Geographic overview: Climate, phenology, and disturbance regimes in steppe and desert communities

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Abstract.—In midwestern steppes, precipitation peaks in summer, whereas west of the Rocky Mountains, steppes are characterized by summer drought. In western deserts, the amount of precipitation is highly variable. These different climatic regimes result in differences in prevalence of and resilience to disturbances such as herbivory, and differences in susceptibility to invasion by exotic plants and animals. The timing and predictability of precipitation influences plant phenology and life forms, which in turn influence the distributions and annual cycles of animals such as bison (*Bison bison*) and prairie dogs (*Cynomys* spp.). Desert organisms are susceptible to disturbances that disrupt cues signaling temporarily favorable conditions. Herbivores such as Bay checkerspot butterflies (*Euphydryas editha bayensis*) that are closely tied to the life cycles of their host plants are vulnerable to climatic changes that disrupt this tight phase relationship.

INTRODUCTION

Western rangelands encompass a variety of steppe and desert communities that are too dry to support trees as their dominant vegetation. Although the ecosystems that are considered in this symposium are all similar in this respect, they differ in climate, topography, and floristic history. This geographic overview focuses on differences in climate, because climate influences the magnitude of ecosystem productivity and the timing of that productivity, both of which influence sensitivity to disturbance and to invasion by exotic species.

This review describes the major climate regimes of western grassland ecosystems and presents examples that illustrate how climate, particularly the timing and predictability of precipitation, influences animal distribution and activity cycles. This study concludes with a brief discussion of some possible consequences of rapid climate change for grassland organisms and a discussion of the implications to sustainability.

The terminology surrounding grassland ecosystems is confusing. The word grassland itself and related words such as desert, desertification, and rangeland are often used without being clearly defined. While I doubt that it is possible to come up with a set of definitions that everyone can agree upon, I hope that this geographic overview will at least reduce some of the confusion surrounding these terms.

MAJOR CLIMATE PATTERNS IN NORTH AMERICAN STEPPE AND DESERT

On the basis of climate, the grassland ecosystems of western North America can be grouped into three major categories the midwestern steppes east of the Rocky Mountains, the western steppes and shrub steppes west of the Rocky Mountains, and the southwestern and Mexican deserts. Patches of grassland also occur as openings or parks within forested landscapes on soils that are incapable of

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supporting trees and on sites where fire prevents trees from becoming established (Daubenmire 1978).

The approximate distributions of the major units of steppe and desert vegetation of North America are shown in figure 1. The term steppe refers to areas where conditions are too dry for trees and the vegetation is dominated by perennial grasses. The steppes of North America fall into two categories. The midwestern or Great Plains steppes (figs. 1B, C, D) are located east of the Rocky Mountains and west of the area capable of supporting fire-maintained grassland. The western steppes of the Intermountain West and California's Central Valley (figs. 1E, F, G) occur west of the Rocky Mountains. In parts of this region such as north-central Oregon, central Washington, and southern Idaho, perennial grasses are accompanied by an overstory of shrubs, particularly big sage-

