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Rising synchrony controls western North American ecosystems

Running title: Rising synchrony in western North America

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Abstract

Along the western margin of North America, the winter expression of the North Pacific High (NPH) strongly influences interannual variability in coastal upwelling, storm track position, precipitation, and river discharge. Coherence among these factors induces covariance among physical and biological processes across adjacent marine and terrestrial ecosystems. Here, we show that over the past century the degree and spatial extent of this covariance (synchrony) has substantially increased, and is coincident with rising variance in the winter NPH. Furthermore, centuries-long blue oak (*Quercus douglasii*) growth chronologies sensitive to the winter NPH provide robust evidence that modern levels of synchrony are among the highest observed in the context of the last 250 years. These trends may ultimately be linked to changing impacts of the El Niño Southern Oscillation on mid-latitude ecosystems of North America. Such a rise in synchrony may destabilize ecosystems, expose populations to higher risks of extinction, and is thus a concern given the broad biological relevance of winter climate to biological systems.

Introduction

Biological impacts of climate change have been widely documented across the world's biomes, yet such responses are almost exclusively described in terms of trends in average conditions (Parmesan & Yohe, 2003; Poloczanska *et al.*, 2013). It is widely acknowledged, however, that global warming is also likely to increase climate variance (Easterling *et al.*, 2000; Coumou &

Rahmstorf, 2012), the extent and consequences of which remain poorly understood. Of concern is that extreme events which often disproportionately influence biological processes and impart long-lasting effects on ecosystems, may increase in frequency (Jentsch *et al.*, 2007; Thompson *et al.*, 2013). Rising climate variability may also induce synchrony in the dynamics of spatially disjunct populations (i.e. the Moran effect (Moran, 1953)), thereby reducing the survivorship of potential emigrants available to “rescue” failing subpopulations in the event of a deleterious climate event. Such a reduction in the regional diversity of biological response to climate could potentially destabilize ecosystem processes and the services they provide to society (Harrison & Quinn, 1989; Palmqvist & Lundberg, 1998; Schindler *et al.*, 2015). Thus, identifying long-term trends in environmental variability or synchrony is of critical importance, especially if a given climate driver is broadly relevant to biology.

Off the coast of western North America, high winter (Jan-Mar) atmospheric pressure (i.e. the North Pacific High; NPH) is associated with more intense northwesterly, upwelling-favorable alongshore winds that lift deep, cold, nutrient-rich waters into the photic zone to stimulate production in the California Current (Huyer, 1983). At the same time, the high pressure ridge deflects Pacific storms, leading to drought on land. Thus, anomalies in winter NPH amplitude and positioning induce negative covariance between metrics of marine and terrestrial biological productivity that are sensitive to cool-season climate. For example, years of robust coastal upwelling, high seabird reproductive success, rapid rockfish growth, and lipid-rich copepod communities are associated with low precipitation and poor blue oak radial growth on land (Black *et al.*, 2014). Although there is almost no trend in average values, centennial-length instrumental records suggest that NPH-induced winter climate variability has increased substantially over the course of the 20th century (Black *et al.*, 2014) with concomitant effects on some biological indicators (Sydeman *et al.*, 2013). Here, we utilize some of the longest spatially-resolved observational records from western North America to explore how the geographic extent, magnitude, and coherence of ecosystem anomalies, including physical and biological indicators, have changed over the past century. We find that rising variance in the NPH has synchronized processes not only within, but also among marine, terrestrial, and freshwater systems of western North America.

