The climate velocity of the contiguous United States during the 20th century

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Abstract

Rapid climate change has the potential to affect economic, social, and biological systems. A concern for species conservation is whether or not the rate of on-going climate change will exceed the rate at which species can adapt or move to suitable environments. Here we assess the climate velocity (both climate displacement rate and direction) for minimum temperature, actual evapotranspiration, and climatic water deficit (deficit) over the contiguous US during the 20th century (1916–2005). Vectors for these variables demonstrate a complex mosaic of patterns that vary spatially and temporally and are dependent on the spatial resolution of input climate data. Velocities for variables that characterize the climatic water balance were similar in magnitude to that derived from temperature, but frequently differed in direction resulting in the divergence of climate vectors through time. Our results strain expectations of poleward and upslope migration over the past century due to warming. Instead, they suggest that a more full understanding of changes in multiple climatic factors, in addition to temperature, may help explain unexpected or conflicting observational evidence of climate-driven species range shifts during the 20th century.

Keywords: climate change velocity, climate velocity vectors, climate change impacts, climatic water balance

Introduction

Anthropogenic climate change is considered a threat to ecosystem services and to global biodiversity because of its magnitude, the potential for novel climatic conditions (Williams *et al.*, 2007), and the rate at which it is occurring (Parmesan & Yohe, 2003; Montoya & Raffaelli, 2010). The consequences of changes in biophysical drivers on biota should be contingent upon the rate at which climate changes vs. a given species' capacity to ameliorate these effects (Ackerly *et al.*, 2010). Indeed, species have always been subject to changing climatic regimes and have responded through adaptation (Davis & Shaw, 2001; Hoffmann & Sgrò, 2011), changes in phenology (Cleland *et al.*, 2007), range shifts (Davis & Shaw, 2001), the use of climate refugia (Dobrowski, 2011; Hampe & Jump, 2011), and extinction (Svenning, 2003).

The ability of species to cope with the rapid rate of climate change projected for this century is a topic of debate. Studies of past and present climate changes suggest that range shifts can lag climate changes (Bertrand *et al.*, 2011), an outcome that may put species at risk of extinction if the rate of climate change, habitat degradation, and fragmentation accelerates. Furthermore, projections of climate change impacts on species extinction rates (Thomas *et al.*, 2004) are alarming and are considered by some to be overestimates (He & Hubbell, 2011). The fossil record suggests that widespread extinctions of plant species were rare during periods of rapid warming (~2–10 °C/century) such as the Pleistocene–Holocene transition (15–11.5 kya) (Willis & MacDonald, 2011). Instead, authors note that ecological turnover and range shifts were common responses to rapid climate changes of the past (Botkin *et al.*, 2010; Hof *et al.*, 2011; Willis & MacDonald, 2011). Despite these uncertainties, the rate of climate change is an important consideration for assessing ecological vulnerability to climate change impacts and quantifying this for the 20th century is an important step in providing a baseline from which to view 21st century climate changes unfold.

One approach to characterizing the rate of climate change is through the use of climate change velocity (Loarie *et al.*, 2009). Climate change velocity is calculated by dividing the rate of climate change through time (e.g. °C yr^{-1}) by the spatial gradient in climate at that location (e.g. °C km^{-1}) yielding an estimate of the velocity (km yr^{-1}) and direction of climate displacement

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across a landscape. Climate velocity describes the rate and direction which an organism would need to migrate to maintain an isocline of a given climate variable. Although the term climate change velocity has been used synonymously with the rate of climate displacement (Loarie *et al.*, 2009), its true vector form also yields a directional component. Recent research has examined the rate of climate velocity both historically (Burrows *et al.*, 2011; Sandel *et al.*, 2011) and under future scenarios (Loarie *et al.*, 2009), but less work has characterized the direction of these vectors (see Burrows *et al.*, 2011 and Ackerly *et al.*, 2010 for exceptions). The direction of climate velocity may be critical to our understanding of biotic responses to changing climate and can provide one basis for our expectation of poleward and upslope shifts of species ranges under warming conditions. Furthermore, the use of climate change velocity is considered more biologically relevant (Ackerly *et al.*, 2010) than the use of climate anomalies as it accounts for regional changes in climate and the ability of topographic heterogeneity to buffer biota against these changes.

Previous analyses of climate change velocity have focused on observed and projected changes in temperature. These estimates of climate velocity have been correlated with patterns of species endemism and biotic specialization (Dalsgaard *et al.*, 2011; Sandel *et al.*, 2011). However, it is well known that species are constrained by multiple interacting climatic factors in addition to temperature (Woodward, 1987). For example, climatic water balance characterizes the concurrent availability of both energy and water for biota and is largely absent from literature on climate change impacts despite its importance in shaping species range limits (Stephenson, 1998; Urban *et al.*, 2000) and richness (O'Brien, 1998; Francis & Currie, 2003). Moreover, the direction of climate velocity may vary by climate variable resulting in multiple or even opposing influences on biota. For instance, vectors of temperature may differ from those describing water availability. Divergence in the direction of climate velocity vectors between multiple climate variables may help explain species specific responses to climate change (Angert *et al.*, 2011; Tingley *et al.*, in press), the lack of evidence for poleward range shifts for some plant taxa (Zhu *et al.*, 2011), and biotic shifts in directions that counter our expectations (Lenoir *et al.*, 2010; Chen *et al.*, 2011; Crimmins *et al.*, 2011).