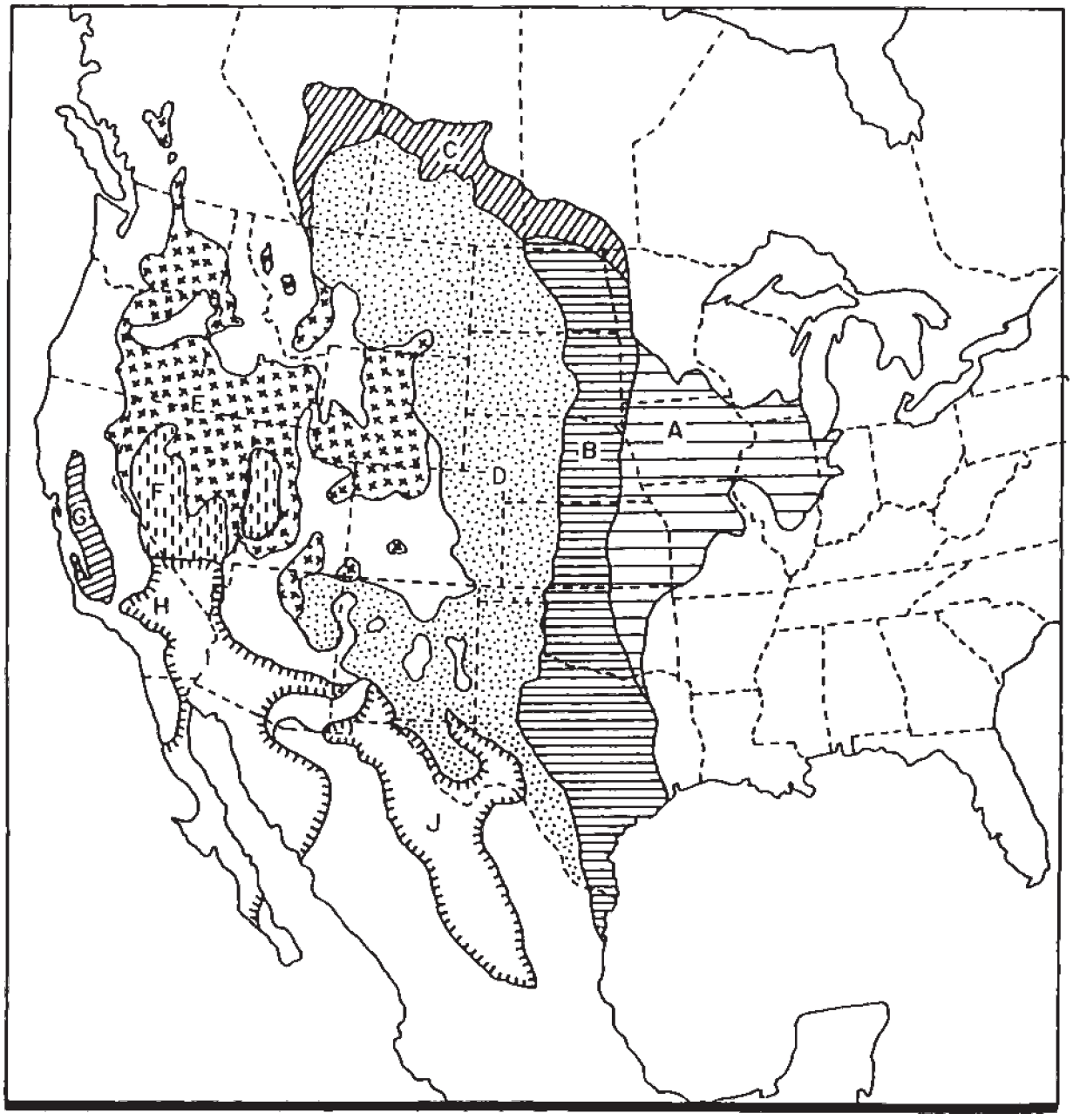

Figure 1. Approximate distribution of major units of steppe and desert vegetation of North America. A) area capable of supporting fire-maintained grassland; B, C, D) Midwestern steppes; E, F, G) western steppes; H, I, J) desert. After Daubenmire, *Plant Geography*, 1978.

brush (*Artemisia tridentata*). This type of community is termed shrub-steppe (Daubenmire 1978).

Desert has been defined in many ways. This review follows Daubenmire (1978) in using the word desert to refer to areas where precipitation is low in relation to heat level, so that the substrate is moist for only brief periods (figs. 2H, I, J). Under these conditions, the climate is too hot and dry to support the perennial grasses characteristic of steppes. Shrubs dominate on zonal soils in deserts, and if grasses are present, they are typically annuals rather than perennials (Daubenmire 1978).

