologists and climate scientists are rapidly advancing our insights into the issue of the response of ecosystems to climate variability and climate change (Stenseth et al. 2002).

The study of large-scale climatic patterns as a synchronizing force in ecological processes occurring in populations separated by long distances has recently re-gained interest in the context of global climate change (Ranta el al. 1997; Koenig and Knops 1998; Stenseth et al. 2002), as it suggests a regional-to-global mechanism through which climate might affect simultaneously widely distributed populations as well as multiple species (Post 2003). Using large-scale climate indices is thus central to the study of global change ecology (Forchhammer and Post 2004).

1.2 Causality and factors linked to synchrony in ecological processes

1.2.1 Causal mechanisms

Stenseth et al. (2002) pointed out the strengths and limitations of seeking for relationships between large-scale climatic indexes and ecological processes: while we are able to find and describe clear patterns occurring over large areas, there is in many cases a great uncertainty regarding the mechanisms that cause such patterns. That is, we need to explain how these spatially correlated climatic variations affect ecological processes and patterns. This is achieved through empirical knowledge of the physical and climatological system together with the physiology and ecology of the studied organisms. Moreover, there is no necessary link between the correlations we find and causality: while we can improve our confidence about the relationships we find through a series of statistical procedures such as bootstrapping, Monte-Carlo simulations, or via more sophisticated timeseries analysis tools like wavelet analyses and phase statistics (see Methods), results need to be sustained on mechanistic links between the ecological process and climate variability.

1.2.2 Proximal and ultimate causes

Individuals respond to local weather conditions such as temperature, wind, rain, snow, and ocean currents, as well as interactions among these. It is through the influence of large-scale climate systems on a set of local weather parameters over a large area that the relationships between ecological patterns and teleconnection indices take place. That is, local weather conditions are the proximal factors to which individuals respond, while large-scale climatic patterns are the ultimate factors of such responses (Post 2003). For example, on a study on the timing of flowering for three species in Norway, Post (2003) found March temperatures to be the proximal factor to which plants were related, while the Arctic Oscillation was the ultimate factor that synchronized March T over a large area and consequently was related to the synchrony in the timing of flowering.

1.2.3. Direct and indirect climatic effects

Local weather may affect individuals directly through their physiology (e.g. individual growth, metabolic rates, reproductive success or mortality), or indirectly through the ecosystem (for example, via trophic relationships and/or competition). Direct effects are the most obvious as they occur over the organism and on a single trophic level, and have generally no lag (e.g. Forchhammer and Post 2004), although not always, since, for example, storage of resources after a climatically favourable year in trees can affect tree-growth during the subsequent years, on top of trees' strong age-related growth trend (Fritts 1976). Indirect effects might be less noticeable and occur temporally lagged (Stenseth et al. 2002). For example, intrinsic density-dependence within populations can interact with climatic variability and originate complex population dynamics in which the climatic signal is difficult to disentangle (Turchin 1995). We thus we need to understand the density-dependent and density-independent structure of the biological system that might interact with climate (Stenseth et al. 2002). Finally, synchrony between spatially contiguous populations might arise from the dispersal capability of the individuals of these populations (i.e. a rise in population in one given area might spread trough other contiguous areas), through trophic interactions (Koenig 1999, Schwartz et al. 2002), or because of past common history between the populations. Thus, interpreting shared variability among populations as a sign of common response to climate needs to take into account these potentially confounding mechanisms.

1.2.4. Spatial and temporal scales of the studied interactions

Interaction between climate and ecological processes can occur at different spatial and temporal scales, which might remain unnoticed if data are not treated adequately. Knowledge about the underlying mechanisms of the interaction is in this case essential, as dimensioning the phenomenon we are interested in studying will define the characteristics of the data needed and the analysis to be performed. For example, the occurrence of a spatially correlated local weather event might not cause major changes over a population (e.g. a moderately cold night causing some mortality), but the iteration of such event during a series of consecutive years might have effects on the ecological process we are studying, causing a low-frequency relationship. Likewise, ecological processes might be controlled by climatic systems operating at very large spatial scales (e.g. the occurrence of persistent high pressure systems with sizes of thousands of km^2), and analyzing data over smaller spatial scales will not help in identifying patterns of synchrony in such ecological processes. Thus, spatial and temporal scales of both the physical and biological systems and of their interaction should ideally be defined prior to analyzing the data. Confidence in the relationships between climate and ecological records will largely depend on the spatial and temporal resolution, and on the length of the ecological and climatic records. High spatial and temporal resolutions will allow manipulating and organizing the data according to the spatial and temporal characteristics of the interaction we are aiming to study, whereas long ecological and climatic records will allow more complex and robust timeseries analyses.

In conclusion, the analysis of the influence of large-scale climate over ecological processes may be done through the careful selection and tuning of complex models that take into account all above-mentioned potential interactions (e.g., Stenseth et al. 1999; Forchhammer and Asferg 2000), or else through research on ecological phenomena sensitive to climate, but largely insensitive to indirect climatic effects (e.g. population density), dispersal, and other trophic interactions. Attributing synchronizing influence of large-scale climatic systems over a given ecological process should be based on mechanisms stemming from empirical knowledge about both the climatic and the biological system, and, as Post (2003) suggested, should be able to provide explicit links between large-scale climate, spatial correlation in local weather, and spatial synchrony in the measurements of the ecological process influenced by both. The use and development of new methods to jointly analyse climatic and ecological timeseries (in space, time, and frequency domains) is essential in the task of studying such couplings, as well as the interaction between biological and physical sciences.