Here we calculate vectors of climate velocity for minimum temperature (T_{min}), actual evapotranspiration (AET), and deficit over the contiguous United States during the period 1916–2005. We focus on these three variables because they represent important limiting factors that are established predictors of plant species occurrence (Woodward, 1987; Stephenson, 1990). For instance, T_{min} profoundly influences the life history

and distributions of species due to the physiological, ecological, and evolutionary impacts of freezing (Inouye, 2000). AET and deficit represent the supply and unmet atmospheric demand components of the climatic water balance (Stephenson, 1990). These variables integrate climate (precipitation and temperature) with meteorological variables (snow melt, solar radiation, vapor pressure deficit, and wind) into a reduced set of biologically relevant and physically based variables that account for the concurrent availability of both water and energy.

Materials and methods

Climate data

We used 30 arc-second (~800 m) resolution gridded climate surfaces for T_{min}, maximum temperature, precipitation, and dew-point temperature from the Parameter-elevation Regression on Independent Slopes Model (PRISM) (Daly *et al.*, 2008) for the period 1916–2005. For trend analysis, we grouped these data into four periods: 1916–1945 (t_1), 1946–1975 (t_2), 1976–2005 (t_3), and 1916–2005 (t_4). The overall study period was chosen to maximize data quality and the first three time periods were chosen to avoid any attribution of observed trends to the Pacific Decadal Oscillation that generally was in a common low-frequency phase during the first three time periods (i.e., t_1 = warm phase; t_2 = cool phase; t_3 = warm phase).

A modified Thornthwaite-Mather climatic water-balance model (*sensu* Lutz *et al.*, 2010) was used to calculate annual estimates of AET and deficit between 1916 and 2005 at the 30 arc-second resolution. The model operates on a monthly time-step and accounts for atmospheric demand (potential evapotranspiration-PET), soil water storage, and includes the effect of temperature and radiation on snow hydrology via a snow melt model (Appendix A). PET was calculated using the Penman-Monteith equation (Allen *et al.*, 1998) and includes (i) terrain and cloud-corrected monthly average climatological downward shortwave radiation derived from NLDAS-2, (Mitchell *et al.*, 2004), (ii) monthly average climatological 10 m wind velocity from the North American Regional Reanalysis (Mesinger *et al.*, 2006), and (iii) monthly average dew-point temperature derived from PRISM data. Due to a lack of data for (i) and (ii) over the entire study period, we fixed these as being constant across time as derived from 1979 to 2010 normals; however, our approach accounts for changes in maximum temperature, T_{min}, dew-point temperature and precipitation. Further details on the datasets used and the development of the climatic water balance model are provided in Appendix A. Code to run the water balance model in R is provided in Appendix B. Additionally, to corroborate temporal trends in T_{min}, AET and deficit identified in the PRISM surfaces, we acquired daily meteorological observations from over 1200 stations from the United States Historical Climate Network Version 2 (USHCN, Oak Ridge National Laboratory, Oak Ridge, TN, USA, http://cdiac.ornl.gov/ftp/ushcn_daily/, last accessed, May 13, 2011) and

compared trends between the point-based measurements and trends identified in the PRISM surfaces (Appendix C). Although trends identified in the USHCN data are not wholly independent from those derived from PRISM data, they do provide a useful check for the presence of artifacts due to the PRISM interpolation procedure.

Climate vectors

Vectors of climate velocity were calculated as follows:

$$\vec{V_l} = \left(\frac{dc/dt}{dc/dx}, \frac{dc/dt}{dc/dy} \right)$$

where $\frac{dc}{dt}$ is the change in a climate variable per unit time (temporal trend) and $\frac{dc}{d_{xy}}$ is the change in the same variable per unit of distance (spatial gradient). Temporal trends were calculated using least squares regression on annual data for each cell over each time interval and significance of trends were estimated following Santer *et al.* (2000), a method that accounts for temporal autocorrelation by reducing the effective sample size of the time series. The spatial gradient for a given variable was calculated using a 3×3 grid cell neighborhood as this maximized the effective spatial resolution of the analysis (Loarie *et al.*, 2009). The direction of the spatial gradient was calculated as the vector sum of the latitudinal and longitudinal gradient and its associated vector angle (Burrows *et al.*, 2011). The temporal and spatial gradients used for calculating climate velocity vectors are presented in Appendix C.

Climate divergence

To assess divergence in the velocity vectors, we first calculated the net mean velocity of the three vectors as follows:

$$\vec{V}_{\text{net}} = \frac{\sum_{i=1}^{n} \vec{V_i}}{n}$$

where the subscript i indexes the three climate covariates $T_{\min}$, AET, and deficit. The net mean velocity implicitly assumes that each vector carries equal weight. We then defined divergence as the mean scalar difference between $\vec{V}_{\text{net}}$ and the $T_{\min}$, AET and deficit vectors:

$$\nabla \cdot F = \frac{\sum_{i=1}^{n} | \vec{V_i} - \vec{V}_{\text{net}} |}{n}$$

When $\nabla \cdot F = 0$, the vectors share the same magnitude and directions. Large values of $\nabla \cdot F$ indicate vectors that diverge in direction and magnitude.