Each of these three ecosystems, the midwestern and western steppes, and southwestern deserts, are characterized by a distinctive seasonal pattern. In figures 2, 3, and 4 mean monthly values for

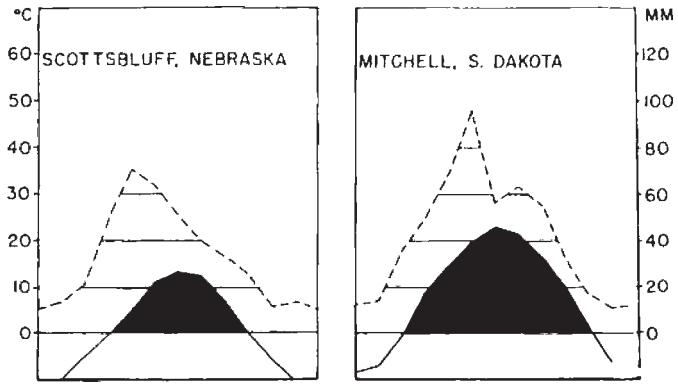

Figure 2. Seasonal trends of mean monthly temperature and precipitation at stations representing Midwestern steppe vegetation. Solid line= temperature; broken line= precipitation. From Daubenmire, *Plant Geography*, 1978.

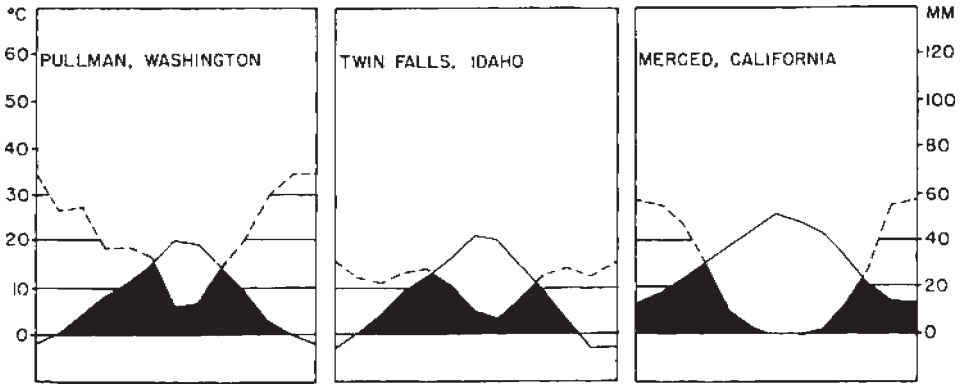

Figure 3. Seasonal trends of mean monthly temperature and precipitation at stations representing western steppe vegetation. Solid line= temperature; broken line= precipitation. From Daubenmire, *Plant Geography*, 1978.

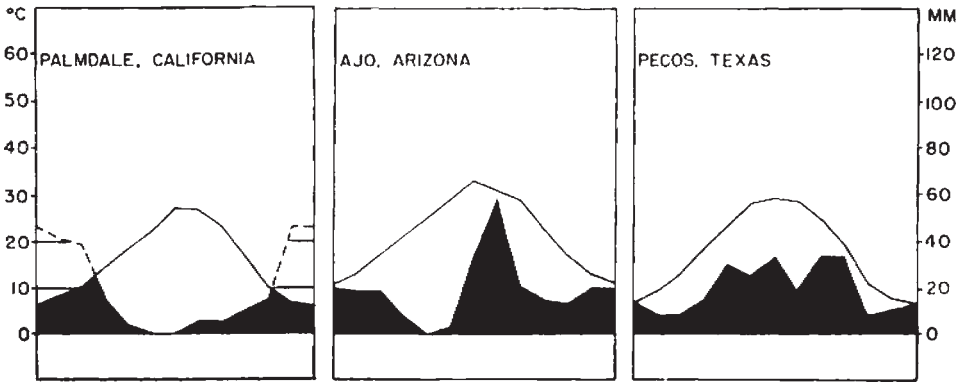

Figure 4. Seasonal trends of mean monthly temperature and precipitation at stations representing desert steppe vegetation. Solid line= temperature; broken line= precipitation. From Daubenmire, *Plant Geography*, 1978.

temperature (solid line) and precipitation (broken line) are plotted throughout a year. These diagrams provide information about both the amount and the timing of precipitation; unfortunately they do not reveal anything about year-to-year variability, which would be useful.

In the steppe ecosystems located east of the Rocky Mountains, precipitation peaks when temperature is high, that is, in spring or summer (fig. 2). The steppes located to the west of the Rockies, however, are characterized by summer drought; note that precipitation in this region is lowest in summer, when temperature is highest (fig. 3). This difference in the seasonal timing of precipitation has important consequences that are discussed below.

