Ecosystem Processes and Human Influences Regulate Streamflow Response to Climate Change at Long-Term Ecological Research Sites

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Analyses of long-term records at 35 headwater basins in the United States and Canada indicate that climate change effects on streamflow are not as clear as might be expected, perhaps because of ecosystem processes and human influences. Evapotranspiration was higher than was predicted by temperature in water-surplus ecosystems and lower than was predicted in water-deficit ecosystems. Streamflow was correlated with climate variability indices (e.g., the El Niño–Southern Oscillation, the Pacific Decadal Oscillation, the North Atlantic Oscillation), especially in seasons when vegetation influences are limited. Air temperature increased significantly at 17 of the 19 sites with 20- to 60-year records, but streamflow trends were directly related to climate trends (through changes in ice and snow) at only 7 sites. Past and present human and natural disturbance, vegetation succession, and human water use can mimic, exacerbate, counteract, or mask the effects of climate change on streamflow, even in reference basins. Long-term ecological research sites are ideal places to disentangle these processes.

Keywords: precipitation/runoff ratio, trend, succession, socioecological systems, Budyko curve

Although many factors affect streamflow, recent concerns have been focused on the effects of climate change on streamflow. Increasing temperature, more-severe storms, advanced snowmelt, and declining snow cover are associated with increased drought and flooding (Groisman et al. 2004, Stewart et al. 2005, Huntington 2006, Barnett et al. 2008, Karl et al. 2009, McDonald et al. 2011, USDOI 2011). Nevertheless, many human actions, natural disturbance effects, and ecosystem processes complicate, mitigate, and potentially counteract the climate effects on streamflow (Meybeck 2003, Jones 2011). Relevant human actions include ongoing disturbance and legacies of past disturbance, as well as global climate change. Understanding how climate change, social systems, and ecosystem processes affect streamflow is critical for mitigating conflicts between economic development and environmental conservation.

Long-term studies of headwater basins, the source areas for water supplies, provide an informative starting point for understanding the effects of climate, social factors, and ecosystem processes on streamflow (figure 1). The US Forest Service (USFS) Experimental Forests and Ranges (EFRs) and the US Department of Agriculture Agricultural Research Service (ARS) established long-term studies in small basins throughout the United States beginning in the early 1900s (see supplemental table S1, available online at *http://dx.doi.org/10.1525/bio.2012.62.4.10*). Four EFRs (AND, CWT, HBR, LUQ; for the site-name abbreviations, see table S1) and one ARS site (JRN) became member sites of the US Long Term Ecological Research (LTER) Network as early as 1980. Some LTER Network sites also utilize streamflow records from the US Geological Survey (USGS) National Water Information Service database. Some headwater basin studies participate in the USGS Hydrologic Benchmark Network; the USGS Water, Energy, and Biogeochemical Budgets (WEBB) program; or the Canadian HydroEcological Landscapes and Processes (HELP) program. Climate and hydrologic data from many sites have been publicly available since the 1990s (*www.fsl.orst.edu/climhy*).
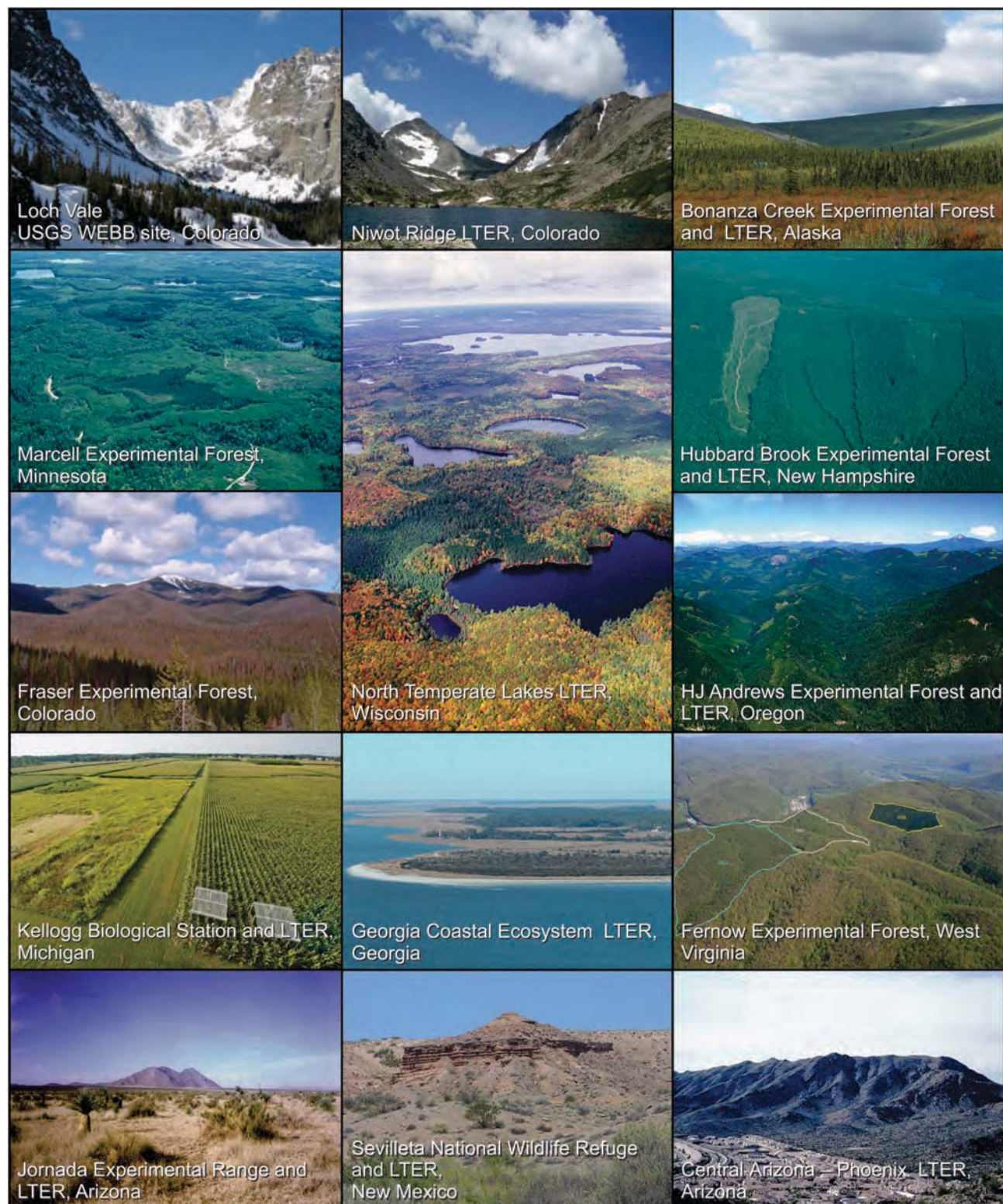
Figure 1. Selected study basins from US Long Term Ecological Research (LTER) sites, US Forest Service Experimental Forests and Ranges, and US Geological Survey (USGS) Water, Energy, and Biogeochemical Budgets (WEBB) sites.

Although they are less numerous than, for example, the USGS reference sites used in studies of climate change (e.g., Poff et al. 2007), LTER study sites provide unique insights into the interacting effects of social systems, ecosystems, and climate change on hydrology. In common with all eco-systems on Earth, the study basins have a long history of

natural disturbances and human impacts. Most of the study basins experienced no management during the period of record, but all of them are experiencing succession from past human disturbances; many continue to experience natural disturbances; and a few have agriculture, forestry, or residential development. Moreover, these study sites have matching records of climate drivers and hydrologic responses from (in most cases) relatively small areas. Therefore, these sites and analyses provide a unique opportunity to compare hydrologic responses to climate drivers over multiple decades and to interpret the responses on the basis of concurrent studies of social and ecosystem processes.