Scale sensitivity

To assess the sensitivity of our velocity estimates to data resolution, we calculated velocity for data at five resolutions: 30 arc-second (native resolution), 1′, 5′, 30′, and 1°. This was accomplished by aggregating the original 30 arc-second resolution climate data to the coarser resolutions using a simple mean. We graphically examined the influence of data resolution on both climate velocity and direction.
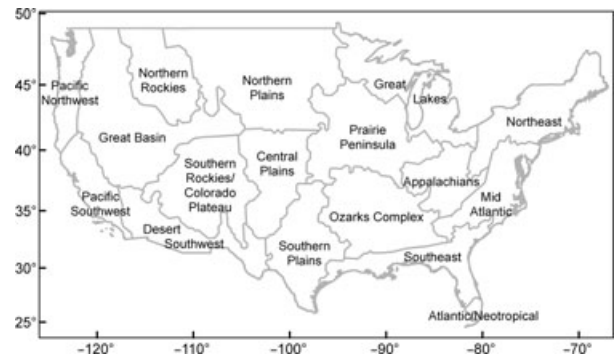
Fig. 1 National Ecological Observatory Network (NEON) domains for the coterminous US.

Climate velocity and divergence were summarized within the eco-climatic domains of the National Ecological Observatory Network (http://www.neoninc.org/news/neonsampling-design) (Fig. 1) using geometric means. National Ecological Observatory Network (NEON) domains were chosen because they represent biophysical and ecologically relevant components of climate in the study region (Hoffman & Hargrove, 1999). They also provide the basis for a national ecological observation network moving forward in time. Both the rate and directional component of the vectors are summarized using 30 arc-second data unless specified otherwise for visualization purposes. All analyses were conducted using R version 2.14.1 (R development Core Team, Vienna, Austria).

Results

Nationally, the geometric mean velocity for $T_{\min}$, AET, and deficit (derived using 30 arc-second resolution data for the period 1916–2005) was 0.081, 0.098, and 0.084 km yr^{-1}, respectively (Table 1). However, the vectors exhibited large spatial variability. The largest rates were found in regions with little topographic relief, principally the central plains region of the country, whereas the lowest rates were found in the mountainous western region of the country (Fig. 2). Likewise, the largest divergence rates occurred in the plains region in areas that experienced incongruent and rapid shifts in both temperature and water balance metrics (Fig. 3). High divergence rates were also found in other isolated areas with low topographic relief that had diverging vectors (e.g. Central Valley of California). Across all variables and time periods, the Southern Plains NEON domain had the highest velocity rates (range = 0.063–2.282 km yr^{-1}) driven principally by changes in climatic water balance (Table 1). In contrast, the Pacific Northwest had the lowest rates (range = 0.013–0.108 km yr^{-1}) across all three variables and time intervals (Table 1).

The direction of velocity vectors varied spatially and among the variables considered. For the period from

Table 1 Geometric means for climate velocity (km yr^{-1}) by National Ecological Observatory Network (NEON) domain for minimum temperature (T_{min}), actual evapotranspiration (AET) and climatic water deficit

| NEON domain	T_{min}				AET				Deficit			
	1916–2005	1916–1945	1946–1975	1976–2005	1916–2005	1916–1945	1946–1975	1976–2005	1916–2005	1916–1945	1946–1975	1976–2005
Appalachians	0.044	0.147	0.242	0.620	0.151	0.134	0.376	0.117	0.146	0.387	0.575	0.094
Atlantic Neotropical	0.175	0.374	0.605	1.101	0.033	0.186	0.360	0.107	0.121	0.344	0.124	0.102
Central Plains	0.110	1.187	0.391	0.596	0.346	0.500	0.711	0.711	0.344	0.415	0.429	0.501
Desert Southwest	0.075	0.164	0.122	0.354	0.060	0.251	0.366	0.613	0.025	0.097	0.277	0.351
Great Basin	0.058	0.142	0.070	0.192	0.056	0.154	0.158	0.105	0.026	0.071	0.101	0.119
Great Lakes	0.133	0.875	0.229	1.214	0.082	0.169	0.166	0.206	0.175	0.141	0.464	0.404
Mid Atlantic	0.099	0.220	0.450	0.668	0.127	0.095	0.353	0.146	0.054	0.180	0.272	0.258
Northeast	0.026	0.119	0.175	0.331	0.046	0.103	0.298	0.073	0.039	0.122	0.281	0.070
Northern Plains	0.257	1.102	0.190	0.873	0.277	0.611	0.631	0.603	0.147	0.447	0.405	0.599
Northern Rockies	0.036	0.096	0.039	0.159	0.029	0.077	0.045	0.063	0.020	0.030	0.041	0.077
Ozarks Complex	0.147	0.236	0.521	1.133	0.133	0.239	0.174	0.216	0.248	0.293	1.054	0.285
Pacific Northwest	0.033	0.102	0.033	0.108	0.013	0.061	0.035	0.105	0.018	0.026	0.034	0.106
Pacific Southwest	0.063	0.131	0.063	0.130	0.027	0.179	0.094	0.099	0.020	0.080	0.075	0.078
Prairie Peninsula	0.076	0.927	0.281	1.223	0.164	0.362	0.376	0.296	0.319	0.290	0.678	0.807
Southeast	0.173	0.201	0.847	1.021	0.118	0.225	0.253	0.245	0.096	0.322	0.565	0.261
Southern Plains	0.063	0.347	0.551	0.940	0.354	1.159	2.064	0.511	0.611	0.889	2.282	0.614
Southern Rockies	0.039	0.080	0.055	0.193	0.030	0.098	0.099	0.121	0.015	0.074	0.118	0.110
*Mean**	0.081	0.284	0.183	0.505	0.098	0.226	0.267	0.216	0.084	0.180	0.311	0.247