Materials and Methods

Physical data

The winter NPH was defined as mean Jan-Mar Hadley Centre HadSLP2 sea level pressure [<http://www.metoffice.gov.uk/hadobs/hadslp2/>] for the region 25°N - 35°N by 125°W - 145°W, the approximate location over which the NPH is centered during the winter months (Schroder *et al.*, 2013). Although NPH data are available prior to 1920, time series were truncated at this date due to concerns about relatively low densities of sea level pressure observations early in the 20th century. Annual water year (Oct 1-Sep 30) discharge data (referred to as “annual discharge”) were obtained from the U.S. Geological Survey [<https://waterdata.usgs.gov/nwis>] for relatively undisturbed watersheds in the western US states of Washington, Oregon, Idaho, California, Nevada, Arizona, New Mexico, Utah, and Colorado (Falcone *et al.*, 2010). Over half of the sites (56%) used in the variance and synchrony analysis (see below) are part of the Hydro-Climatic Data Network, a subset of U.S. Geological Survey streamgage sites for which flow of the watercourse is natural and record length sufficiently long to analyze discharge patterns over time (Slack *et al.*, 1993) (Table S1). The coastal upwelling index represents the magnitude of offshore Ekman transport (Bakun, 1973; Schwing *et al.*, 1996), and monthly means were obtained from the National Oceanic and Atmospheric Administration (NOAA) Pacific Fisheries Environmental Laboratory [<http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html>]. Monthly-averaged sea level data were obtained from the University of Hawaii Sea Level Center [<http://uhslc.soest.hawaii.edu/>] for all records along the west coast of North America that exceeded at least 30 yr in length. All linear trends were removed from sea level data given their possible association to tectonic processes or anthropogenic sea-level rise. Monthly-averaged precipitation data were obtained from two sources, the first of which was NOAA divisional data for Washington, Oregon, Idaho, California, Nevada, Arizona, New Mexico, Utah, and Colorado, available at (<https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp>). The second source was the Climate Research Unit TS3.24 gridded 0.5° precipitation data for North America (Harris *et al.*, 2014). With the exception of river discharge, winter (Jan-Mar) means were used in all analyses.

Tree-ring data

Blue oak (*Quercus douglasii*) tree-ring data were obtained through the NOAA International Tree-Ring Databank [<http://www.ncdc.noaa.gov/paleo/treering.html>]. Only growth chronologies that significantly ($p < 0.01$) correlated with the winter NPH, extended past 2003, and had measurement time series > 400 yr in length were retained ($n=16$ time series). Measurements were standardized using negative exponential detrending in the program ARSTAN (Cook & Krusic, 2005). The Expressed Population Signal (EPS) was used to quantify how well the chronology developed from a given number of trees represents the theoretical population from which it was sampled. The “standard” chronology was retained and truncated where the Expressed Population Signal (EPS) fell below 0.85 (Wigley *et al.*, 1984). Albeit arbitrary, an $\text{EPS} \geq 0.85$ is often used as a threshold at which the chronology is considered sufficiently robust for climate reconstruction.

Trends in variance and synchrony

The focus of this study was on those variables that related to the NPH. Thus, time series were screened for a winter NPH Pearson correlation at values of $r < -0.4$ for river discharge, $r > 0.4$ for upwelling, $r < -0.5$ for sea level and NOAA divisional precipitation, and $r < -0.6$ for CRU gridded precipitation) over the interval 1948 through 2015. These thresholds accounted for the fact that some variables were inherently more strongly correlated with NPH than others and helped focus the geography of the analysis. Note that the findings of this study were insensitive to a single correlation threshold of 0.4 (data not shown). Prior to subsequent analysis, all time series were normalized to the common interval of 1948-2015.

To identify trends in the variance structure of time series, a running standard deviation was calculated in a 31-year window and then averaged for each variable (e.g., upwelling, sea level, river discharge, etc.). Trends in synchrony were quantified by calculating mean pairwise correlation in a running 31-year window and then fitting the resulting time series with a linear regression. Mean pairwise running correlation (\bar{r}) was calculated within each variable (e.g. the eight upwelling time series and then the five sea level time series, etc.). Next, \bar{r} was calculated among the means of each variable type (NPH, mean river discharge, mean upwelling, mean sea level, and mean CRU precipitation) to identify trends in synchrony across marine, terrestrial, and freshwater systems. For the blue oak, \bar{r} (synchrony) was calculated for each subset of chronologies, beginning with all 16 and then repeating with the 15 longest, the 14 longest, etc.,

to maximize the length of the synchrony history. Results were highly consistent for 14 or more chronologies, but became less stable at lower sample depths (data not shown). This is likely due to the concentration of relatively short chronologies to the north and the resulting changes in geographic representation farther back through time.

Significance of trends in \bar{r} was evaluated by comparing observed slopes in \bar{r} to those in simulated, bootstrapped data ($n = 10,000$ iterations). For each iteration, time series of identical number, length, and autocorrelation as the observational records were generated after which \bar{r} was calculated and fit with a linear regression. The \bar{r} regression slope from observed data was compared to the distribution slopes in the simulated data. To verify the cause of synchrony trends, each instrumental time series was regressed against winter NPH and the running correlation and regression analysis repeated on the residuals. The \bar{r} slopes were compared between the observed (unaltered) data and that from which the NPH signal had been removed.