A conceptual model of social systems, climate, ecosystems, and water

The fundamental premise of the present article is that streamflow responds to ecosystem processes, which, in turn, respond both to climate drivers and to social drivers (figure 2). Social systems are a primary driver of streamflow through human water use and regulation and may indirectly affect streamflow through human-induced climate change. However, even in headwater ecosystems lacking human residents, social factors, including population dynamics, economic development, political conflicts, and resource policies, produce ecosystem disturbances, including forest harvest or clearance, grazing, agriculture, mining, and fire. In turn, these disturbances influence ecological succession, evapotranspiration, and streamflow.

Climate drivers—especially precipitation, temperature, snow and ice, and extreme events—also create ecosystem disturbances (e.g., wildfires, floods, wind and ice storms). Ecosystems continuously respond to disturbances (both human and natural) through ecological succession, and disturbances and responses differ among biomes. Ecosystems, social systems, and climate also respond to streamflow. Headwaters provide water for downstream ecosystems and communities, and ecosystem processes drive climate through evapotranspiration and energy exchange (figure 2).
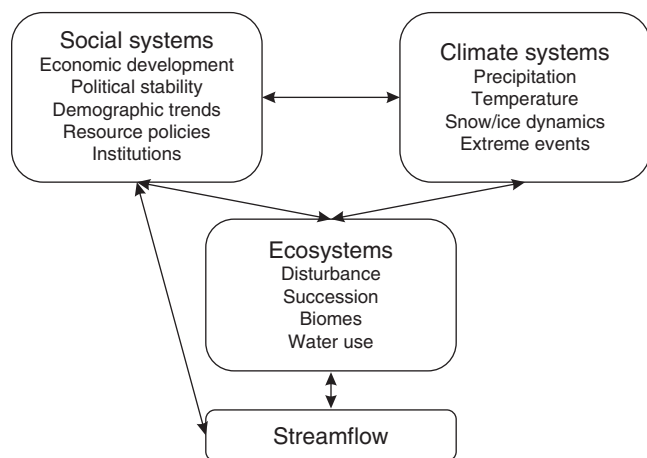
Figure 2. Conceptual model of social, ecological, and climate influences on streamflow.

Many of the study sites experienced social effects on ecosystem processes prior to becoming LTER sites. Most of the temperate forest in the eastern half of the United States and Canada and tropical forests in Puerto Rico experienced forest harvest, land clearance for agriculture, and grazing, followed by land abandonment (Swank and Crossley 1988, Foster and Aber 2004). Sites in the southwestern United States experienced intensive grazing of domestic animals during the past four centuries (Peters et al. 2006). Boreal forest, temperate wet forest, and tundra sites experienced varying fire regimes, mostly driven by climate but, in some cases, affected by prehistoric peoples (e.g., Weisberg and Swanson 2003). Some sites contain agriculture, forestry, and urban development.

In this study, we primarily examine the relationship between climate and streamflow on the basis of energy exchange. In cases in which streamflow behavior cannot be explained purely by climate, other hydrologic processes, as well as past and present human and natural disturbance effects on ecosystems, are considered as possible explanations.

Study sites and questions

In this study, we examined long-term records of air temperature (T), precipitation (P), and streamflow (Q) from 35 basins at US LTER Network sites, USFS EFRs, USGS WEBB sites, and Canadian sites (table S1, figure 3a, 3b). The study sites were headwater basins that have mostly experienced no management since their records began. Nevertheless, the study basins have undergone succession in response to earlier natural or human disturbance, and some basins experienced natural disturbance during the periods of record. The records of T, P, and Q were obtained from the US LTER Network's Climate and Hydrology Database Projects (ClimDB/HydroDB; *http://climhy.lternet.edu*), supplemented by USGS streamflow data (*http://co.water.usgs.gov/lochvale, http://waterdata.usgs.gov/nwis*) and data from the Canadian HELP program (table S1).

The study basins ranged from 0.1 to 10,000 square kilometers; 2 were less than 10 hectares (ha), 5 were 10–100 ha; 10 were 100–1000 ha; 5 were 1000–10,000 ha; 8 were 10,000–100,000 ha; 2 were 100,000–1 million ha; and 2 were undefined (FCE, MCM; see table S1). The two largest basins were near ARC and GCE; eight additional large basins are located in the vicinity of CAP, HFR, JRN, KBS, NTL, OLY, PIE, and SEV. The smallest basins (smaller than 100 ha) are mostly associated with USFS or Canadian sites, at AND, BES, CWT, DOR, FER, HBR, MAR, and TLW.

The study sites represent many biomes (potential vegetation) (figure 4). More than half of the sites were temperate forest (CAS, CWT, DOR, HBR, HFR, FER, KEJ, MAR, MRM, NTL, PIE, TLW), temperate wet forest (AND, CAR, MAY, OLY), and boreal forest (ELA, FRA, LVW, TEN, UPC). The remainder includes tundra or cold desert (ARC, MCM, NWT), warm desert (CAP, JRN, SEV), cool desert or woodland (BNZ), woodland or grassland (BES, FCE, GCE, KBS, KNZ, SBC), and tropical rainforest (LUQ). Actual
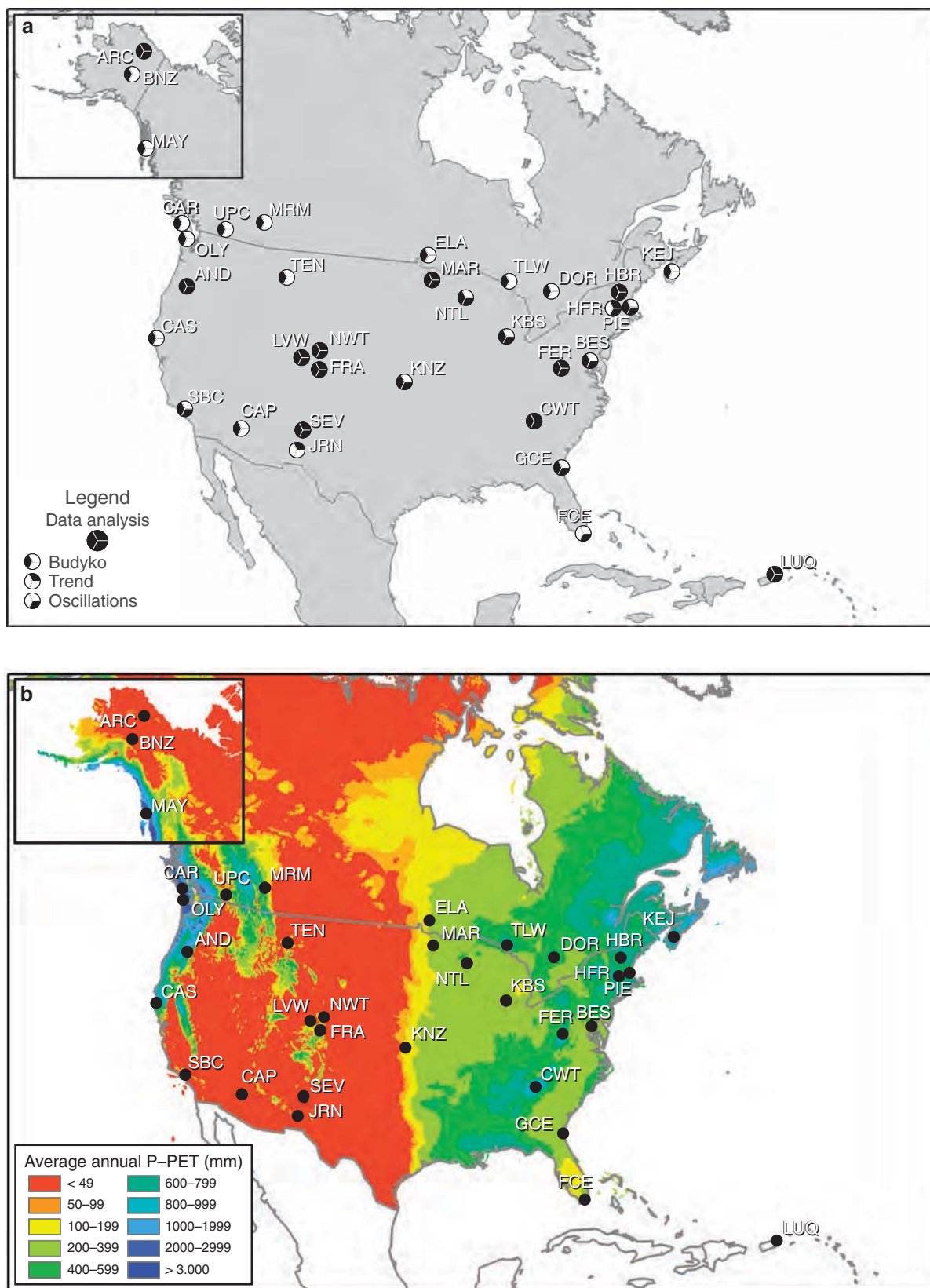
Figure 3. (a) Map of sites used in this analysis. The study-site characteristics and abbreviations are in supplemental table S1, available online at **http://dx.doi.org/10.1525/bio.2012.62.4.10.** *The symbols indicate which of the three analyses (Budyko curve, trends, and correlation with climate indices [oscillations]) were conducted with data from that site. (b) Map of average annual precipitation (P) minus potential evapotranspiration (PET) in millimeters (mm) with study-site locations.*
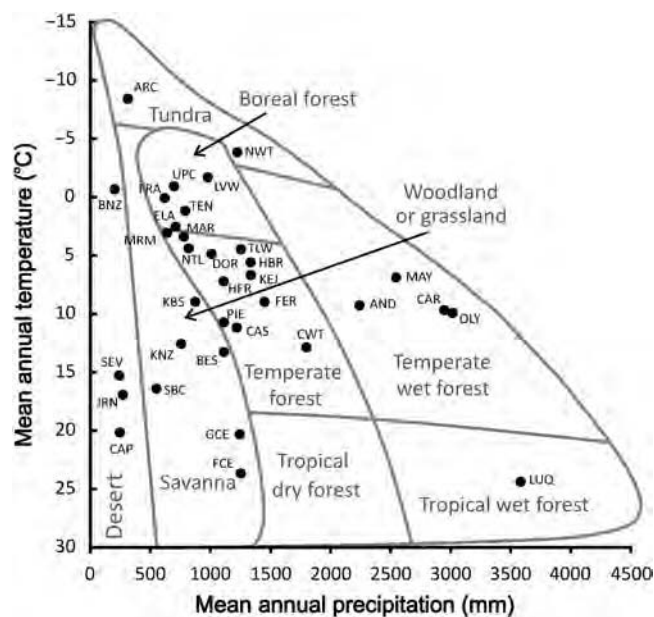
Figure 4. Mean annual temperature, mean annual precipitation, and biomes of the study sites. The study-site abbreviations are in supplemental table S1, available online at **http://dx.doi.org/10.1525/bio.2012.62.4.10.** *Data for the MCM site are not shown. Abbreviations: °C, degrees Celsius; mm, millimeters.*