*Means are geometric means calculated across the study area using 30 arc-second resolution data.
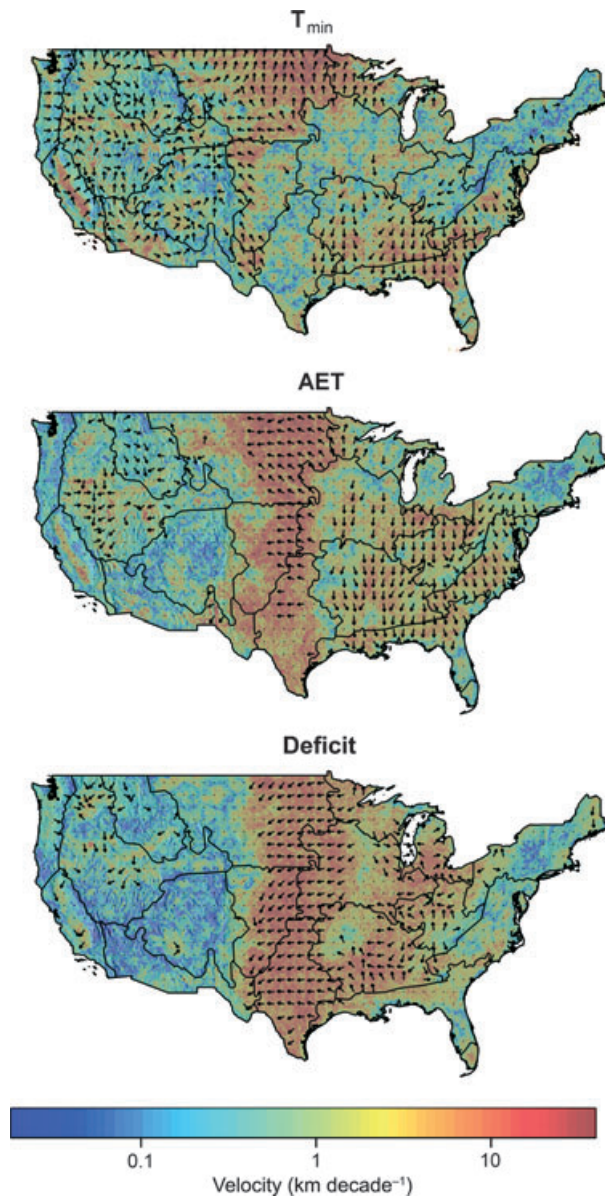
Fig. 2 Climate velocity for coterminous US calculated between 1916 and 2005 for minimum temperature (T_{min}), actual evapotranspiration (AET), and climatic water deficit. Arrows portray the directional component of velocity vectors and were calculated using 1° resolution data. Arrows are displayed in regions with significant climate trends (determined at the $P < 0.10$) based on a linear model fit to annual data and corrected for serial autocorrelation.

1916 to 2005, T_{min} vectors in the Northern Plains and Great Lakes domains were northward. For the Ozarks, Southeast, and Mid Atlantic domains, T_{min} vectors were principally southward, resulting in an apparent dipole of temperature vectors in the eastern half of the country (Fig. 2). For AET and deficit, vectors were principally toward the west in the plains regions. In the Ozarks, Southeast, and Central Atlantic regions, vectors
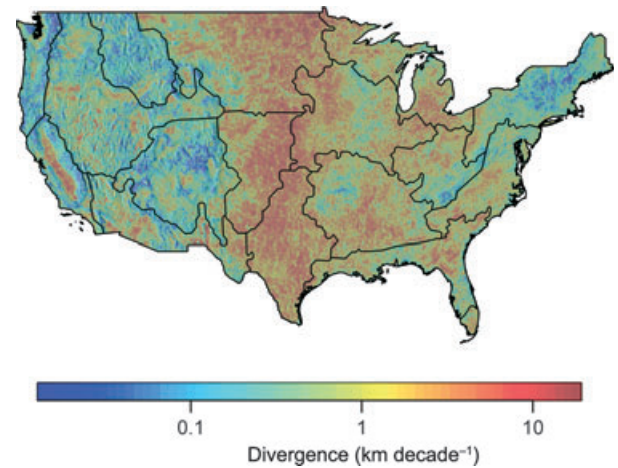

Fig. 3 Rate of climatic divergence between T_{min}, AET, and climatic water deficit velocity vectors for the period 1916–2005.

for AET were toward the south (Fig. 2). For the mountainous western region of the country, T_{min}, AET, and deficit vectors had low rates and variable (sometimes bimodal) directional distributions (Fig. 2) driven by the orientation of mountain ranges within each NEON domain. At local scales, the direction of velocity vectors was variable, showed divergent directions between T_{min} and AET, and was driven by the physiography of the local landscape (Fig. 4).