1.3 The changing nature of the relationships between climate and ecological processes

The nature of large-scale relationships between climate and ecological processes is dynamic and so it greatly oscillates over a range of timescales (e.g. Ranta et al. 1997; Briffa et al. 1998; Vaganov et al. 1999; Barber et al. 2000; Biondi 2000). The reasons for such changes might be found in climate change-related responses of the individuals. For example, a strong precipitation increase over a given area might reduce or stop the drought signal in the tree-growth, or an oscillating precipitation regime might cause oscillating strength on the relationships between tree-growth and precipitation. Moreover, land-use changes, such as grazing, trampling, recreational uses, fishing, logging, mining, oil and gas development, among many others, can greatly affect such relationships over large areas by changing the physical structure and the composition of the systems (e.g. Kershaw 1978; Forbes et al. 2004; den Herder et al. 2003; Pavlov and Moskalenko 2003; Olofsson et al. 2004). Increasing anthropogenic disturbances, which act on top of the various natural (both physical and biological) disturbances to which ecological systems are adapted, may result in the systems entering a 'new ecological domain', that is, not recovering (Paine et al. 1998), with the consequent change in their relationship with climate. For example, Stenseth et al. (2002) report on the sudden crash in anchovy abundances as a result of an interaction between overfishing and unfavourable environmental conditions.

Such constant changing scenario, presently enhanced by human-caused disturbances at a global scale, makes it impossible to define the climax, stasis, or equilibrium over a given ecosystem (e.g. Raup 1951; Forbes et al. 2004). Without taking into consideration these potentially changing relationships, we reduce our ability to understand ecosystem's responses to climate and climate change, and we may also fail to successfully reconstruct past environments using long records of biological proxy data such as tree-rings.

1.4 Paleo-environmental studies

Interdisciplinary collaboration with geophysical scientists was constant and intense during this Ph.D. Such joint work has greatly improved the understanding of the interactions between ecological and physical processes, and has allowed the implementation of novel timeseries analysis methods. Moreover, it has produced scientific results beyond the pure research of ecological process vs. climate interactions, extending the Ph.D. into the field of paleo-environmental reconstructions. Paleo-environmental reconstructions are important in putting current environmental changes into a wider temporal context, and thus essential to understand ecosystem response and functioning. Moreover, paleoclimatology can also benefit from knowledge on current climate *vs.* ecological processes interactions when studying paleo-environmental data.

2. Brief description of the main tasks done in the papers

Paper I analyzed tree-growth variability and the dynamic relationships between climate and tree-ring width over a Scots pine (*Pinus sylvestris* L.) chronology network in the timberline region in northern Fennoscandia, located along a strong W-E continentality gradient. The role of land-use (grazing) in these relationships was studied in **Paper VII**.
Paper II analyzed tree-growth variability and the dynamic relationships between climate and

tree-ring width over a network of chronologies in the southernmost populations of European Silver fir (*Abies alba* Mill.), located along a strong climatic gradient due to the rainshadow effect of the Pyrenees Mountains: 5 chronologies were sampled in the mesic Main Ranges and 5 more in the drier southern Peripheral Ranges (Fig. 1, **II**).

Paper III described the mechanisms that originate large area burnt by lightning-caused fires in the North American boreal forest as a basis to suggest potential effects of climate change on wildfires. Being a review paper, it had no explicit methods: however, it was partly based on previous research done in my M.Sc. at the University of Calgary (Canada) and reported in Macias Fauria and Johnson (2006). Large lightning-caused fires are a substantial ecological process in the boreal forest of North America as they allow forest recruitment and control its stand age and species composition. The concepts of fire ecology relevant to the study are summarized in results and further explained in **III**.

Paper IV analyzed the synchrony of area affected by mountain pine beetle (MPB; *Dendroctonus ponderosae*)-caused tree mortality in British Columbia (BC), western Canada, using a spatially explicit database, as well as its relationships with local and large-scale climate.

Paper V consists on a multi-proxy reconstruction of April sea ice extent in the western Nordic Seas combining tree-ring chronologies from the timberline area in Fennoscandia and $\delta^{18}O$ from the Lomonosovfonna ice core in Svalbard. Special attention was put on the quality and autocorrelation of proxy *vs.* environmental data relationships during the overlapping period, exploring possible tests of significance for reconstruction statistics. Reconstructed sea ice variability was analyzed in the context of the main climatic drivers in the area.

Finally, **Paper VI** is a purely methodological paper which explored a new procedure to confidently calculate climatic reconstruction statistics from highly autocorrelated data. More information on this method is available in Methods and in Results, as well as in **VI**.

3. Data

3.1. Selection of the ecological processes: characteristics of the data-sets

Three ecological processes were selected to maximize their climatic signal and minimize indirect climatic effects, dispersal, and trophic interactions. These are:

- Ring-width growth variability from Scots pine (*Pinus Sylvestris* L.; **I**, **V**, **VI**, **VII**) in the timberline area of northern Fennoscandia and European silver fir (*Abies alba* Mill.; **II**) in its south-western distribution limit (Pyrenees and nearby ranges).
- Area affected by tree mortality caused by mountain pine beetle (*Dendroctonus ponderosae*; **IV**) in its northern distribution limit in North America (British Columbia, Canada).
- Area burnt by wildland fire in the boreal forest of North America (**III**).

Generally, analyses involved large-scale spatial networks of timeseries of ecological and climatological measurements, spanning the longest period and the highest spatio-temporal resolution possible, and overlapping in time. Climatic influence in the ecological process was maximized by collecting data close to the geographical distribution limit of species (e.g. Root 1988). Overall, the main idea present in most works of this study is that synchrony between ecological records was largely caused by climate.