and potential vegetation may differ because of disturbance (table S1).

In our analyses, we examined three questions, using successively more-stringent requirements of data sets and interpreted these results in the light of ecological and social factors: (1) How is potential evapotranspiration (PET) related to actual evapotranspiration (AET) at each site, and how do these relationships compare with the theoretical Budyko curve ($n = 30$ sites)? (2) How is streamflow correlated with climate indices (e.g., the El Niño–Southern Oscillation [ENSO], the Pacific Decadal Oscillation [PDO], the North Atlantic Oscillation [NAO]; $n = 21$ sites)? (3) How have temperature, precipitation, and streamflow changed over time ($n = 19$ sites)?

Energy- and water-balance relationships to observed water use

The values of T, P, and Q from 30 sites with matched T, P, and Q (table S1, figure 3) were used to calculate PET and AET (i.e., P – Q). These values were plotted on the Budyko curve (Budyko 1974), which displays the relationship between PET and AET, each indexed by P (figure 5a). Thirty of the 35 sites had data on T, P, Q, and basin area for a common 10-year period (1993–2002), although a slightly adjusted period was used for 10 of the sites (figure 5b). PET was calculated from T (after Hamon 1963) on the basis of the number of daylight hours, mean monthly temperature, and the saturated vapor pressure. Annual PET was calculated as a sum of monthly values. The Budyko curve assumes that the

water balance is Q = P – ET (evapotranspiration), with no significant losses to or gains from groundwater, and that the basins are at steady state, unaffected by vegetation dynamics (Donohue et al. 2007).

The distribution of study basins on the Budyko curve reveals that observed water use in ecosystems in small basins deviated systematically from its expected dependence on energy and water balances. As was expected, observed ecosystem water use (AET ÷ P) was positively correlated to energy and water inputs to evapotranspiration (PET ÷ P) in sites with a water surplus (P > PET) and insensitive to increases in energy at sites with a water deficit (P < PET), following the theoretical Budyko curve (figure 5b). However, only 7 of 30 sites (ARC, DOR, FRA, HBR, KEJ, KNZ, and OLY) fell on the Budyko curve, where observed water use (AET ÷ P) was equal to predicted water use (PET ÷ P) (figure 5b). Of the 19 sites with a moisture surplus (P > PET) that did not fall on the Budkyo curve, 14 were above it, with higher than expected evapotranspiration (AET ÷ P > PET ÷ P). Of the five sites with moisture deficits (P < PET), four fell below the Budyko curve, with lower than expected evapotranspiration (AET ÷ P < PET ÷ P) (figure 5b).

This result may indicate that ecosystems evaporate, transpire, and store more water than would be expected on the basis of temperature and day length at wet sites and less than would be expected at dry sites. Ecosystem structure (e.g., rooting depth, leaf area) and processes (e.g., adaptations to water deficits) may produce lower streamflow in wet sites and higher streamflow in dry sites than would be predicted from energy and water balances alone. However, other factors may also explain the departures of the sites from the theoretical Budyko curve. For instance, the PET value estimated from climate-station T records may not represent PET over entire basins, especially in mountain sites (e.g., AND, NWT, LVW). AET ÷ P is also considerably overestimated from P – Q in basins in which the groundwater recharge bypasses the stream gauge (Graham et al. 2010, Verry et al. 2011).

When the annual values of T, P, and Q are plotted on the Budkyo curve, the interannual variation of AET relative to PET varies among biomes (figure 5c, 5d). Variation in AET ÷ P was less than in PET ÷ P at the desert sites (CAP, SEV) and at forested sites (AND, CAS, CWT, FER, HBR, MAR, NTL) (figure 5d). In contrast, at alpine sites (LVW, NWT), the interannual variation in AET ÷ P was large relative to the variation in PET ÷ P. This behavior of sites relative to the Budyko curve implies that ecosystems are capable of adjusting AET to compensate for climate variability at desert, grassland, and forest sites, but less so at alpine sites.