Velocity vectors exhibited sensitivity to data resolution. Estimates of climate velocity increased as the spatial resolution of the climate data was coarsened (Fig. 5). In addition, coarsening the resolution of the input data resulted in a reduction in the variance of vector directions (Fig. 5). Velocity vectors were also sensitive to climate variations over multi-decadal time periods suggesting that inferences to trends should
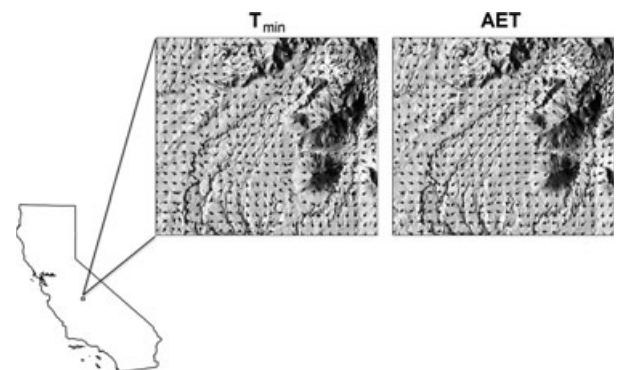
Fig. 4 Direction of climate velocity for T_{min} and AET for a subset of the study region in California, USA. Vectors are calculated using data at the 30 arc-second resolution from the period 1916–2005.
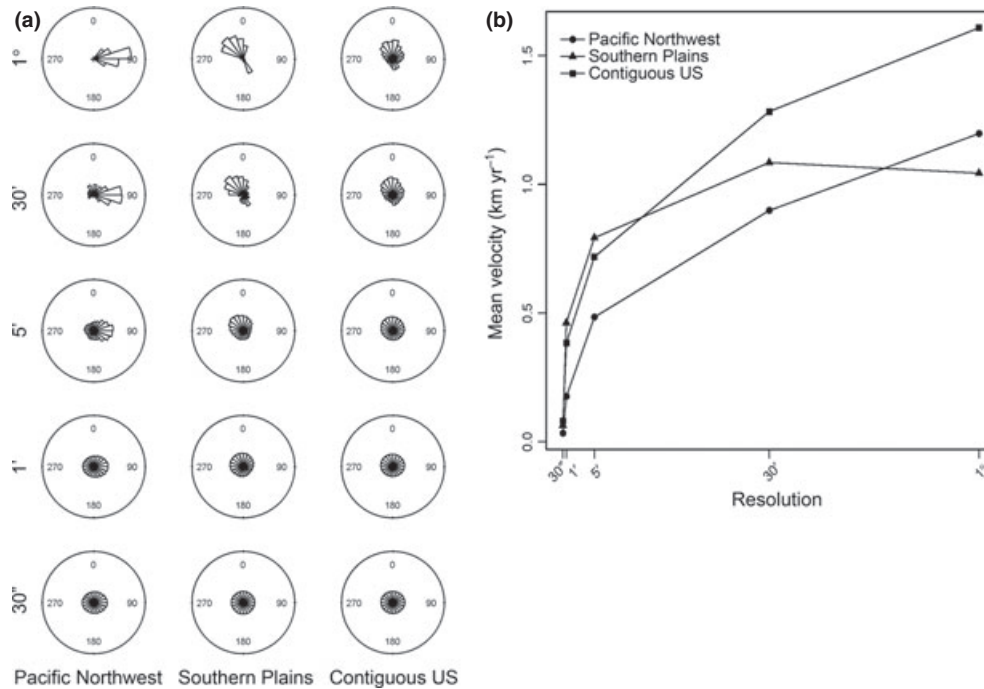
Fig. 5 Influence of climate data resolution on velocity estimates for T_{min} in the Pacific Northwest and Southern Plains NEON domains, and in the contiguous US as a whole. Rose diagrams (a) summarize the distribution of vector directions at each spatial resolution determined for the period 1916–2005. Climate velocity rates for each spatial resolution are summarized in (b).

consider transient decadal-scale variability. Velocities for T_{min} increased in the most recent time interval (t_3) reflecting a recent acceleration in warming whereas the same pattern was not observed for AET and deficit. In addition, the interval influenced vector directions. For example, from 1916 to 1945 and between 1976 and 2005, T_{min} vectors in the central and eastern regions of the country were principally northward showing a reversal between 1946 and 1975 associated with a temporary multi-decadal cooling trend (Fig. 6). For the 30-year time intervals examined here, statistically significant temporal trends in AET and deficit were often limited to regions with the highest rates, primarily in the central plains and eastern regions of the country (Fig. 6).