3.2. Environmental data

3.2.1. Ring-width series: Scots pine from Northern Fennoscandia and European Silver fir from the Pyrenees

Tree-ring data for northern Fennoscandia (**I**) consisted on a network of 21 existing ring-width chronologies: 14 had been previously published (Lindholm 1995, 1996; Kirchhefer 2000, 2001), whereas 7 were built by Mauri Timonen in 2001, and were unpublished at the time the study was carried out. Tree-ring data for the long northern Lapland regional chronology (**V**, **VI**) had been described in Eronen et al. (2002) and Helama et al. (2002). Tree-ring data from a NE Fennoscandian stand (**VII**) was collected for that study by Timo Helle and Aarno Niva. Finally, tree-ring data for the Pyrenees (**II**) consisted on 10 chronologies produced for that study.

Tree-ring width series show a clear age-related decreasing trend, as well as a high degree of temporal autocorrelation, most evident in the timberline sparse forests of northern Fennoscandia (**I**, **VII**). Moreover, logging history, stand density, or other disturbances (e.g. insect outbreaks) might also disrupt the climatic signal (e.g. intense logging in the Pyrenean fir forests until mid-20th century caused strong growth releases in the ring-width chronologies, **II**). On the plus side, tree-ring width measurements are free of potential dispersal effects, and long records are relatively easy to obtain.

3.2.2. Large fire data: area burnt in Canada and Alaska

Although being a review study, **Paper III** was partially based on a database of lightning-caused large (>200ha) fires for Canada and Alaska (1959 -1999), obtained from the Canadian Large Fire Database (Stocks et al. 2003) and the Alaska Historical Fire Database (Bureau of Land Management, Alaska Fire Service).

Contrary to the other processes considered in this Ph.D. (which are biologically-based), forest fires are physically-based phenomena, and logically area burnt data poses no problems neither in dispersal (at a continental scale) nor in density-dependence or any potential trophic interactions. Log-transformation of the area burnt data is recommended due to the high correlation between mean and variance. Long and spatially large records of such data are difficult to obtain and early records are unreliable at regional scales due to the fact that most areas in northern Canada and Alaska were not monitored until the second half of the 20th century.

3.2.3. Mountain pine beetle: area affected by tree mortality caused by mountain pine beetle in British Columbia, Canada

Spatially explicit records of area affected by MPB-caused tree mortality in British Columbia (**III**) consisted of province-wide aerial surveys of forest insect outbreaks for the period 1959–2004. During 1959-1996, data was collected by the Forest Insect and Disease Survey, Canadian Forest Service, and since 1996, data collection was assumed by the BC Ministry of Forests.

The data was interpreted as a proxy for the population numbers of mountain pine beetle. Heteroscedasticity of data suggested it should be log-transformed prior to analyses. As with area burnt, long records of area affected by mountain pine beetle are difficult to obtain, early records being unreliable at a regional scale as many areas were not monitored until the second half of the 20th century.

3.2.4. Phenological data for south-western Finland

Plant phenological data from south-western Finland (Holopainen et al. 2006) was used as an example of a paleoclimatic timeseries in the methodological **Paper VI**.

3.2.5. Data on sea ice extent in the western Nordic Seas and ice core data from Svalbard

Records of sea ice extent in the Nordic seas were collected by Vinje (2001), and the $\delta^{18}O$ series from Svalbard was obtained by Isaksson et al. (2001; **V**).

3.3. Climatic data

3.3.1. Indices of teleconnection patterns

Several teleconnection patterns operating over the Northern Hemisphere were considered in the study of the relationships between climate and ecological processes. Their main characteristics are described in the Papers where they were used, and a short description is provided in here:

Arctic Oscillation (AO)/ North Atlantic Oscillation (NAO) — **I**, **III**, **IV**, **V**, **VII**

The Arctic Oscillation (AO) or northern annular mode (NAM; Trenberth and Paolino 1981; Wallace and Gutzler 1981; Thompson and Wallace 1998, 2000) is defined as the dominant pattern of sea-level pressure (SLP) variations north of 20°N and is characterized in its positive (negative) phase by negative (positive) SLP anomalies in the Arctic and positive (negative) anomalies at mid-latitudes (Fig. 5, **III**). AO index correlates strongly with northern hemisphere and Eurasian temperature anomalies (Thompson and Wallace 1998).

The North Atlantic Oscillation (NAO) is a large-scale meridional seesaw between the Icelandic Low and the Azores High (Van Loon and Rogers 1978). NAO indices are calculated by computing the difference between the SLP in these two areas: positive NAO situations imply large SLP differences between the two air masses and strong westerly winds in the north Atlantic region. A positive (negative) NAO is thus associated with strong (weak) moist and mild air advection and consequently wetter (drier) and warmer (colder) weather in Northern Europe (Hurrell 1995).

The NAO may be regarded as a subset of the spatially broader AO (the AO being a hemispheric version of the more regional NAO; Thompson and Wallace 1998; Deser et al. 2000). They are essentially equivalent in the Atlantic sector. Although the NAO and the AO operate throughout the year, the greatest variability is seen during winter (Hurrell 1995). Besides having a high inter-annual variability, they also exhibit low-frequency variability and are strong determinants of both interannual variation and decadal trends in temperatures and precipitation in northern latitudes: the last 25 years of the 20th century were characterized by an unrecorded series of high positive NAO/AO values (Hurrell 1995). Persistent positive NAO/AO situations were predicted by climate models as a consequence of human-caused increases in CO2 and CH4 atmospheric concentration (e.g. Thompson et al. 2000; Gillett et al. 2004). However, the NAO/AO system has shown an episodic behaviour since the end of the 1990s (Overland and Wang 2005).