Ecosystems have more-similar rates of net primary productivity per unit precipitation in dry than in wet years (Huxman et al. 2004). Comparisons of long-term AET and PET from study basins to the theoretical Budyko curve (figure 5) suggest that AET varies in a narrower range than would be expected from energy and water balances alone, which underscores the importance of ecosystem process effects on streamflow.
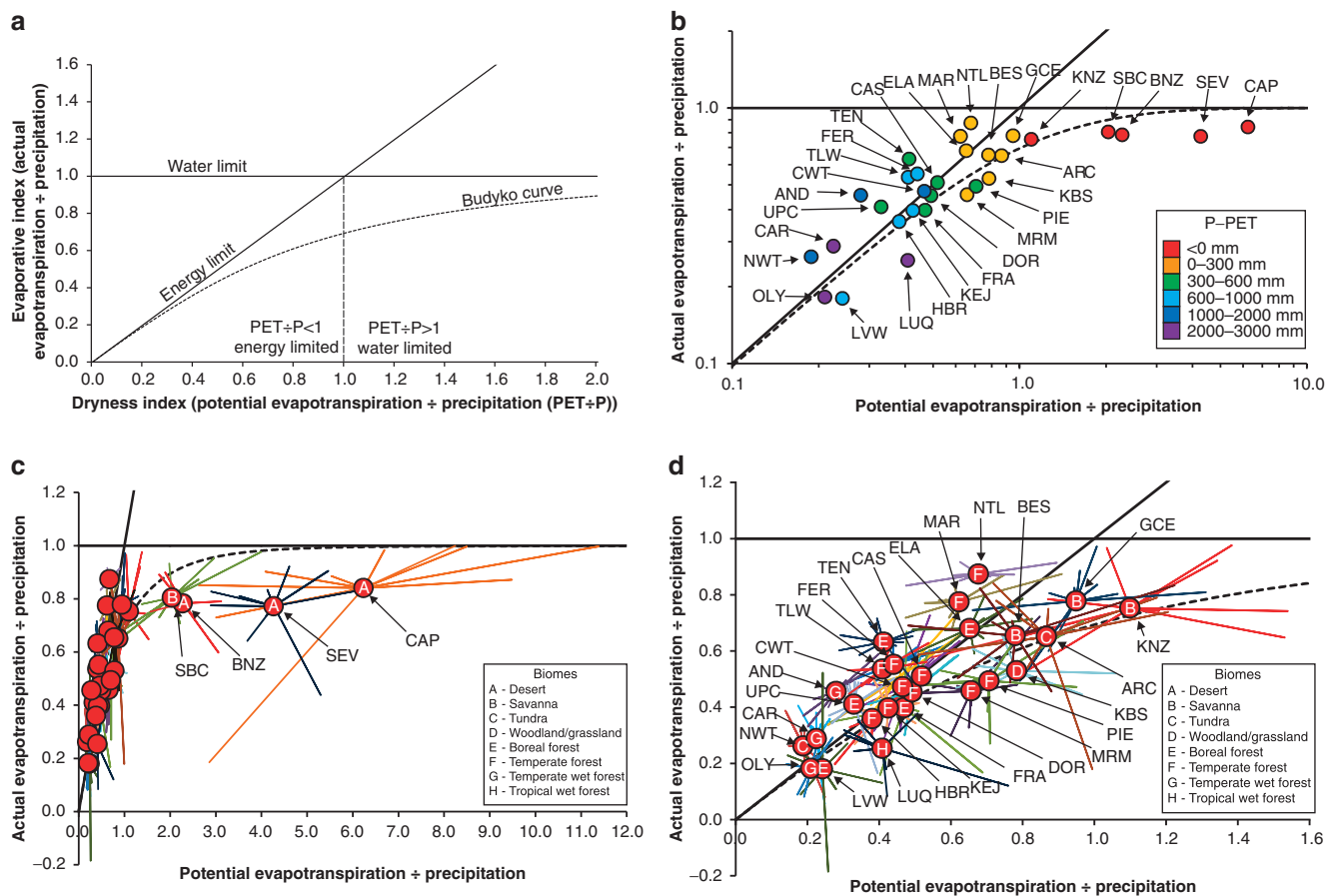
Figure 5. (a) The theoretical Budyko curve is a plot of the evaporative index, which is actual evapotranspiration (AET) divided by precipitation (P), where AET = P − Q, and Q = streamflow) as a function of the dryness index, which is potential evapotranspiration (PET) divided by P. PET is calculated from T (temperature), so it is a measure of energy balance, whereas AET is the difference between inputs (P) and outputs (Q), or observed water use (AET = P − Q). Values of PET ÷ P that are greater than 1 indicate an arid climate, whereas values of PET ÷ P that are less than 1 indicate a humid climate. Because AET is calculated as P − Q, AET ÷ P is simply 1 − (Q ÷ P), and high values of AET ÷ P represent low runoff ratios. For values of PET ÷ P that are less than 1 (wet sites), the theoretical Budyko curve approaches the energy limit, where AET = PET, the line where observed ecosystem water use equals PET based on T. For values of PET ÷ P that are greater than 1 (dry sites), the curve approaches the water limit, where AET = P, the line where observed ecosystem water use equals P inputs. (b) Observed Budyko curve showing points for 30 sites. (c) Interannual Budyko curve showing variation over a 10-year period for the dry sites. (d) Interannual Budyko curve showing variation over a 10-year period for the wet sites. In panels (c) and (d), each annual value of AET ÷ P as a function of PET ÷ P is connected to the 10-year mean by radial lines. The study-site characteristics and abbreviations are in supplemental table S1, available online at http://dx.doi.org/10.1525/bio.2012.62.4.10. Abbreviation: mm, millimeters.

Streamflow and regional climate oscillations

We examined the relationship of three climate indices (ENSO, PDO, and NAO) to Q at 21 sites (tables S1 and S2). These indices measure multiyear or multidecadal oscillations of sea-surface temperatures and atmospheric-pressure differentials in the east–central tropical Pacific (ENSO), the northern Pacific (PDO), and the northern Atlantic (NAO). They are correlated with local and regional temperature, precipitation, and streamflow in the United States (Cayan et al. 1999, Barlow et al. 2001, Enfield et al. 2001). The sites included in this analysis had fewer than 10 years of continuous (monthly) Q at one or more gauging stations, separated

into a cool season (November–April) and a warm season (May–October). Correlated streamflow records (Pearson's $r > .80$) were pooled at study sites with multiple stream gauges. Climate indices were obtained from online databases (NAO, *www.cgd.ucar.edu/cas/jhurrell/indices.html*; ENSO, *www.cdc.noaa.gov/ClimateIndices/List*; PDO, *www.esrl.noaa.gov/psd/data/correlation/pdo.data*). The streamflow–climate oscillation relationships were tested using generalized least squares models with autoregressive moving average functions; the models were evaluated with the Durbin–Watson test statistic and Akaike's information criterion. The results are shown as the sign (+ or −) of the relationship of streamflow

to climate oscillation variables that were significant at $\alpha < .10$ in the models (table S2).

The cool-season (November–April) and warm-season (May–October) streamflow values were significantly correlated with at least one climate index or interaction term at all sites except FRA, KNZ, NWT, and PIE (table S2). Significant correlations of streamflow were more frequent with ENSO (11, plus six interactions) and PDO (10, plus one interaction) than with NAO (4, plus six interactions) (table S2). Significant correlations were also slightly more frequent in winter (18) than in summer (14). These findings extend Greenland and colleagues' (2003) analysis of climate indices, temperature, and precipitation at US LTER Network sites and corroborate the results of other studies. Molles and Dahm (1990) noted that streamflow in two rivers in New Mexico was significantly higher during El Niño (warm sea-surface temperatures in the eastern Pacific) than during La Niña conditions. Cayan and colleagues (1999) showed that days with high daily precipitation and streamflow were more frequent than average in the US Southwest and less frequent in the Northwest during El Niño because of effects on snowpack accumulation and the subsequent melt. Enfield and colleagues (2001) found that sea-surface temperatures in the northern Atlantic are correlated with those in the northern Pacific and are associated with variations in streamflow in the Mississippi River and in Florida. Sea-surface temperature and pressure anomalies originating in the North Pacific affect cyclonic circulation over the East Coast and summer precipitation, streamflow, and drought (Barlow et al. 2001).