Discussion

Climate: complex dynamics in space and time

In this study, we show that climate velocity vectors during the 20th century for temperature and climatic water balance demonstrate a complex mosaic of rates, directions, and changes through time. Our estimates of climate velocity for T_{min} between 1916 and 2005 (geometric mean = 0.081 km yr^{-1}) are lower than those presented by Loarie *et al.* (2009) for average temperature for the A1B emission scenario for the period

2000–2100 for biomes present in the United States. (range = 0.11–0.71 km yr^{-1}). Our estimate for T_{min} for the period 1976–2005 (0.505 km yr^{-1}) is more consistent with those presented by these authors; however, a direct comparison is difficult given that we examine T_{min} as opposed to average temperature. Our velocity estimates are two orders of magnitude lower than those presented by Burrows *et al.* (2011) for the northern hemisphere (~3 km yr^{-1}) for the period 1960–2009 principally due to their use of coarse resolution (1°) data which underestimates the capacity of terrain to buffer changing climate (Loarie *et al.*,2009). We also demonstrate that climate velocity for variables that characterize the climatic water balance for the period 1916–2005 was similar in magnitude to those derived from temperature, but differed in direction, thus emphasizing what we consider an understudied facet of climate in global change science.

Velocity vectors for the variables considered were predominantly constrained by regional climate patterns in the eastern half of the country and physiographic influences in the western US. For instance, vectors for T_{min} calculated between 1916 and 2005 reflect the influence of regional warming in the Northern Plains (resulting in northerly vectors) and cooling (resulting in southerly vectors) in the Southeast, Ozarks, and Central Atlantic regions. The cooling trend identified in the
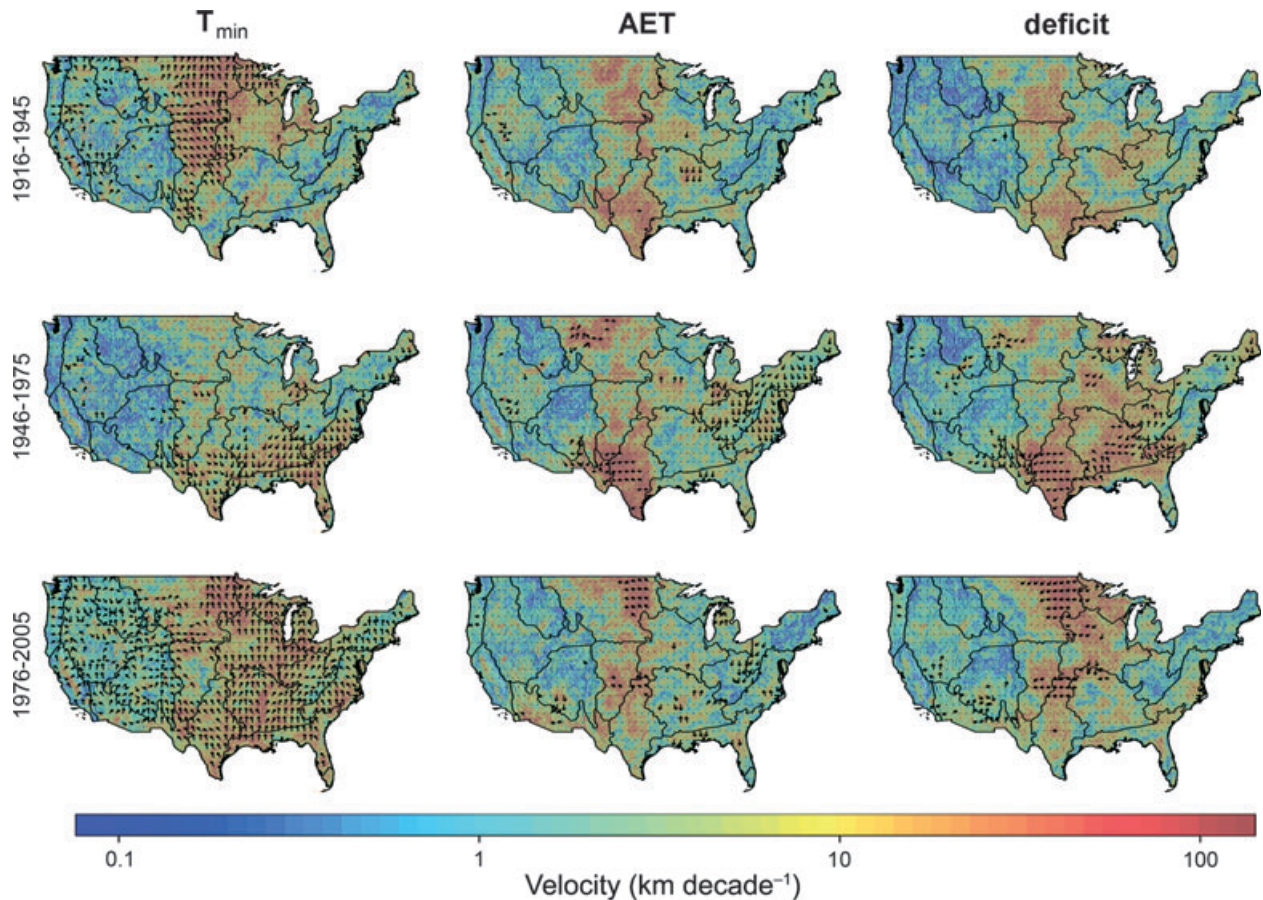
Fig. 6 Climate velocity for coterminous US calculated for three 30 year intervals (1916–1945; 1946–1975; 1976–2005) for minimum temperature (T_{min}), actual evapotranspiration (AET), and climatic water deficit. Arrows portray the directional component of velocity vectors and were calculated using 1° resolution data. Arrows are displayed in regions with significant climate trends (determined at the $P < 0.10$) based on a linear model fit to annual data and corrected for serial autocorrelation.