Results

Rising variance and synchrony

Running standard deviations indicate that variance has increased over the 20th century within our network of marine, freshwater, and terrestrial indicators (Fig. 1a). Patterns in exceptionally long sea level records at San Francisco and San Diego closely track those in regional precipitation and the NPH (Fig. 1a). Furthermore, centennial-length trends in rising variance are accompanied by rising synchrony, calculated within each variable type (rivers, upwelling, precipitation, etc.) as mean pairwise correlation (\bar{r}) (Fig. 1b). Strikingly, synchrony not only rose within these variable types, but also among them (Fig. 1c, d). Collectively, these findings suggest that climate-driven covariance is strengthening concurrently across marine-terrestrial-freshwater environments. Observed directional changes in synchrony are unlikely due to chance alone, as confirmed by comparing slopes in \bar{r} to those in simulated data ($n = 10,000$ iterations) (see Methods; Fig. S1, Table S3). When NPH signals were removed from instrumental records, trends in synchrony were no longer significant (Table S3), indicating that variability in NPH was a dominant factor driving synchrony among time series considered in the study.

Enlarged NPH footprint

Coincident with rising \bar{r} , the climatological “footprint” of the winter climate pattern has expanded as evidenced by stronger correlations across the region between NPH and sea level, upwelling, precipitation, and river discharge during the latter half compared to the first half of the instrumental record (Fig. 2). What was previously a signal specific to north-central California has in recent decades extended across the southwestern United States and northern Mexico. Moreover, river discharge at many sites in Oregon and Washington that were positively correlated with the NPH early in the 20th century now negatively correlate, and agree in sign, with rivers farther south in California (Fig. 2). A similar landscape-level pattern of correlations occurs if the closely related ($r = -0.85$; $p < 0.0001$) and consistently sampled record of sea level at San Francisco is substituted for the NPH (Fig. S2). Notably, those pairs of variables that correlated the least with one another at the beginning of the record experience the greatest increase in \bar{r} over time (Fig. S3). This suggests that the spread of the NPH signal across the region is likely a key driver of rising synchrony as is the intensification of this NPH signal in those areas where NPH has been historically important. Pairs of variables that are well-correlated early in the record remain as such over time (Fig. S3).

Historical context

The 16 blue oak tree-ring chronologies are highly sensitive to winter climate and strongly correlate with winter precipitation (Stahle *et al.*, 2013; Black *et al.*, 2014), the NPH, and sea level at San Francisco (Table S2). Variance has risen in these chronologies over the past century (Black *et al.*, 2014), as has synchrony among them (Fig. 3), suggesting that environmental patterns have affected biotic phenomena, increasing coherence in interannual variability of tree growth. Indeed, the uniquely long history provided by the blue oak suggests that levels of synchrony (\bar{r}) in the 20th century have risen to among the highest levels in the multi-centennial context (Fig. 3). Although \bar{r} varied considerably over the past 250 years, and in tandem with levels of variance, confidence intervals around maximum \bar{r} values (peaking in the 31-year window of 1972-2002) at least marginally exceed those of all other decades in the proxy record (Fig. 3).

Origins of rising synchrony

The century-length rise in variance and synchrony within and among western North American ecosystems may have linkages to the tropical Pacific. The winter NPH has in recent decades become much more strongly related to low-latitude atmospheric pressure fields in the vicinity of the western Pacific warm pool (Fig. 4). Correlations between these regions are negligible over the 1920 through 1966 interval, intensifying to highly significant ($p < 0.001$) levels over the more recent 1967 through 2013 interval (Fig. 4). This suggests that covariance between the NPH and the tropical Pacific has substantially increased over the past hundred years. To better explore the timing and nature of these changing relationships, mean Jan-Mar Hadley Centre HadSLP2 sea level pressure was extracted from the region of the tropical western Pacific over which correlation to the NPH has increased ($15^{\circ}\text{S} - 20^{\circ}\text{N}$ by $110^{\circ}\text{E} - 145^{\circ}\text{E}$). A running (31-year) correlation between sea level pressure in the tropical Pacific and the NPH indicates a sharp increase in coupling beginning in the mid-1960s (Fig. S4). However, this strengthening relationship occurs as soon as the 31-year running window of correlation envelops the extreme El Niño event of 1983. Given their leverage on correlation coefficients, subsequent El Niño events in 1992 and 1998 help to maintain these strong relationships through present.