Pacific Decadal Oscillation (PDO)/ El Niño-Southern Oscillation (ENSO) — **III**, **IV**

The PDO is the leading mode of monthly sea surface temperature (SST) in the North Pacific Ocean north of 20°N (Fig. 6, **III**; Hare 1996; Mantua et al. 1997; Zhang et al. 1997). It is manifested by a low-frequency pattern of SST over the Tropical and North Pacific Ocean — PDO events have persisted for 20 to 30 years during the 20th century — and it is strongly linked to the atmospheric circulation over North America and the North Pacific, as commonly expressed by the Pacific North American (PNA) index (Mantua et al. 1997). Warm (cool) PDO phases are characterized by a strengthened (weakened) Aleutian low, enhancing (reducing) the advection of warmer air onto the west coast of North America and causing positive (negative) temperature anomalies over northern North America, with the largest anomaly located over central Canada (Minobe 1997; Mantua and Hare 2002). Moreover, warm PDO phases tend to produce persistent high-pressure anomalies over northern North America, especially over western Canada and Alaska (Zhang et al. 1997). Finally, the PDO is related to SST, precipitation and convection variability in the Indian and tropical Pacific Oceans, and its spatial climatic patterns are similar to the ENSO pattern (Mantua et al. 1997; Zhang et al. 1997): it can be thought of as a long-lived El Niño-like pattern of Pacific climate variability. The physical mechanisms responsible for the PDO are yet not fully understood (Mantua and Hare 2002).

Low Frequency Oscillation (LFO) — **V**

Although not being a proper teleconnection pattern, the Low Frequency Oscillation (LFO) is referred in here because this long-wave Arctic climatic pattern was observed to be an important component in the reconstructed western Nordic Seas sea ice variability (**V**). Low-frequency interdecadal variability (~50-80yr), is seen in a large part of the observed environmental variability in the Arctic during the last century and a half (e.g. Polyakov et al. 2003; Divine and Dick 2006) and has been linked to the thermohaline circulation in the north Atlantic (Polyakov and Johnson 2000) and to multi-decadal variability in Atlantic Ocean SST (Atlantic Multidecadal Oscillation – AMO; Delworth and Mann 2000; Polyakov et al. 2004). However, direct observational evidence on these long cycles is very limited, and modelling using coupled global circulation models (GCMs) shows rather ill-defined power on these timescales (Knight et al. 2005).

3.3.2. Local climate data: temperature, precipitation, and date of snowmelt

Monthly temperature and precipitation, as well as records of the number of days with snow on the ground for Fennoscandia (**I**, **VI**, **VII**) were obtained from the NordKlim data set (Tuomenvirta et al. 2001). Paper II used monthly T and P series for the Pyrenean area from the National Institute of Meteorology of Spain (INM). Daily T and monthly P for western Canada (**IV**) were obtained from Environment Canada, and the 50km-gridded monthly P and T dataset CANGRID for Canada (Zhang et al. 2000) was obtained from the Meteorological Service of Canada.

4. Methods

Methodology mainly dealt with timeseries analyses. Both ecological and climatic data form timeseries, that is, a sequence of observations usually spaced at uniform intervals. Timeseries analyses do not constitute a fixed set of methods and are mostly defined by the subject being analyzed (Grinsted 2007). Methods relevant to this Ph.D. and mentioned in this section belong in this field.

4.1. Dendrochronology — I, II, V, VI, VII

4.1.1. Cross-dating

Cross-dating is the procedure of matching variations in ring-width or other ring characteristics among several tree-ring series, allowing the identification of the exact year in which each tree-ring was formed (Fritts 1976). It is an essential step prior to any dendrochronological study. Visual cross-dating is done by identifying conspicuous years which help comparison between the series; statistical comparison is performed by inter-series correlations (Holmes 1983).

4.1.2. Standardization and chronology building

Removal of the age-related growth trend in tree-ring series, as well as of other growth variations that might mask the information we are aiming to obtain, is normally performed by dividing or subtracting each individual series by a smoothing function (e.g. negative exponential, cubic smoothing spline; Cook and Peters 1981). This procedure produces dimensionless tree-ring indexes for each individual series that can be averaged into a mean chronology: in averaging, variations present only in a few trees non-related to a common (climatic) signal are expected to be reduced, and the common signal within the chronology is strengthened. A bi-weight robust mean can be used in the averaging process instead of the simple arithmetic mean in order to reduce the effect of potential outlier values in the group of individual series (Cook 1985). The mean chronology arising from this procedure is called standard. Standard chronologies are autocorrelated due to the effect that the growth performance of one year has in the growth performance of the following years on trees (physiological preconditioning; Fritts 1976). Such autocorrelation can be further removed by auto-regressive-moving average models (ARMA; Cook 1985), producing white noise series (residual chronologies), which are useful in assessing the influence of one year's climate on tree-growth on that year.

Smoothing functions effectively remove long-term age-related tree-ring variability. If flexible enough (**II**) they might also remove relatively abrupt growth disturbances. However, they also remove relevant climatic information occurring at the same or longer timescales than the process we aim to eliminate. Thus, a trade-off exists between removing what we consider noise and what we want to preserve: this is not a problem if we don't aim to use tree-ring data as proxy to perform climatic reconstructions, or to assess long-term tree-growth trends.