Southeast has been previously noted (Portmann *et al.*, 2009) and is likely associated with concurrent changes in precipitation (Portmann *et al.*, 2009) and subsequent land-atmosphere feedbacks (Pan *et al.*, 2004). There have also been well-documented changes in low-frequency climate variability that have resulted in asymmetric temperature trends across the continental US with enhanced warming across the northern and western tier of the United States and reduced warming or even cooling in the southeast (Abatzoglou & Redmond, 2007). These dynamics resulted in a dipole of vectors for T_{min} between the Northern Plains and the Southeast with a neutral region of statistically nonsignificant vectors centered on the Prairie Peninsula and Central Plains regions (Fig. 2). In contrast to the eastern half of the country, the mountainous west showed low rates on average and variable directions driven principally by physiographic features. For example, at the 1° resolution, T_{min} vectors in the Pacific Northwest and Pacific Southwest were oriented toward

the east (Fig. 2) given that temperature trends were positive and cooler temperatures were found upslope along the north–south-oriented Cascade and Sierra Nevada Mountain ranges. At more local scales, velocity vectors sometimes exhibited opposing directions with T_{min} pointing upslope and AET vectors pointing downslope (Fig. 4).

Climate velocity estimates were sensitive to the spatial resolution of analysis, but scaled in a predictable fashion. Coarsening the resolution of the input data often resulted in the maintenance of the mean direction and a reduction in the variance of the directional distribution (Fig. 5a). This is the commonly observed 'support effect' for regionalized spatial variables (Olea, 1990). In addition, estimates of the rate of climate velocity increased as the spatial resolution of the climate data was coarsened (Fig. 5b). The sensitivity of the rate to data resolution varied with topographic complexity. Areas with little topography showed an asymptotic response; i.e. high sensitivity at fine spatial resolutions and no sensitivity at

coarser resolutions. In contrast, areas with complex terrain did not exhibit asymptotic behavior over the range of data resolutions examined. We attribute these scaling characteristics to the spatial structure in the underlying climate variables. These data exhibit greater self-similarity at short lag-distances (results not shown) for topographically homogenous regions as compared to topographically complex regions. The high sensitivity of velocity rate to spatial resolution at fine grain sizes also suggests that the use of topographically informed climate data (Dobrowski, 2011) will result in lower climate velocity estimates than those presented here. This is an important consideration for assessing the capacity of organisms to keep pace with changing climate in areas of complex terrain.

Climate velocity estimates were sensitive to the time interval over which they were calculated. Rates calculated over a 90-year interval (1916–2005) were lower on average than those calculated from the 30 year subsets that comprised the study period. Larger rates for the shorter 30 year intervals are expected given that longer intervals average out low-frequency natural variability of the climate system, especially decadal to multi-decadal variations in precipitation. However, we note greater ambiguity in identifying climate velocity vectors at shorter time intervals due to a decrease in the signal to noise ratio. This was most apparent for the water balance metrics we examined over the 30-year intervals assessed (Fig. 6).

Multiple limiting climatic factors

A large body of evidence suggests that species abundance, richness, and range limits are determined in part by multiple climatic factors. This is supported by research in various disciplines including species distribution modeling (Dobrowski *et al.*, 2011; Smith, in press), ecological ordination studies (Austin, 1985; Pausas & Austin, 2001), Quaternary paleoecology (Jackson & Overpeck 2000), and biogeography (Woodward, 1987; Stephenson, 1990; Francis & Currie, 2003; Woodward *et al.*, 2004). Despite this longstanding recognition, climate change studies predominantly focus on the biotic consequences of temperature changes, and in particular changes in mean annual temperature (T_{mean}), a metric of energy availability that has a limited direct mechanistic relationship with plant distribution (Woodward *et al.*, 2004). Changes in T_{mean} have been related to changes in phenology (Cleland *et al.*, 2007; Parmesan, 2007), growth rates (Millar *et al.*, 2004), and a host of other biotic responses (Parmesan, 2006). In many instances the proximal mechanism of influence in these studies is not clear and may simply be due to the correlation between T_{mean} and other bioclimatic factors (e.g.

minimum temperature, growing degree days, AET, etc.) in which a more direct causal relationship between climate and biotic response is known. The focus on temperature also belies the fact that biota, and in particular plants, require the concomitant availability of both energy and water for growth and reproduction.

Not only are multiple climate factors important to shaping the biotic response to climate change but interactions between climate factors are relevant. The temporal covariance between energy and moisture availability plays a key role in determining how species respond to changes in each of the climatic variables independently. For instance, changes in temperature (e.g. warming) may occur during periods of the year in which available moisture is limited (thus increasing climatic water deficit), during periods of the year in which water is not limited (increasing AET and productivity), or both. This complex interplay between climate trends and the seasonal timing of water and energy availability illustrates the need for mechanistic bioclimatic predictors that can account for these contingencies (Stephenson, 1990). It also highlights the limitation of using univariate or bivariate changes in T_{mean} and precipitation to describe what are intrinsically complex temporal interactions. In addition, these metrics cannot accommodate for the fact that the temporal covariance of water and energy can vary in sign being negative (e.g. positive temperature trend and lower water availability) or positive (e.g. positive temperature trend and greater water availability) depending on a range of factors including large-scale climate variability, local meteorology, and land-cover changes (Roderick & Farquhar, 2002; McVicar *et al.*, 2012). In contrast to the use of T_{mean} and precipitation anomalies in climate change impact studies, changes in climatic water balance can account for the temporal covariance of water and energy and thus have a more mechanistic link to the limiting resources that define the range of plant species, constrain growing season length, and drive productivity (Stephenson, 1990; Gavin & Hu, 2006; Littell *et al.*, 2008).