Discussion

Evidence in biological indicators

Rising variance in the amplitude of the NPH in winter has induced a pervasive signal of rising variance and synchrony among marine, terrestrial, and freshwater ecosystems of western North America. Biological impacts consistent with such trends have been previously documented in terrestrial environments of California. Near San Francisco, extreme variability in interannual precipitation induced temporal mismatches between larval development and the availability of host plants, collapsing two populations of checkerspot butterfly (*Euphydryas editha bayensis*) (McLaughlin *et al.*, 2002). Along a 700-km latitudinal gradient from San Diego to San Francisco, *Artemisia californica* shrubs from sites in which interannual precipitation regimes are highly variable have greater capacity to exploit favorable moisture conditions compared to individuals from sites in which precipitation regimes are relatively stable (Pratt & Mooney, 2013). However, over the past several decades, variability in interannual precipitation has increased, and to the greatest extent at historically stable sites where plants are less well adapted to accommodate such change (Pratt & Mooney, 2013).

With respect to the marine environment, variance in the a) reproductive success (offspring raised per pair) of a seabird, the Cassin's auklet (*Ptychoramphus aleuticus*) at the Farallon Islands, California, and b) the abundance of Sacramento River fall run Chinook Salmon (*Oncorhynchus tshawytscha*) have increased (Sydeman *et al.*, 2013), as have the variance and synchrony in survival rates of Coho (*O. kisutch*) and Chinook Salmon from Alaska through California (Kilduff *et al.*, 2015). Rising variance in these marine populations has been attributed to rising variance in the North Pacific Gyre Oscillation (NPGO), a mode of climate variation that correlates to patterns of nutrients, salinity, and plankton dynamics in the northeastern Pacific (Di Lorenzo *et al.*, 2008; Sydeman *et al.*, 2013). In turn, the variance increase of the NPGO has been linked to stronger expressions of the Central Pacific El Niños (Kilduff *et al.*, 2015), which energizes the low-frequency variability of NPGO (Di Lorenzo *et al.*, 2010). The forcing pattern of the NPGO is an atmospheric pressure dipole with a climatological low centered on Kodiak, Alaska, and a climatological high that overlaps considerably with the winter NPH (Di Lorenzo *et al.*, 2008). Thus, rising variance in the NPGO and NPH are likely related, though the NPH is much more strongly coupled to the geophysical indicators in this study, as well as a wide range of biological indices (Black *et al.*, 2011; Thompson *et al.*, 2012; Garcia-Reyes *et al.*, 2013; Schroder *et al.*, 2013). Our ability to detect trends in variance or synchrony in observational biological records is, however, hindered by the lack of records that span multiple decades.

Origins of rising synchrony

Strengthening correlations between the winter NPH and atmospheric pressure in the western Pacific warm pool suggest that rising synchrony and variance may be linked to changes in tropical climate and/or teleconnections to western North America. The NPH is closely coupled to a region of climatological low pressure north of Australia (Schwing *et al.*, 2002; Hartmann, 2015; Seager *et al.*, 2015), the same area for which correlations between SLP and winter NPH have increased in recent decades (Figure 4). Both the NPH and western tropical Pacific are centers of action for North Pacific Hadley / Walker atmospheric circulation, which are heavily influenced by ENSO (Schwing *et al.*, 2002; Di Lorenzo *et al.*, 2010; Furtado *et al.*, 2012), the variability of which has been increasing over the past hundred years to unusually or unprecedentedly high levels in the context of the past several centuries (Cobb *et al.*, 2003; Li *et al.*, 2011; Cai *et al.*, 2015; Liu *et al.*, 2017). Thus, greater amplitude in ENSO is likely to be