Moreover, even the most rigid curve-fitting (negative exponential curve; **I**, **VII**) will remove all variability at longer wavelengths than the length of the series. This was termed the *segment length curse* (Cook et al. 1995), and might constitute a problem when reconstructing past climatic variability from long tree-ring chronologies built from overlapping segments of cross-dated ring-width series (as in **V**). Such problem can be surmounted by the application of the Regional Curve Standardization (RCS) procedure (Erlandsson 1936; Fritts 1976; Briffa et al. 1992, 1996; **V**, **VI**), specifically designed to preserve low frequency variability in tree-growth chronologies. RCS is based on the idea that trees of the same species growing within a homogeneous region share a single idealized model of tree-age ring-growth, which can be estimated if a large number of trees are used. Applying the time-invariant RCS growth model as the expectation of ring-width at any particular tree age allows the overall level of tree-growth at any particular time to systematically over- or underestimate the curve when climate causes the rate of tree-growth to exceed or reduce the expected growth rate (Helama et al. 2002), preserving long-term variability.

4.1.3. Dendroclimatology

Correlation and response function analyses are empirical models commonly used to describe the statistical relationships between climate and dendrochronological records. The term 'function' indicates a sequence of coefficients computed between the tree-ring chronology and the monthly climatic variables (Biondi and Waikul 2004). The coefficients in correlation functions are univariate estimates of Pearson's product moment correlation (Morrison 1983). The response function (Fritts 1976) avoids the problem of multi-colinearity, commonly found in multi-variable sets of meteorological data, by performing a stepwise multivariate regression between the pre-whitened tree-ring indices (residual chronology) and the principal components of the monthly climatic predictors. Finally, pseudo-datasets may be produced by random sampling of the data (artificially increasing its sample size) so as to test the significance of each monthly variable (bootstrapping; Till and Guiot 1990): bootstrapping might be applied to both correlation and response functions.

Evolutionary response and correlation functions (Biondi 1997; 2000) were used to assess temporal changes in growth/climate relationships (**II**, **VII**). **Paper I** was written before this technique was reported, and simply divided the studied period into 2 sub-periods for such analysis. Finally, running correlations have been applied in several occasions when the data were univariate (**V**, **VII**).

4.2. Paleoclimatic reconstructions — V, VI

The overall methodology of climatic reconstructions can be found in detail in the methodological **Paper VI** (e.g. Fig. 1, **VI**). In short, a paleoclimatic reconstruction starts with a model of the relationship between the proxy data and the climatic or environmental data to be reconstructed (transfer function; Fritts 1976), involving in most cases a simple or multiple linear regression. The time frame over which such relationship is modelled is called full calibration period. Ideally, the validity of the calibration should be tested using independent data not used in the training process. Hence, the full calibration period is typically divided into 2 sub-periods (calibration and verification periods). The model parameters are optimized over the calibration period and the predictive skill is tested over the verification period: this is important as it may reveal potential over-fit of the calibration model or decreased sensitivity to climatic variations over the non-calibrated period. Finally, this process can be re-done by considering the old verification period as a new calibration period, and the old calibration period as a new verification period: such a procedure is called cross-calibration-verification.

4.3. Advanced timeseries analyses

4.3.1. Autocorrelation and its implications in the assessment of climate-ecological process relationships —IV, V, VI

Short timeseries and autocorrelation reduce the amount of independent observations in the data. Consequently, conventional statistical methods (e.g. Pearson correlation and statistics commonly used to assess the robustness of dendroclimatic reconstructions) may be analytically intractable due to appropriate assumptions not being satisfied. Moreover, many reconstruction statistics lack of proper significance tests. Working with such timeseries fostered the development of a new method to estimate the significance of ecological (or proxy) *vs.* climatic data relationships, based on combining autoregressive modelling and Monte-Carlo simulations. The method is explained in detail in the methodological **Paper VI**, and will not be further discussed in here.

4.3.2. Time-frequency domain methods —V, VII

Traditional timeseries methods (e.g. regression, but also correlation and response function analyses) assume that data come from linear systems and stationary processes, and will not be further commented. However, timeseries from climate and ecological systems are (and interact) non-linear in many cases, and exhibit non-stationarity (i.e. time-varying probability distribution functions of their relevant statistics).

Moreover, timeseries might be analyzed in the temporal and frequency domains. The assumption of stationarity can be partially overcome by applying successive moving windows (e.g. moving averages or correlations). Applying moving temporal windows to frequency methods (e.g. moving Fourier transforms) permits the joint analysis of frequency and time domains. However, this is an inaccurate and inefficient method due to the aliasing of high- and low-frequency components that do not fall between the frequency range of the window and to the fact that a window of a given size will sample more short wavelengths oscillations than long (Torrence and Compo 1998).

Continuous wavelet transform (CWT) attempts to solve these problems by decomposing the timeseries into time-frequency space simultaneously, determining not only the dominant modes of variability but also how these modes vary in time. A wavelet is a function with zero mean and localized both in time and frequency space (Farge 1992). CWT applies the wavelet as a series of band pass filters to the timeseries: it has the advantages of not assuming stationarity and of a readily visible region affected by boundary conditions (Torrence and Compo 1998). In this Ph.D., a Morlet wavelet approach was used following Grinsted et al. (2004). CWT is a powerful tool for analyzing intermittent oscillations in a time series (Fig. 5, **V**), whereas cross-wavelet transform (XWT; Fig. 4, **V**) calculates the common power between two series and their relative phase in the time-frequency space, and wavelet coherence transform (WCT; Fig. 4, **V**) measures the coherence of the cross wavelet transform in the time-frequency space. WCT is usefully thought of as a localized correlation coefficient in the time-frequency space. Monte Carlo methods were used to assess the statistical significance against a red noise background, following Grinsted et al. (2004).