These findings underscore the importance of separating the effects on streamflow of climate variability from long-term trends. Because the ENSO oscillation has a wavelength of 2–7 years, trends in climate and streamflow data sets over fewer than 20 years may simply reflect ENSO. Similarly, the PDO has a wavelength of 4–16 years (MacDonald et al. 2005), with mostly negative PDO in the 1950s to the mid-1970s and mostly positive PDO from 1976 to 1998. The NAO was predominantly negative between the 1950s and the early 1970s and was mostly positive between the 1980s and the early 1990s. As a result, climate and streamflow trends from the 1950s to 2000 may be strongly affected by these climate oscillations. For example, at ARC, streamflow increased between 1988 and 2003, but declined between 1988 and 2008, so lengthening the record shifted the direction of apparent change. The lack of statistically significant increases in minimum temperature at the tundra ARC and boreal forest LVW sites (see the next section) may also be attributed to confounding effects of climate oscillations on these relatively short-term records.

Climate oscillations influence ecosystem processes through streamflow and moisture. Streamflow was slightly more weakly correlated to climate indices in summer than in winter, perhaps because precipitation and streamflow are more closely related when ecosystems are dormant. ENSO is linked to aquatic-community structure in the Southwest

(Sponseller et al. 2010), PDO is related to salmon returns in the Northwest (Mantua et al. 1997), and NAO is linked to stream salamander abundance in the Southeast (Warren and Bradford 2010). Headwater streamflow records are just beginning to be long enough to relate climate variability and trends to ecosystem processes and population dynamics.

Climate and streamflow trends at long-term headwater basin study sites

Nineteen sites had long-term records suitable for testing trends in T, P, and Q (table S1). Sites were included in the analysis if they had overlapping records of T, P, and Q that exceeded 20 years. The climate and streamflow record lengths used for trend estimation ranged from 20 to just over 60 years; five were 20–30 years; one was 30–40 years; four were 40–50 years; seven were 50–60 years; and two were more than 60 years (table S1). The records exceeding 40 years are from USGS gauges and nearby climate stations (CAP, GCE, JRN, OLY, SBC, SEV), USFS EFRs that became US LTER Network sites (AND, CWT, HBR), other LTER Network sites (HFR), and USFS EFRs (FER, MAR) that did not become LTER Network sites. The records less than 40 years in length were USGS gauges and nearby climate stations at LTER Network sites, WEBB sites, and EFRs (ARC, FRA, LUQ, LVW, NTL, and NWT).

Interannual trends in minimum and maximum daily T, P, Q, and runoff ratios (Q:P) were estimated using linear regression and the Mann–Kendall nonparametric trend test (Helsel and Hirsch 2002). In these analyses, we used the period of record or from 1950 onward. Linear regressions and Mann–Kendall tests produced almost identical results (Hatcher 2011). The water year was defined as 1 October to 30 September. Tests were conducted using daily data. The daily P and Q values were log transformed before analysis. Data were tested for autocorrelation before analysis, and residuals from linear regression analyses were also tested for autocorrelation. Significant trends in annual T, P, and Q were defined as 10 or more days (out of 365) with significant trends (at $\alpha \leq .025$) and no autocorrelation before regression or in the residuals, and an average slope of the trend in daily values exceeding its standard error.

Annual minimum or maximum daily temperature increased significantly at 17 of the 19 sites (minimum temperatures increased at 13 sites and maximum temperatures increased at 7 sites), but only two sites experienced significant changes in precipitation over the period of available record (figure 6). Minimum daily temperatures increased by several degrees Celsius since 1980 at NWT and FRA, high-elevation, snow-dominated sites in the Rocky Mountains, but not at the other high-elevation Rocky Mountain site (LVW). Minimum daily temperature also increased by several degrees Celsius since the 1950s at climate stations near JRN and SEV in New Mexico, since the 1950s at a southeastern temperate forest site (CWT), and since the 1960s at a northern hardwood site (MAR) but not at its neighbor
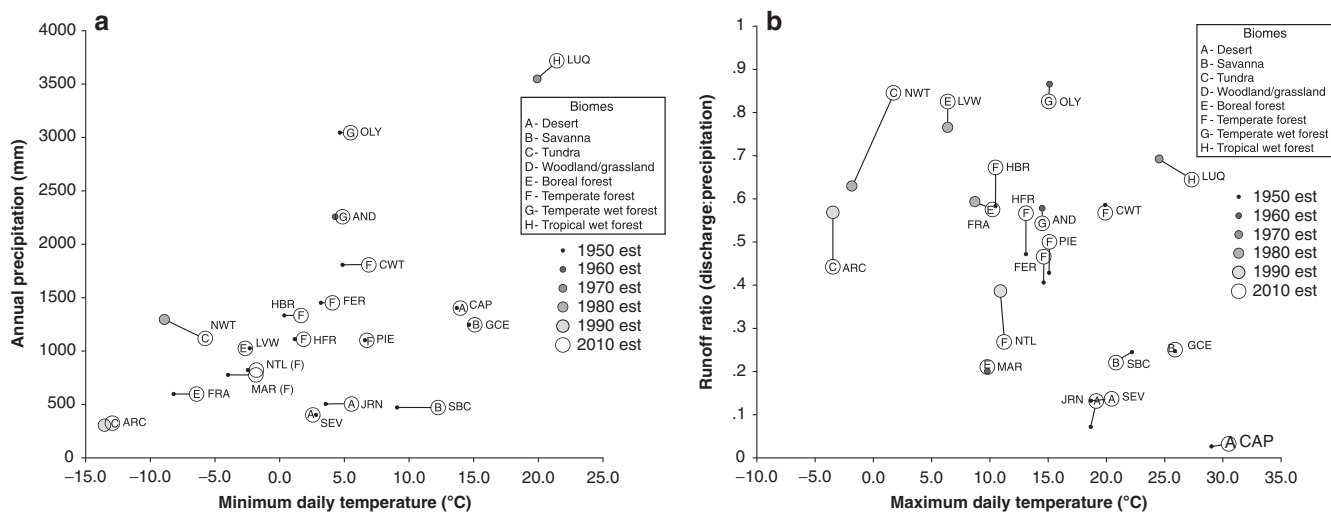
Figure 6. (a) Multidecade trends in minimum daily temperature (in degrees Celsius [°C]) and precipitation (in millimeters [mm]) at long-term watershed study sites. Each site is designated by the minimum daily temperature and precipitation at the beginning and end of the decades spanning the period of record, based on the statistically significant trend in that variable over the period of record. The initial observation is connected to or contained within the 2010 estimated (est) observation for each site. The radius of the 2010 estimated symbol is 0.5°C and 125 mm. Statistically significant increases in minimum daily temperature occurred at all sites except ARC, CAP, JRN, PIE, and SEV (the study-site characteristics and abbreviations are in supplemental table S1, available online at http://dx.doi. org/10.1525/bio.2012.62.4.10). Statistically significant changes in annual precipitation occurred only at LUQ and NWT. (b) Multidecade trends in maximum daily temperature and runoff ratios at long-term watershed study sites. Each site is designated by the maximum daily temperature and runoff ratio at the beginning and end of the decades spanning the period of record, based on the trend in that variable over the period of record. The initial observation is connected to or contained within the 2010 estimated observation for each site. The radius of the 2010 estimated symbol is 0.5°C and 0.125. Statistically significant increases in maximum daily temperature occurred at CAP, FRA, JRN, LUQ, NWT, and SEV. Statistically significant changes in annual streamflow occurred at FER, GCE, HFR, HBR, JRN, LVW, MAR, NWT, NTL, PIE, and SEV.

(NTL, for which the record began in 1990). Mean annual precipitation increased significantly at LUQ and NWT. The first day of spring (defined as the last day of freezing temperature) moved earlier by between 0.31 and 1.98 days per year—that is, by more than 15 days in 50 years—at eight sites (AND, ARC, CWT, FER, FRA, HBR, LUQ, MAR, NWT) (Hatcher 2011).