associated with rising variability of the winter NPH and synchrony among associated physical and biological populations in western North America. Indeed, rising variance in the tropics has been associated with a rapid succession of recent climate extremes in western North America including record-breaking El Niño events in 1982-1983, 1997-1998, and 2015-2016, and the unusually persistent 2014-2015 North Pacific Ocean heat wave known as “The Blob,” which was linked to the recent exceptional California drought (Griffin & Anchukaitis, 2014; Wang et al., 2014; Bond et al., 2015; Williams et al., 2015; Di Lorenzo & Mantua, 2016). The apparent step-change in connectivity between the NPH and sea level pressure in the western tropical Pacific appears to coincide with this series of extreme events beginning with the 1983 El Niño. Other possible mechanisms include changes in ENSO phenology or expression (Ashok & Yamagata, 2009; Zhou *et al.*, 2014) as well as interactions with other broad-scale climate phenomena such as the Pacific Meridional Modes (Liguori & Di Lorenzo, 2018), Pacific decadal variability (Mantua & Hare, 2002), or North Pacific Gyre Oscillation (Di Lorenzo *et al.*, 2008), among others. Ultimately, how these factors interact to influence apparent changes in the connectivity between the NPH and the tropics is unknown and worthy of study. However, the balance of evidence suggests that part of the rise in NPH variability and related patterns of synchrony have origins in the tropics, and that the intensity of these relationships has changed over the past century.

Historical context

Blue oak tree-ring chronologies confirm that the level of variance (Black *et al.*, 2014), and especially synchrony, have risen over the past hundred years to levels that are among the highest of the 250-year reconstruction. A conspicuous feature of this longer-term history, however, is the occurrence of three low-variance events. The most recent of these occurs in the late 1950s and 1960s and is associated with a period of relatively low variability between the large 1941 and 1983 El Niño events. Comparisons with North Pacific climate variability is complicated by poor agreement among existing reconstructions (Kipfmueller *et al.*, 2012). However, the relatively quiescent period of the 1760s in the blue oak record coincides with a period of low variability in several ENSO reconstructions that span marine and terrestrial archives across both hemispheres and provide at least some corroborating evidence that this was a period of low tropical variability (Braganza *et al.*, 2009; Wilson *et al.*, 2010). Yet the record

with the greatest similarity appears to be a reconstruction of the North Atlantic Jet (NAJ) positioning derived from European tree-ring chronologies (Trouet *et al.* 2018). All three periods of low synchrony in the blue oak record correspond to periods of low interannual NAJ variability. Further mirroring patterns in blue oak synchrony, NAJ variability is conspicuously elevated during the 1790s and also sharply increases late in the record, beginning around 1960 (Trouet *et al.* 2018). This suggests that general patterns of mid-latitude variability may be coherent across broad spatial domains.

Broader implications

The effects of climate variability on biological synchrony are widely documented. For example, growth synchrony is a central principle of modern dendrochronology that not only enables the exact dating of growth-increment time series, but also illustrates the pervasive influence of climate among individuals, habitats, and species from high-elevation forests to marine fish, corals, and bivalves (Douglass, 1941; Fritts, 1976; Black *et al.*, 2016). Beyond growth rate, climate variability has also been linked to synchrony among population sizes with examples from insects (McLaughlin *et al.*, 2002; Jepsen *et al.*, 2009; Ojanen *et al.*, 2013; Allstadt *et al.*, 2015; Sheppard *et al.*, 2016) to vertebrates (Post & Forchhammer, 2002; Hansen *et al.*, 2013). The synchronizing effects of climate on biology are particularly apparent following climate regime shifts, such as occurred in the North Pacific in 1977 or on an even broader global scale in the 1980s, with the potential to profoundly reorganize ecosystem structure and functioning across a range of trophic levels and spatial scales (Anderson & Piatt, 1999; Mantua & Hare, 2002; Defriez *et al.*, 2016; Reid *et al.*, 2016).

Less common are studies that document directional trends in biological synchrony. Beyond those examples specific to this study region (McLaughlin *et al.*, 2002; Kilduff *et al.*, 2015), the spatial synchrony in North American wintering bird species has increased as a consequence of rising synchrony in maximum air temperatures (Koenig & Liebhold, 2016). In Eurasia, tree-ring records indicate that forests in central Siberia have become more synchronous with those in Spain via the effects of long-term warming on growing-season length in the north and drought intensity in the south (Shestakova *et al.*, 2016). Thus, over these broad scales, physical and biological synchrony have been enhanced by rising temperatures. Furthermore, rising temperatures have also enhanced the synchrony of snowpack as well as the occurrence of

wildland fire across western North America (Kitzberger *et al.*, 2007; Pederson *et al.*, 2013). As for the winter climate pattern described in the present study, there is no evidence that regional temperature is a factor in synchrony trends. Instead, synchrony trends appear to be driven instead by variability in the North Pacific High and its effects on precipitation and meridional winds. This is consistent with Ganguli & Ganguly (2016) who found that drought, as defined only by precipitation and not temperature, had over the past century increased in spatial coverage across the southwestern region of the United States.