Wavelet methods were designed for long records with many data points, such as many geophysical records. When records were short (**IV**), high- and low-pass running average filters were applied to obtain a minimum and purely explorative frequency resolution (e.g. interdecadal *vs.* interannual variability).

5. Results and discussion

5.1. Tree-ring width and climate in Northern Fennoscandia — I, VII

Radial tree-growth in northern Fennoscandia was significantly related to July T (as in Briffa et al. 1988; Lindholm 1996; Kirchhefer 2001), spring T and P, and, to a lesser degree, autumn T prior to the growing season (Tab. 5, **I**; Fig. 6, **VII**). High early summer T enhance the formation of a wider cambial zone, with higher cell production through the growing season and thus a wider ring (Vaganov et al. 1999). Spring climate controls soil warming, and consequently the timing of the start of the growing season (e.g. Bonan and Shugart 1989; Hollinger et al 1999; Vaganov et al. 1999): spring T was highly related to the date of snowmelt in northern Fennoscandia, whereas May P was more probably related to soil-warming rain once the snow had melted. Finally, autumn cold spells might damage trees through the occurrence of early winter deep soil freezing and thus potential root damage or severe water stress (e.g. Benninghoff 1952; Bonan and Shugart 1989).

The North Atlantic Oscillation (in particular in early winter prior to the growing season and late spring) showed a strong link with tree-growth (Tab. 6, **I**; Tab. 3, **VII**). NAO/tree-growth relationships occurred over the whole chronology network. The NAO correlates local weather parameters important for tree-growth over northern Fennoscandia, such as spring and autumn temperatures.

The spatial dimensions of the chronology network, and the presence of the Scandes mountains dividing the studied area, enabled the identification of growth differences between the Norwegian and Finnish chronologies (Fig. 3, **I**), attributed to a strong gradient of continentality caused by the trapping of North Atlantic mild and wet air masses by the mountain ranges. Moreover, the dimensions of the chronology network (spanning distances over 500km; Fig. 1, **I**) permitted the study of the NAO influence on tree-growth at a northern Fennoscandian scale: overall, chronologies showed high correlations, even at long distances. However, a larger network size (e.g. one extending east into Siberia or even a pan-boreal dendrochronological network) would have allowed the investigation of different large-scale patterns of tree-growth synchrony, and to define limits of NAO-related forest areas.

5.1.1. Temporal changes

Tree-ring data in **I** spanned the period 1880-1991, whereas the more recent dendrochronological data in **VII** covered the period 1864-2003. The 12yr difference in last year of record implied that trends found in the climate/growth relationships in I were partially outdated in **VII**.

The signal of July T weakened towards the end of the 20th century (Fig. 6, **VII**). **Paper I** did not assess temporal changes in the strength of tree-growth/July T relationships, so this result is restricted in the Ph.D. to the study case of a stand of NE Fennoscandia (VII). Exploratory analyses performed with the chronology network showed a general decreasing July T signal over the region, also reported in Briffa et al. 1998. Such phenomenon is known as the divergence problem of northern forests (e.g. D'Arrigo et al. 2007). Delayed snowmelt due to higher winter precipitation, and consequently delayed and shorter growing seasons was proposed as the cause of such divergence in Eurasia (Vaganov et al. 1999). Our data supported this idea.

Relationships between the NAO and tree-growth were unstable and dropped in the second half of the 20th century (Tab. 6, **I**). The more recent data in **VII** (final year 2003 instead of 1991) revealed that such relationship recovered in the last 2 decades of the 20th century.

Finally, W-E growth differences were also dynamic and increased during the 2nd half of the 20th century (up to 1990). This was interpreted as a stronger climatic gradient between Norway and Finland. That is, at least some climatic parameter significant to tree-growth diverged between both sides of the Scandes during that period.

5.1.2. The impact of reindeer grazing on tree-growth

Trees growing in the grazed part of a previously ungrazed forest stand in NE Fennoscandia showed larger tree-growth than those in the ungrazed part of the stand (Fig. 4, **VII**). Removal of the lichen mat by reindeer grazing increased the coupling of soil T at depths up to 20cm with air T, causing faster soil spring warming and autumn cooling, higher summer and lower winter T, and deeper soil frost in winter (Fig. 2 & 3, **VII**). An earlier start of pines growing season due to faster spring soil warming in the grazed part of the stand was suggested to enhance tree-growth. Larger tree-growth started a decade after lichen removal: this delay was attributed to the reorganization of newly exposed roots right after the first grazing event.

Trees in the ungrazed part of the stand were more strongly related to spring T and P (i.e. snowmelt and associated soil warming; Fig. 6, **VII**). Although this was a case study, the high agreement between spring NAO, date of snowmelt, and tree-growth, together with the widespread grazing activity over northern Eurasia, suggests that such process might occur synchronously over large areas, and provides evidence that land-use (grazing in this case) can be an important component in climate/taiga interactions, and thus on carbon uptake by boreal forest trees. The rarity of stands where the differential effects between trees growing in grazed and ungrazed terrain can easily be measured limits the otherwise convenient possibility of performing such studies over a large area.

5.2. Tree-ring width variability in the Pyrenees — II

The frequent and abrupt growth releases from logging events in Pyrenean Silver fir stands were treated by a trade off between selecting the most flexible standardization method and the maximum inter-chronology common signal (climatic signal) possible. Chronology variability was thus restricted to high time frequencies (decadal to annual): ecological data quality limited in this case the information that could be extracted from it.