Runoff ratios (Q:P) changed at 8 of 19 sites (figure 6b). Tundra and boreal forest sites with ice and permafrost (LVW, NWT) experienced increases in runoff ratios, and so did temperate deciduous forest sites in the northeastern United States (HBR, HFR, PIE), which have a seasonal snowpack. An increase in runoff ratio means either that AET has decreased, or that there is a net addition of water to the system, such as from melting ice or interbasin water transfers. The observed increases in runoff ratios at LVW and NWT may be associated with the melt of ice, snow, and permafrost in response to warming temperatures during seasons in which these ecosystems are dormant (not taking up water). However, warming did not result in increased runoff ratios at other sites with permafrost (ARC, which has a short record) or seasonal snowpacks (e.g., AND, FRA, MAR, NTL). Runoff

ratios did not change at most other sites, which mostly lack significant snow and ice (Hatcher 2011).

Streamflow changes vary according to the season and differ among various biomes (figure 7). At undisturbed desert sites in Arizona (CAP) and New Mexico (SEV), streamflow did not change at any time of year (figure 7a, 7b). However, in a desert mountain basin northeast of JRN (New Mexico) and in a semiarid mountain basin near SBC (southern California) containing residential and urban development, streamflow increased during low-flow periods (figure 7c, 7d). In a large basin in coastal Georgia containing agriculture and forest plantations (GCE), streamflow declined in early and late summer (figure 7e).

At tundra sites on the North Slope of Alaska and in the Rocky Mountains (ARC, NWT; figure 7f, 7g), streamflow increased in early spring and late fall, during time periods adjacent to freezing periods. Streamflow changed in spring at boreal forest sites in the Rocky Mountains (FRA, LVW; figure 7h, 7i). At a temperate forest site in western North Carolina (CWT), where seasonal snowpacks do not form, streamflow did not change at any time of year (figure 7j), but at a temperate forest site in West Virginia (FER), streamflow
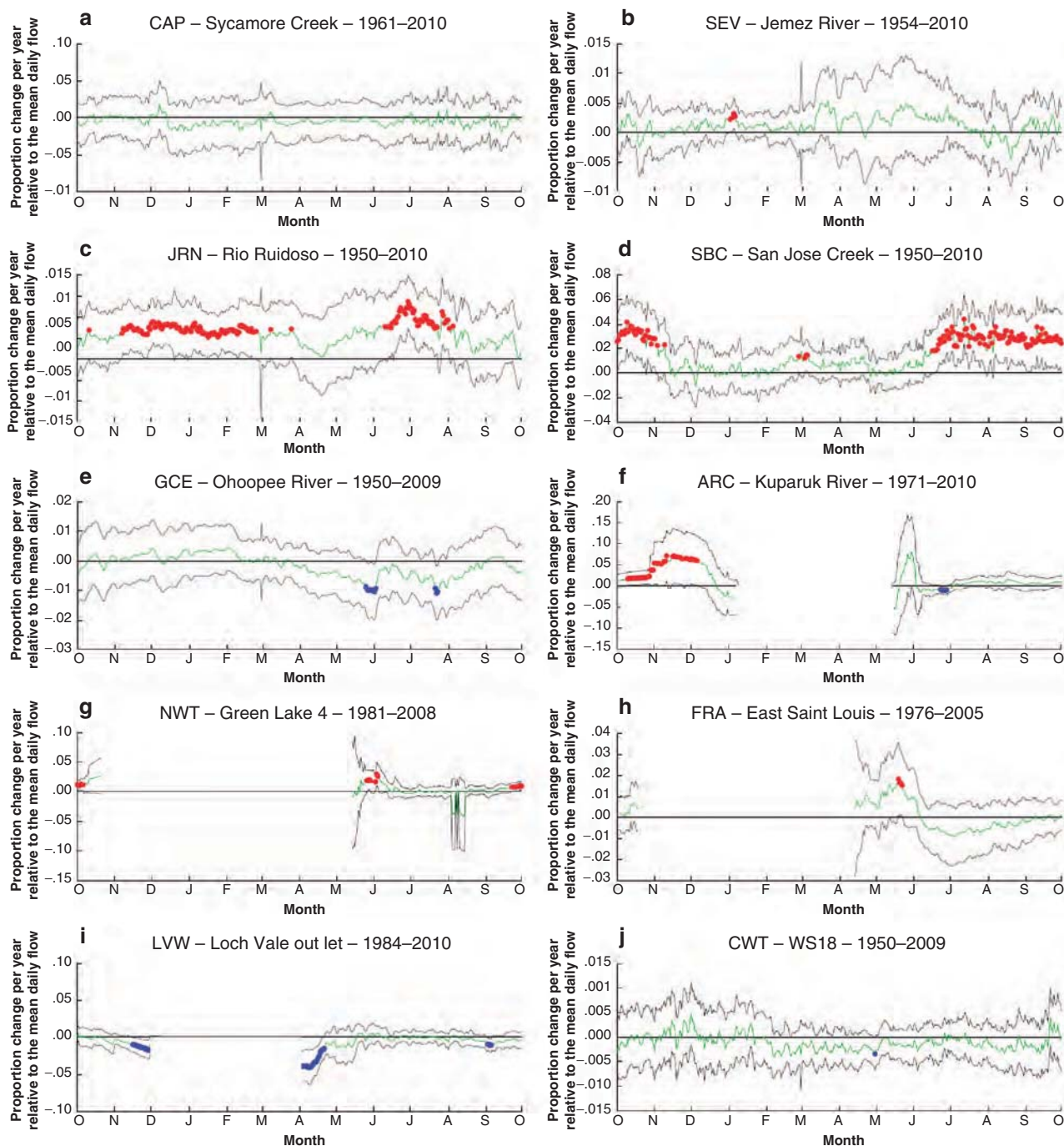
Figure 7. *Daily changes in streamflow at 19 US Long Term Ecological Research sites, US Forest Service Experimental Forests and Ranges, and US Geological Survey Water, Energy, and Biogeochemical Budgets sites arranged by biome (from figure 4) as a function of the day of the water year (1 October to 30 September). (a–c) Desert sites (CAP, SEV, JRN); (d), (e) savanna sites (SBC, GCE); (f), (g) tundra sites (ARC, NWT); (h), (i) boreal forest sites (FRA, LVW); (j–p) temperate forest sites (CWT, FER, HFR, HBR, MAR, NTL, PIE); (q), (r) wet temperate forest sites (AND, OLY); (s) wet tropical forest site (LUQ). The vertical axis and the green line are the slope of regression of log-transformed streamflow for each day of the water year over the period of record (see supplemental table S1, available online at* http://dx.doi.org/10.1525/ bio.2012.62.4.10*). The vertical axis units are the proportion change per year relative to the mean daily flow. The percentage change can be calculated as* $(1 + p)^n$, *where* p *is the proportion change and* n *is the number of years. Note the different vertical axis scales. The horizontal black line represents no change (a proportion change of 0); the wiggly black lines are the upper and lower bounds on the 97.5% confidence interval. The red dots represent significant increases, and the blue dots represent significant decreases in daily streamflow, where* $\alpha \leq .025$.
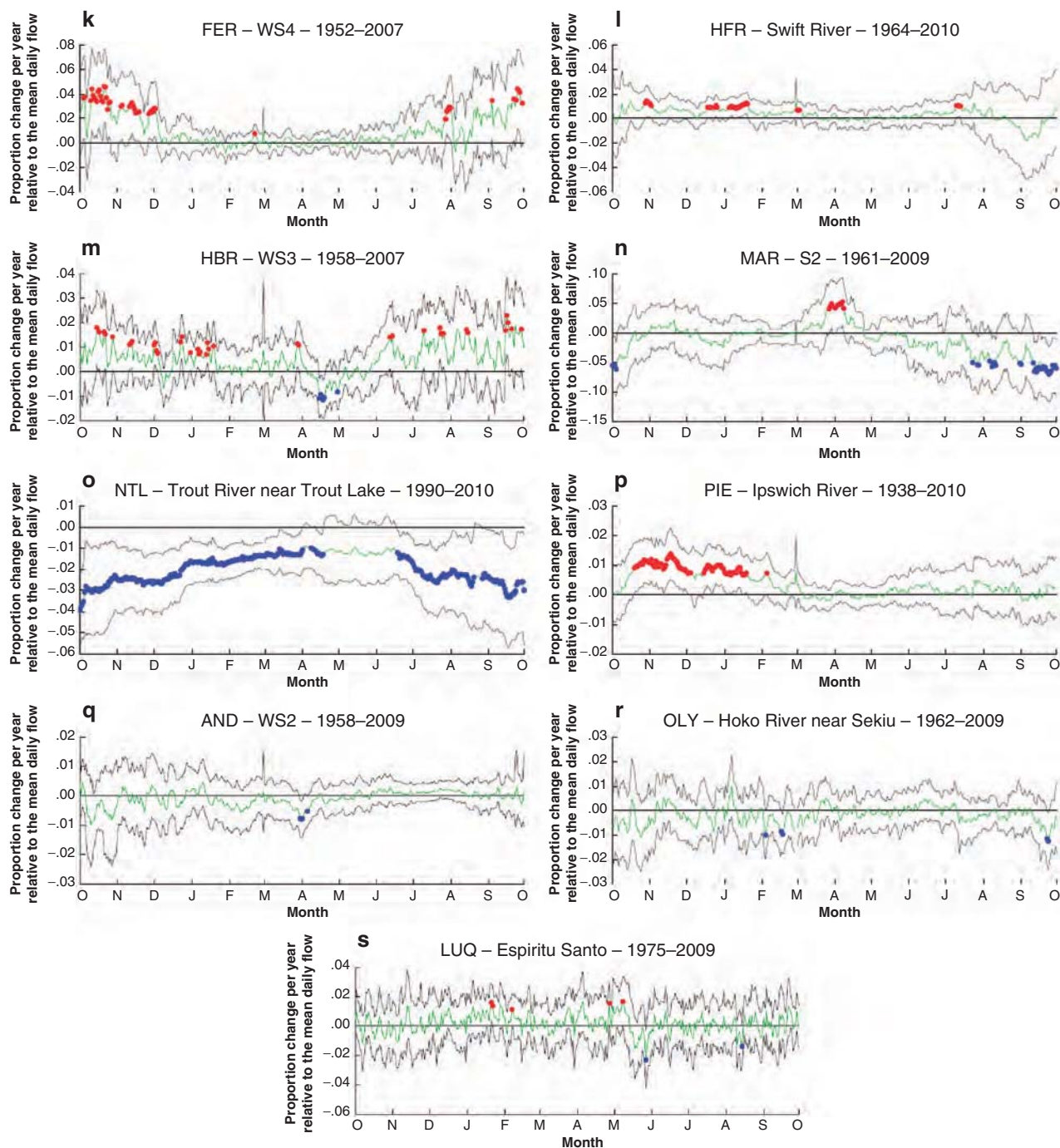
Figure 7. (Continued)