Ultimately, the bottom-up forcing by the NPH illustrates that rising synchrony can be far-reaching and pervasive, simultaneously impacting marine, terrestrial, and freshwater systems. Thus, not only is this an issue within, but also among ecosystems, and species that utilize more than one of these habitats to complete their life cycle may be particularly vulnerable. One notable example is Pacific salmon, for which increasing temporal and spatial synchrony may lead to decreased population production and viability (Schindler *et al.*, 2010; Schindler *et al.*, 2015). Given the limited length of observational biological records and even instrumental records, high-resolution proxies will be key to establishing pre-industrial, baseline ranges of synchrony as well as assessing the extent to which resilience, the stability of ecosystem processes, and diversity of biological responses to climate are reduced. Considering their possibly widespread prevalence and biological relevance, such trends in variance and synchrony should be more broadly quantified and prominently addressed in the mitigation and management of climate change impacts.

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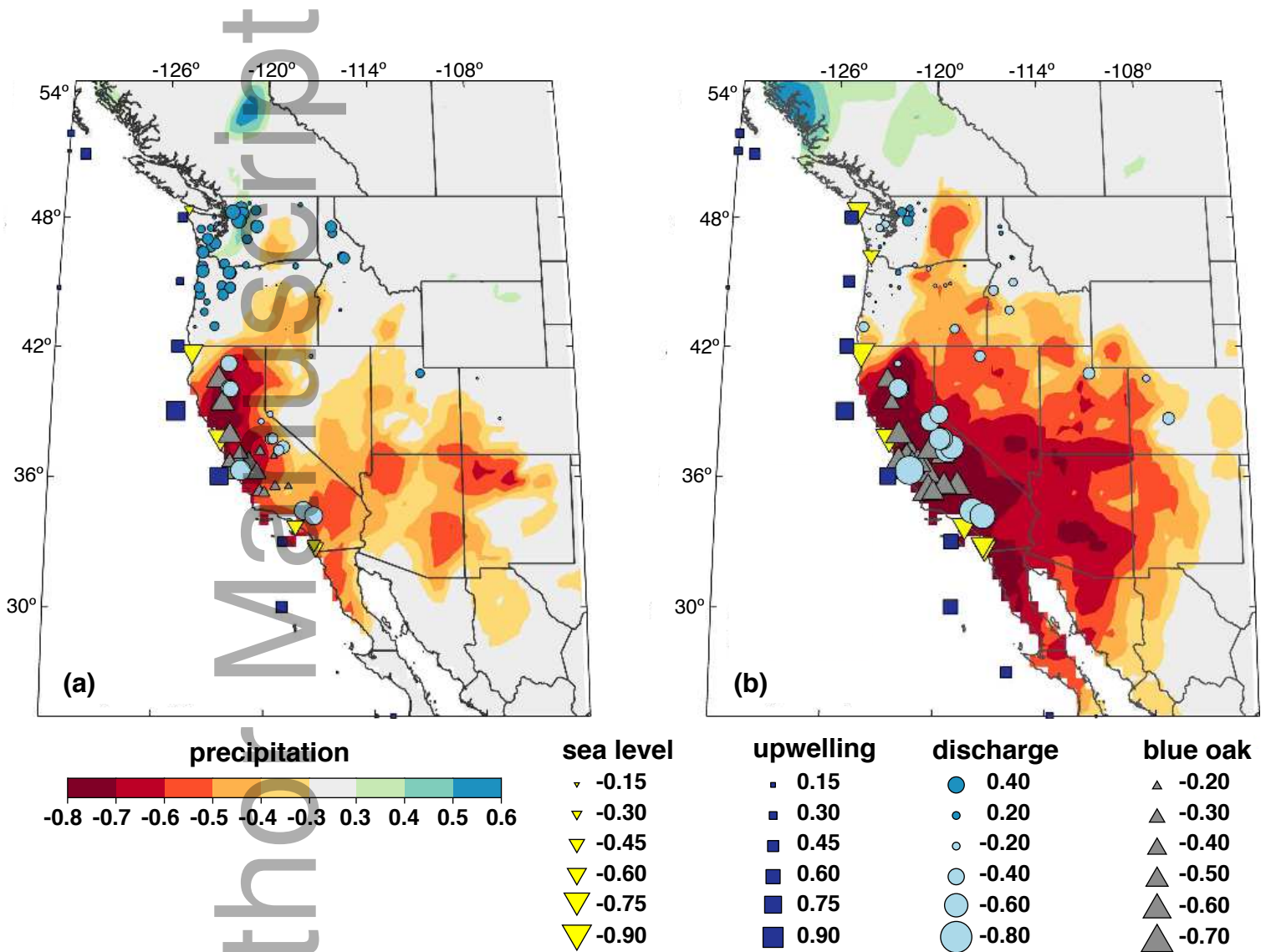