Climate velocity and species response

Climate velocity vectors are well suited to assessing the effects of multiple climate factors on biota because they allow for standardizing multiple climate variables to a common response type (displacement rate and direction) that can be related to the dispersal capacity of organisms. A recent global meta-analysis of observational studies (Chen *et al.*, 2011) found that latitudinal shifts for a range of taxa (not including plants) averaged 1.6 km yr^{-1}, a rate that is consistent with expectations for a few regions (Great Lakes, Prairie Peninsula),

but is more than double our highest calculated rate for the entire study area (T_{min} for 1976–2005) based on our 30 arc-second estimates. Our results are more consistent with estimates presented by Parmesan & Yohe (2003), who found average latitudinal shifts of 0.61 km yr^{-1}. This latter rate is consistent with paleoecological estimates for tree migration which range from 0.1 to 1 km yr^{-1} (Clark et al., 1998). However, the choice of scale affects comparisons between climate velocity and observed shifts in species' distributions. Species' responses are likely affected by dispersal ability and their ability to take advantage of fine-scaled climate variation. One scale may be inappropriate for all comparisons (Fig. 5), even among species with similar climatic requirements.

Our results suggest that the expectation of poleward and upward shifts associated with all taxa, previously referred to as a 'globally coherent fingerprint' (Parmesan & Yohe, 2003), may be derived from an oversimplification of the climate dynamics that have been observed over the 20th century. For instance, in the US T_{min} vectors calculated over decadal and century scales demonstrate complex dynamics (e.g. northerly and southerly directions, direction reversal through time) that vary regionally. Similarly, climate displacement vectors for metrics of the water balance were predominantly oriented toward the west and south, showing regional variability. Divergent climate vectors between temperature and water balance may help explain why roughly 10–30% of species assessed in previous climate change studies have not shifted their ranges whereas nearly 25% of species have shifted their ranges in a direction counter to expectations (Parmesan & Yohe, 2003; Chen et al., 2011; Crimmins et al., 2011; Tingley et al., in press). For instance, over the 20th century in the Sierra Nevada, Tingley et al. (in press) report that only half of the bird species they examined shifted their range upslope and that range shifts varied regionally and could be better predicted using both changes in temperature and precipitation as opposed to temperature alone. Similarly, in a novel study of eastern North American trees, Zhu et al. (2011) examined the distribution of conspecific seedlings and adults for 92 tree species using Forest Inventory and Analysis data. The authors found little evidence of northerly range expansion, but instead found evidence for range contractions for a majority of the species studied. The authors suggest that the incongruence between their observations and expectations could be due to multiple factors including data limitations, successional changes, and source sink dynamics, among other possibilities. Range expansion for tree species is likely sensitive to changes in climatic water balance. For instance, mortality of juvenile trees has been shown to be influenced by drought (deficit) in western US forests (van Mantgem & Stephenson, 2007) and growth rates/productivity (AET) in eastern forests (Kobe, 1996; Caspersen & Kobe, 2011). Our results show that velocity vectors for AET and deficit during the 20th century in the eastern US were not poleward, but instead were principally to the south and west or were ambiguous when calculated at shorter time intervals. Thus, Zhu et al.'s (2011) findings are not surprising if one reassesses the climatic basis for the expectation of northerly shifts.

Conclusions

Our analysis paints a complex picture of the climate in the contiguous US during the 20th century; one in which velocity vectors vary regionally, show variable and opposing directions among the variables considered, and shift direction through time. The complexity of velocity vectors emphasizes that individual organisms in different locations experience different climate forcings, and that the location and interval over which biotic responses are observed should influence our expectation of the direction and magnitude of potential response. In addition, given that limiting climatic factors vary among taxa, our observations of divergent vectors between temperature and water balance could result in taxonomic variability in species responses to climate change and potential asynchrony in species interactions (Parmesan, 2006).

The analysis presented does not provide a direct evaluation of 20th century climate change impacts for individual taxa, but instead provides a geographic assessment of the climate forcings that organisms have experienced during the study period. Accordingly, additional research is warranted to assess whether climate velocity of individual or multiple climate variables can be used to better characterize observed changes in phenology or range shifts for specific taxa, and to estimate climate velocity of water balance for the 21st century. Beyond global change studies, the use of climate velocity has potential utility in conservation science including identifying climatic refugia, prioritizing protected areas, and assisted migration planning. In conclusion, we emphasize that moving away from viewing climate as simple monotonic changes in temperature is a necessary step in advancing our understanding of how species have and will respond to climate shifts.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix A. Detailed methods for water balance model.
Appendix B. Code for replicating water balance calculations in R.
Appendix C. Validation of climate gradients used in water balance model.

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