increased in the summer (figure 7k). Winter streamflow increased at three temperate forest sites in New England (HFR, HBR, PIE) and declined at one (NTL) (figure 7l, 7m, 7o, 7p). In addition, streamflow increased in March and decreased in April at HBR (figure 7m), and it increased in March and declined in summer at MAR (figure 7n). At wet temperate forest sites in Oregon (AND, OLY), streamflow declined in spring (figure 7q, 7r). Streamflow did not change at any time of year at a wet tropical forest site in Puerto Rico (LUQ) (figure 7s).

Social, ecological, and climate factors influencing streamflow trends

Multiple social and ecological factors may explain the streamflow trends at long-term headwater basin sites, even though humans do not directly affect most of these sites (figure 2). Economic development, population growth, and the use of fossil-fuel resources have increased atmospheric carbon dioxide, warmed the Earth, contributed to more-intense precipitation events, and increased evapotranspiration

(Min et al. 2011, Pall et al. 2011), which in turn have been linked to increased flooding and drought (Barnett et al. 2008, Karl et al. 2009). Yet direct climate-trend effects on streamflow in headwater basins may be mitigated by ecological processes, including disturbance, succession, and vegetation adaptations to water scarcity. In many cases, the vegetation—and, therefore, evapotranspiration in headwater basins—is affected by human activities, such as past logging, grazing, agriculture, and fire suppression. Moreover, in some headwater basins, land-use changes, including agriculture and exurban expansion, may mitigate or overwhelm climate-trend effects on streamflow.

Some observed trends in streamflow appear to be direct effects of climate trends. For example, increased streamflow in fall and spring at ARC, FRA, and NWT is probably the result of the expanding period of thaw at these tundra and boreal forest sites (figure 7f, 7g, 7h). Increases in streamflow at these sites may be driven by permafrost melt; changes in the chemical composition of streamflow support this hypothesis (Bowden et al. 2008, Caine 2010). In addition, increased spring streamflow at temperate forest sites with seasonal snowpacks in New England (HBR) and in the upper Midwest (MAR) is probably the result of earlier snowmelt, whereas increased winter streamflow at temperate forest sites in New England (HFR) may be the result of a shift from snow to rain. These responses are consistent with the results of published studies (Hodgkins et al. 2003, Stewart et al. 2005, Clow 2010, Campbell et al. 2011).

Some observed trends in streamflow may be the result of biological responses to climate change. For example, declining streamflow at a woodland site (summer at GCE), a boreal forest site (LVW), temperate forest sites (MAR, NTL), and wet temperate forest sites (spring at AND, OLY) may be the result of increased evapotranspiration in response to warmer temperatures. Conifer forests, which occur at MAR, NTL, LVW, AND, and OLY, are adapted to photosynthesize and respire when conditions are favorable; warmer temperatures may lead to an earlier onset of transpiration and to declining streamflow (e.g., Moore KM 2010). Streamflow trends at wet temperate and boreal forest sites (LVW, AND, OLY; figure 7) are restricted to the immediate period of snowmelt, and declines may reflect increased evapotranspiration (Moore KM 2010, Oishi et al. 2010, Campbell et al. 2011). In contrast, streamflow trends are largest during the nonsnowmelt periods at temperate forest sites in the upper Midwest (NTL, MAR), where wetlands (bogs and lakes) occupy a large proportion of basin area (Verry et al. 2011). Increased evapotranspiration associated with declining ice cover (Magnuson et al. 2000) or increased radiation associated with decreased precipitation may account for declining flows at these sites.

Some sites experienced no trends in streamflow, despite increases in temperature. For example, desert sites (CAP and SEV) and the wet tropical site (LUQ) experienced significant increases in minimum and maximum daily temperatures, no change in precipitation (figure 6), and almost no changes in streamflow (figure 7a, 7b, 7s). Vegetation adaptations to drought might explain the lack of a streamflow response to warming at the desert sites. At the wet tropical forest site, the effects of the 1996 Hurricane Hugo on leaf area, evapotranspiration, and streamflow (Scatena et al. 1996) may have overwhelmed climate-trend effects.

Some sites experienced trends in streamflow that appear to be biological responses to past disturbances. For example, forest succession and declining evapotranspiration may explain increased summer streamflow at two temperate forest sites (FER, HBR), which were logged in the early nineteenth century (figure 7k, 7m). At a third temperate forest site (CWT), streamflow and runoff ratios have not changed, despite increases in air temperature (figure 6, figure 7j). Forest succession following disturbances in the early 1900s at all three sites (table S1; Swank et al. 2001, Adams et al. 2006) and associated changes in species composition or leaf area may have influenced streamflow trends. Analyses of long-term paired-basin experiment data (e.g., Jones and Post 2004) indicate that streamflow continues to change over decades or centuries of forest succession after disturbance.