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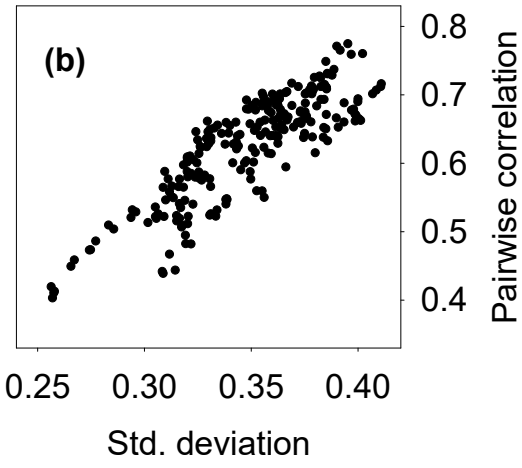
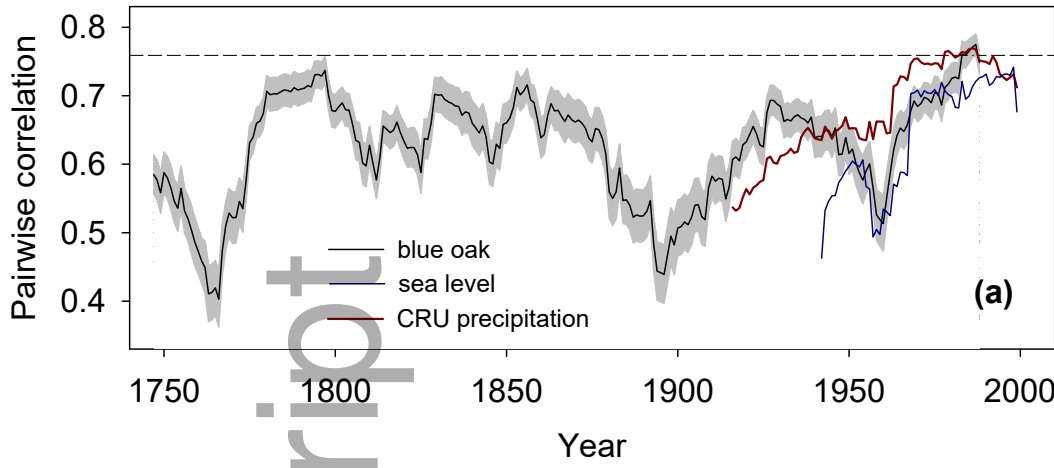
Figure 1. Trends in variance and synchrony for winter climate indicators in western North America. (a) Running std dev (31-year window) for the North Pacific High, annual river discharge (n=7), winter sea level (n=5), winter upwelling (n = 8), winter precipitation across NOAA climate divisions (n=13) and winter precipitation across CRU gridded data (n=76). (b) Mean running pairwise correlations (31-year window) within time series of annual river discharge, winter sea level, winter upwelling, winter NOAA precipitation, and winter CRU gridded precipitation. (c) Mean running pairwise correlations (31-year window) between all possible combinations of the North Pacific High (NPH), sea level averaged across 5 sites (SL), annual river discharge averaged across 7 sites (rivers), upwelling averaged across 8 sites (UW), and CRU precipitation averaged across 76 grid cells (precip). (d) Mean running pairwise correlation among these five variables (all) and a subset of the longest four variables (rivers, sea level, NPH, and CRU precipitation). Dotted line is linear trend for the “longest” subset; slope = 0.005; p = 0.04