Radial fir growth in its south-western distribution limit was related to September T prior to the growing season (negative) and late summer P prior to the growing season (positive; as in Rolland 1993; Desplanque et al. 1998; Rolland et al. 1999; Tab. 4, **II**). Moreover, radial growth also responded positively to July P in the chronologies located in the drier Peripheral Ranges. Such tree/climate patterns agree with the "drought-avoidance" strategy of the species (Rolland et al. 1999; Aussenac 2002). Indeed, silver fir has lower water-use efficiency than other fir species from more xeric areas (Guehl and Aussenac 1987; Guehl et al 1991).

All pairs of chronologies were highly correlated, and common variability was interpreted as a regional response to summer drought stress experienced by trees in all stands. Moreover, chronologies from trees growing in the mesic conditions of the Main Ranges could be distinguished from chronologies in the drier Peripheral Ranges in their different chronology statistics and response to climate. As with the study in northern Fennoscandia, the spatial dimensions of the network (inter-forest distances up to ~300km; Fig. 1, **II**) were large enough to detect the influence on tree-growth of climatic gradients due to the presence of mountain ranges (Pyrenees) and their role in trapping moisture from the Atlantic Ocean, creating a strong rain-shadow effect over the southern Peripheral Ranges. A larger network (e.g. continental or distribution-wide) would have probably allowed defining the limits of the area over which fir's drought response occurs, which was not however the initial purpose of the study.

5.2.1. Temporal changes

Inter-series correlations significantly increased (Fig. 4, **II**) and showed a trend towards not decreasing with distance along the 20th century (Fig. 5, **II**). This was interpreted as an intensified common response to large-scale climate. Indeed, climatic data showed a warming trend in the second half of the 20th century across the Pyrenees, with more severe summer droughts (Fig. 7, **II**). The longer dataset of Pic du Midi (2880m.a.s.l.) indicates that such trend has occurred during the whole 20th century. Increased water-stress response (i.e. extended period of response to drought; Fig. 8, **II**) and higher year-to-year variability (especially in the Peripheral Ranges; Fig. 6, **II**) further suggested this.

5.3. Climate and wildfires in the North American boreal forest - III (Review Paper)

Area burned by large fires in the North American boreal forest is controlled by the frequency of persistent positive mid-troposphere anomalies (>10 days), characterized by lack of precipitation and prevailing meridional flow of warm air that cause rapid fuel drying. Fuel dryness, as measured by the Canadian Fire Behaviour System (e.g. Johnson and Wowchuk 1993), strongly associates with blocking highs, providing a causal explanation for large fire occurrence. Ultimately, the dynamics of large-scale teleconnection patterns (Pacific Decadal Oscillation/El Niño Southern Oscillation and Arctic Oscillation) set the frequency and location of blocking highs over the continent at different timescales, controlling area burned on the North American boreal forest (Macias Fauria and Johnson 2006): thus, an increase in T alone need not be associated with an increase in area burned.

5.3.1. Temporal changes

Climate has been moist and variable since the end of the Little Ice Age, with large fire years occurring in unusual years and decreased fire frequency. Prolonged and severe droughts were common in the past and were partly associated with changes in the PDO/ENSO system, characterized by common large fire years and increased fire frequency. Constantly changing fire regimes imply that the term 'natural fire regime' cannot be defined as a static concept in any part of the boreal and subalpine forests of Canada and Alaska, nor can we define equilibrium, climax or stasis in the same way. Instead, the boreal forest is a reflection of a dynamic fire cycle carrying the memory of different past fire cycles (Johnson et al. 1998).

5.4. Forest area affected by mountain pine beetle in British Columbia, Canada - IV

Area affected by MPB-caused tree mortality in British Columbia was found to be highly synchronous even at large distances (Fig. 3, **IV**; Tab. 1, **IV**). Multivariate spatiotemporal analysis of the data enabled the identification of three major modes of MPB variability: the 1st and 3rd modes (Fig. 6, **IV**; Fig 7, **IV**), accounting together for ~60% of the dataset variability, were found to be largely related to both local and large-scale climate. Moreover, the 1st mode of variability strongly suggested that province-wide synchrony was the main characteristic of the dynamics of MPB-caused tree mortality in BC. The 2nd mode (accounting for 18.6% of the total variability) was found to be unrelated to climate and attributed to internal variability potentially related with the two major outbreaks that occurred in the period of record.

Overall, area affected by MPB was positively related to minimum winter T (Fig. 8, **IV**; Tab. 2, **IV**). Cold winter temperatures, often related to Arctic air invasions (Stahl et al. 2006), are able to kill large numbers of MPB larvae population living within the bark of trees (Wygant 1942). Moreover, area affected by MPB in BC was highly related to the Pacific Decadal Oscillation (PDO), and, to a lesser extent, to the Arctic Oscillation (AO). These relationships were stronger at low frequency timescales (Tab. 2, **IV**). PDO synchronized winter T over the whole studied area: warm PDO phases reduced the frequency of extreme winter T and Arctic air invasions through an enhanced Aleutian low, an eastwards-displaced western Canadian ridge, and warm air advection into western Canada (e.g. Stahl et al. 2006). AO, on the other hand, was responsible for a smaller portion of MPB variability, and also related to extreme winter events in the southernmost and northernmost parts of the range of MPB-activity in BC. Thus, ultimate factors (PDO and AO) synchronized proximal factors (minimum winter T) over BC, which largely controlled area affected by MPB through a known mechanism (larvae mortality).