Responses to land use and disturbance, such as advanced snowmelt or declining summer streamflow, may be misconstrued as responses to climate change. In paired-basin experiments (see the discussion of long-term experiments in Knapp and colleagues 2012 [in this issue]), forest harvest advanced the timing of peak snowmelt and associated streamflow by up to three weeks in temperate forest sites with a seasonal snowpack (AND, HBR); the effect lasted for more than 10 years (Jones and Post 2004). By 25 to 35 years after forest harvest in temperate forest basins (AND, CWT, HBR), summer streamflow declined by up to 30%–50% relative to the reference basins (Hornbeck et al. 1997, Swank et al. 2001, Jones and Post 2004). Regenerating species in early forest succession may transpire more water per unit of leaf area and, in some cases, have greater total leaf area than the species that were removed, which would reduce summer streamflow (Swank et al. 2001, Moore GM et al. 2004).

Historic legacies from past disturbance in these long-term studies demonstrate that streamflow and timing responses to forest disturbance are at least as large as responses associated with climate trends over the past 20–60 years at the study sites. Daily streamflow during the late summer and early fall increased by up to 300% in the 1–5-year period after experimental forest harvest (AND, CWT, HBR), but most daily changes were on the order of 50% or less (Jones and Post 2004). By comparison, trends in daily streamflow associated with climate trends at the 19 study sites were on the order of 10%–50% over 20- to 60-year periods, although a few days, especially those adjacent to freezing periods, experienced larger changes (figure 7).

Finally, some observed trends in streamflow may be direct human effects on the hydrologic cycle. For example,

increased irrigation using groundwater or water imported from other basins may explain increasing streamflow during dry seasons at a desert site in New Mexico (JRN) and a savanna site in southern California (SBC), which have some agriculture and residential development (figure 7c, 7d). Increasing winter streamflow trends at a temperate forest site (PIE) may reflect urban expansion (Claessens et al. 2006). Therefore, human effects on streamflow may mimic, exacerbate, counteract, or mask climate effects on streamflow, making it challenging to determine the vulnerability of human communities (*sensu* Polsky et al. 2007) to variations in water supply.

Headwater basins in this study drain into major river systems that supply water to major agricultural areas and medium and large cities. Climate change is expected to increase the variability of future streamflow and to stress municipal water supplies (Milly et al. 2008, Covich 2010, McDonald et al. 2011, USDOI 2011). Long-term studies of headwater basins can help distinguish biophysical from social causes of variability in water supply and, hence, the relationships between ecological and social resilience (Adger 2000). Water scarcity may be perceived even in areas with abundant rainfall, where politics rather than true scarcity may govern water restrictions (Hill and Polsky 2006). Meanwhile, residents, professional policymakers, and academics in Phoenix (CAP) implicated population growth, climate change, and drought as the most important causes of water scarcity, rather than their own water-use habits (Larson et al. 2009). Adding to this research, in this study, we suggest that rather complex interactions among historical social factors, ecosystem processes, and climate influence the long-term water supply from headwater basins.

The role of information management
Long-term ecological data are critical to answering societal questions of national concern and significance. Long-term data are the only way to distinguish trends from short-term variability in key environmental indicators, such as climate and streamflow. However, many long-term data remain inaccessible or difficult to access. Many valuable data sets are stored in inconvenient file formats with limited metadata. Variations in methods, variables, units, measurement scales, and quality-control annotation complicate data integration and prevent automated approaches to data synthesis.

Until the 1990s, the difficulty of identifying, accessing, and integrating climate and hydrologic data from the LTER Network, EFRs, and related networks precluded cross-site studies. ClimDB/HydroDB (*http://climhy.lternet.edu*), a collaborative effort between LTER Network and USFS information managers, was initiated in 1997 to overcome these limitations. ClimDB/HydroDB is a Web harvester and data warehouse that provides uniform access and visualization of daily streamflow and meteorological data through a single portal. Participating sites manage original data within their local information systems but periodically contribute data to the warehouse. Although the ClimDB/HydroDB approach is not a complete solution to data-access and -integration issues, it has served as an effective bridge technology between older, more rigid data-distribution models and modern service-oriented architectures (Henshaw et al. 2006).

The LTER Network has made great strides in collecting, archiving, and integrating long-term data sets online, enabling synthesis activities such as this one, and providing an example for other environmental observatories. Information managers at LTER Network sites have led the development of metadata standards, data dictionaries, and software for data integration. The LTER Network data-management system serves as a model for emerging national observatories and existing programs.

Conclusions
This study provides an example of the special kinds of science that are possible from networks of long-term study sites. Climate and streamflow records are sufficiently long that averages, variability, and trends can be meaningfully analyzed. The climate and streamflow properties are simple and comparable because they are consistently measured across sites. Climate and streamflow data are broadly relevant to ecosystem processes and ecosystem services. Above all, multisite synthesis is fostered by and contributes to an open, inclusive culture of science collaboration.

This study showed that actual evapotranspiration was predicted by PET at only 7 of 30 sites with 10-year-long records (the Budyko curve). Taken individually, these departures might simply reflect the inability of a climate station to represent the conditions of a whole basin or the fact that streamflow depends on groundwater and other forms of storage, as well as precipitation and temperature. But taken collectively, the departures of these sites from the Budyko prediction suggest the intriguing hypothesis that water-scarce ecosystems evapotranspire less and water-abundant ecosystems evapotranspire more than would be predicted from their climates. Moreover, streamflow at many of these sites was significantly related to one or more climate index (ENSO, NAO, or PDO), which is not surprising, but the slightly more frequent significant correlations of streamflow with climate indices in winter than in summer imply that ecosystem processes mediate climate–streamflow coupling. Finally, 17 of 19 sites had significant increases in their minimum or maximum daily temperatures or both, but streamflow trends were directly related to climate trends at only 7 of the sites, all of which have permanent or seasonal ice and snow. In contrast, at other sites, and during certain seasons at these seven sites, streamflow trends were contrary to those expected from climate drivers.

A key finding from this study is that the past and present human uses of ecosystems and human water-use practices can mimic, exacerbate, counteract, or mask the effects of climate change on streamflow. Social factors, including

past land management and disturbance and the resulting ecological succession, all influence trends in streamflow, even at sites that are considered to be "reference" basins. In other words, exogenous (climate) factors are not the only drivers of nonstationarity (e.g., Milly et al. 2008) in streamflow from headwaters: Ecosystem processes and their social drivers are also important controls. In order to understand reference conditions for natural flow regimes (e.g., Poff et al. 2007), we need to better understand how ecological processes and social drivers mediate the expression of climate on streamflow. Long-term study sites, where all these processes are being studied, are ideal places for this ongoing work.

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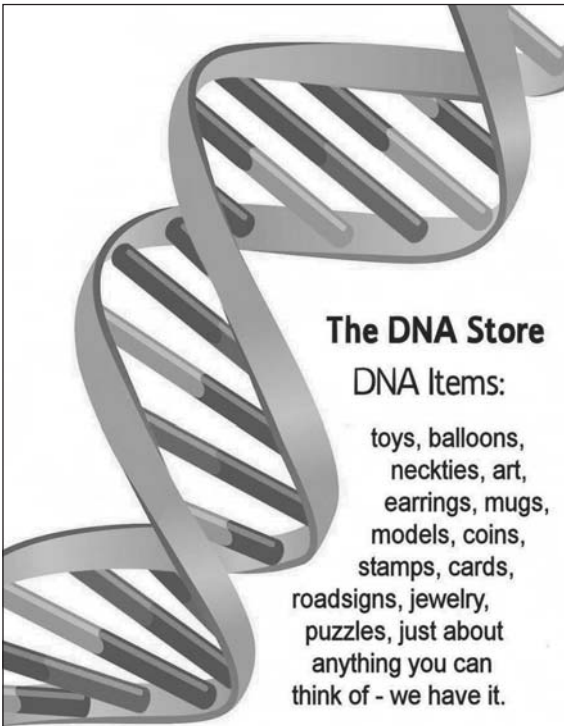
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