Figure 2. Correlation between winter North Pacific High and winter climate indicators during the first half of the record and the second half of the record. (a) First half of the record: CRU gridded winter precipitation (1920-1967), annual river discharge (1940-1977), winter upwelling (1946-1980), winter sea level (1935-1974), and blue oak tree-ring chronologies (1920-1961). (b) Second half of the record: CRU gridded winter precipitation (1968-2014), annual river discharge (1978-2015), winter upwelling (1981-2015), winter sea level (1975-2014), and blue oak tree-ring chronologies (1962-2003).

Figure 3. A multicentennial history of synchrony. (a) Mean running pairwise correlations (\bar{r}) for 16 blue oak chronologies as well as instrumental records of winter precipitation and sea level. Dotted horizontal line is the lower confidence interval for 1987, the year with the maximal \bar{r} value (corresponding to an \bar{r} window of 1972 through 2002). (b) Relationship between average running standard deviation and running \bar{r} for blue oak.

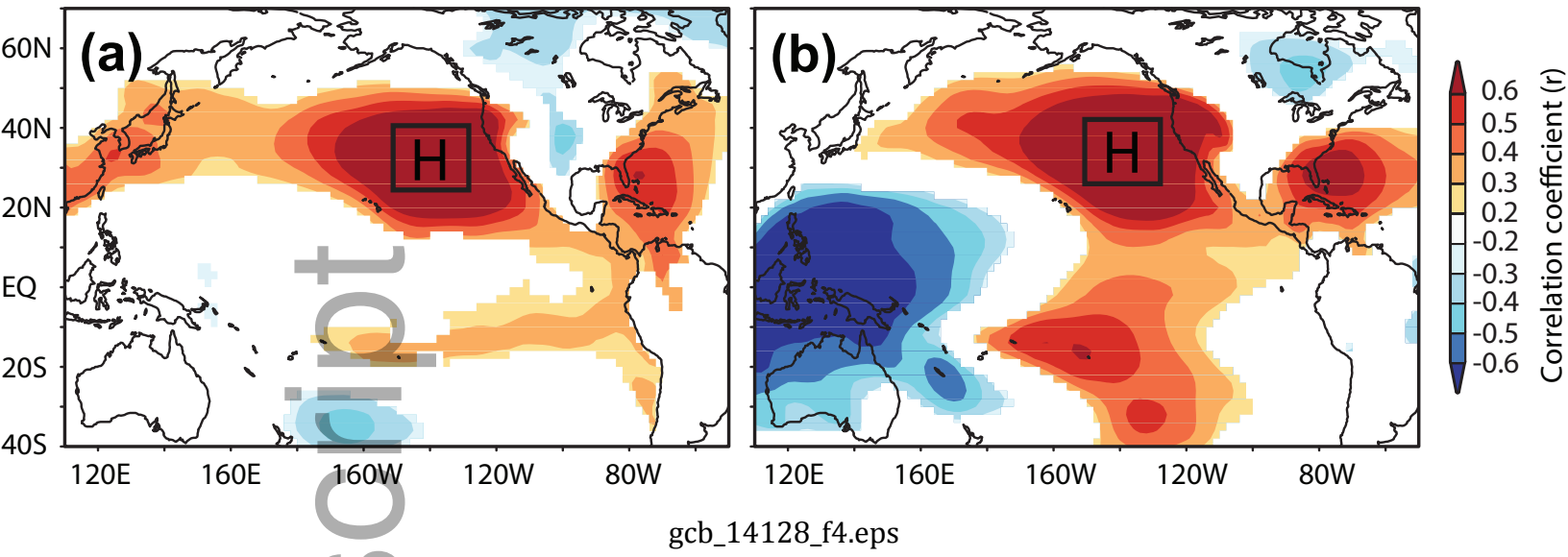
Figure 4. Correlation between the winter North Pacific High (square with “H”) and winter gridded sea level pressure (20th Century Reanalysis). (a) Over the interval of 1920-1966 and (b) over the interval of 1967-2013.





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