The province-wide study on the relationships between large-scale climate and area affected by MPB for the period 1959-2002 provided the adequate spatial and temporal scales to identify the ultimate factors controlling MPB populations in the region. A longer record would have allowed richer timeseries analyses and a more detailed definition of the frequencies at which climate affects population dynamics. Information on the temporal evolution of host abundance (i.e. mature pines) during the period analyzed would have improved the synchrony analyses.

5.4.1. Temporal changes

PDO conditions since its phase shift of 1976/77 reduced the occurrence of extreme low winter T (increasing larvae survival) in BC. Likewise, the persistent and intense positive phase of the Arctic Oscillation during the late 1980s and 1990s also decreased the frequency of extreme cold events in the area, thus favouring MPB survival. All this favoured the occurrence of large MPB outbreaks in BC during the recent decades.

5.5. Reconstruction of April sea ice extent in the western Nordic seas — V

Timeseries were smoothed prior to any computation due to potential dating errors in the early part of the ice core data and complications caused by summer melt, which does not penetrate more than about 5 years (Pohjola et al. 2002). The reconstruction was thus restricted to decadal/interdecadal variability. Records of $\delta^{18}O$ were highly related with T in Longyearbyen (Svalbard; Isaksson et al. 2001), whereas the tree-ring chronology was related with summer T in northern Fennoscandia (Helama et al. 2002). Both records were significantly related with the record of April sea-ice extent from the western Nordic Seas (Tab. 1, **V**), suggesting a potential influence of sea ice extent on regional air T.

The 20th century sustained the most persistent and lowest sea ice extent values since AD 1200 (Fig. 2, **V**), which was largest from the 17th to the 19th centuries (Little Ice Age - LIA), smaller in the 16th century, and moderate during 13th to 15th centuries. Proximally, sea ice extent is sensitive to sea surface T, air T, and wind direction and strength, which may compact sea ice and reduce its extent, or enlarge it and import/export sea ice from/to other areas (e.g. Vinje 2001). Ultimately, large-scale atmosphere and atmosphere/ocean dynamics control the proximal factors over large areas at typical timescales: Low Frequency Oscillation (LFO) and North Atlantic Oscillation (NAO) associated timescales dominated sea ice extent variability during the reconstructed period (Fig. 5, **V**). Moreover, sea ice extent and NAO showed a non-stationary relationship during the observational period (Fig. 7, **V**). Variability at centennial scales also played a major role in the region: the present low April sea ice extent, unique over nearly a whole millennium, results from a climatic amelioration started in mid-19th century after the LIA.

5.6. Estimation of the significance of timeseries statistics from autocorrelated and/or short timeseries — VI (Methodological Paper)

This method permitted handling highly autocorrelated and relatively short ecological and climatic timeseries which otherwise would have not been analyzable or at least confidently testable. Moreover, values of reconstruction statistics which were traditionally considered as threshold for reliable climatic reconstructions were found non-significant even when dealing with white noise timeseries. This work warns against the widespread use of statistics that assume independent observations in the very often autocorrelated timeseries of natural phenomena.

A Matlab package and a Windows executable file for non-Matlab users were produced and made available to perform the analysis (Figs. 3, 4, **VI**).

6. Conclusions

Conclusions particular to each study can be found in the Conclusion sections of each paper. Conclusions in here are more general and address the research done as a whole.

- Organisms interact with local weather phenomena which might be correlated in space by large-scale climatic systems, causing ecological synchrony over large areas. When studying patterns of synchrony between ecological and climatological data, knowledge on the physical and biological processes of the studied systems, as well as of their potential interactions is essential: it will help us to identify other factors potentially masking the climatic signal or causing synchrony.
- When studying patterns of synchrony between ecological and climatological data, defining the scales (both spatial and temporal) at which those occur is basic. Failing to do so will most certainly result in noisy patterns, or in no patterns found. Knowledge about the underlying mechanisms of these interactions defines their range of scales.
- Temporal and spatial scales of large-scale climatic patterns have a large influence on ecological processes. They correlate local weather over large areas and thus produce regional to global responses of organisms to climate. Moreover, they set the frequency of occurrence of extreme weather events which might be lethal or critical for populations.
- Interdisciplinary collaboration between physical and biological research is needed to understand the nature of climate/ecological systems.
- The nature of the relationships between ecological processes and climate is essentially dynamic. It is thus impossible to define climax, stasis, or equilibrium of an ecosystem from a static point of view. Recent climate change might have helped ecological science in general to acknowledge the constant changing nature of these relationships: static visions of ecosystems are at present outdated.
- Land use (grazing in this case) has shown to strongly affect relationships between ecological processes (tree-growth) and climate. Moreover, reindeer grazing is such a widespread human activity in the boreal region that it might affect the global carbon budget.
- Mountain ranges play a major role in creating regional (i.e. sub-continental to continental) climatic gradients and thus strongly influence relationships between climate and ecological processes (e.g. Scandes in tree-growth, Pyrenees in tree-growth, Rocky Mountains in large fire occurrence and mountain pine beetle infestations).
- In many cases, length and spatial-temporal resolution of records limit the extent of large-scale climate-ecological studies. The existence and enlargement of large and intensive datasets across the globe is thus absolutely necessary, as well as the collection and study of proxy environmental data that can lengthen records and put recent changes in perspective.
- There is a need to take into account autocorrelation when calculating statistics from timeseries which assume independent observations. Methods of the nature of the ones presented in V and VI should be applied whenever some of the records have significant temporal persistence.
- Finally, as many ecological processes occur during the growing season, there is a need from ecologists for climatologists to study large-scale climate less focused on wintertime teleconnections.

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