In the deserts of western North America, a rainy season may occur in autumn, winter, or summer (fig. 4); however, the amount of annual precipitation is highly variable. This variability has important consequences for desert organisms, which I will discuss shortly.

PRODUCTIVITY AND SENSITIVITY TO DISTURBANCE

Climate influences productivity both directly, through its influence on plant phenology, and indirectly, through its influence on soil development. Where primary productivity is low, as in deserts and some steppe communities, sensitivity to disturbances that remove vegetation and to invasion by exotic species that exploit resources unavailable to native organisms is high. For example, arid rangelands have been adversely impacted by introduced feral burros (*Equus asinus*), which are able to utilize high-fiber foods that cannot be digested by native ungulates (Seegmiller and Ohmart 1981). Similarly, the alien shrub tamarisk, or salt cedar (*Tamarix* spp.), which is able to reach water sources that are unavailable to native plants, has disrupted plant communities and hydrology in arid rangelands in many parts of the West. Unlike native species, salt cedar extends deep roots to the water table and uses prodigious amounts of water. As a result, salt cedar invasions have been accompanied by major changes in local hydrological cycles (Vitousek 1986; Horton 1977).

CONSEQUENCES OF CLIMATE PATTERNS

The timing of productivity is as important a consideration as the magnitude of that productivity. For example, seasonal trends in productivity influence grassland fire regimes, because fires are most likely to occur when there is abundant, dry fuel available.

In addition, the timing of productivity has other important consequences for western steppe and desert ecosystems, because of its influence on the prevalence of biotic disturbances such as grazing, trampling, wallowing, and digging. If animals are unable to inhabit an area because of inhospitable climate or because of insufficient seasonal productivity, they may be entirely absent from the area, they may be seasonally absent (because they migrate elsewhere), or they may be present but temporarily inactive (because they undergo diapause or torpor). To illustrate this, let us consider the distribution, abundance, and annual cycles of bison (*Bison bison*) and prairie dogs (*Cynomys* spp.) in steppe communities.

Summer Precipitation vs. Summer Drought in Steppe Environments

Distribution of Bison Herds

Although small, scattered bands of bison formerly inhabited this region, sizable herds of bison or other large, hooved grazers never persisted west of the Rocky Mountains (Guthrie 1970; Gustafson 1972; Schroedl 1973). Mack and Thompson (1982) suggest that summer drought was the primary factor excluding large herds of bison from the steppes of the Intermountain West. The greatest energy demand for bison occurs in early summer during lactation; however, intermountain grasses set seed and dry up by early summer. Thus, there is insufficient forage available when bison cows need it most. Consequently, the grasses of the Intermountain West were never confronted with large numbers of bison or other massive mammalian grazers and never adapted to large-scale grazing, wallowing, and trampling (Mack and Thompson 1982). A variant of this explanation was proposed by Van Vuren, who suggested that low bison numbers west of the Rocky Mountains

resulted from a combination of low forage production and low recolonization rates following local extinctions in discontinuous habitat (Van Vuren 1987).

As a result of this lack of significant selective pressure from large herbivores, the dominant species of native intermountain grasses never evolved adaptations that allowed them to rapidly revegetate large disturbed areas. This lack of coevolution between ungulates and intermountain grasses left native grasses vulnerable to invasion by exotics when agriculture and livestock grazing disturbed the region's vegetation on an unprecedented scale (Daubenmire 1970; Mack 1981). In contrast to the native grasses, however, cheatgrass (*Bromus tectorum*), Kentucky bluegrass (*Poa pratensis*), and other Eurasian grasses had coevolved with large herbivores and were well adapted to germinate in disturbed areas (Hulbert 1955; Mack 1981; Mack and Thompson 1982; Mack and Pyke 1983, 1984; Mack 1986; Pyke and Novak 1994). The vulnerability of the intermountain steppes to disturbance from agriculture and grazing, and to invasion by exotic plants is rooted in the evolutionary histories of the native steppe grasses, which have been profoundly constrained by summer drought.

Distribution and Annual Cycles of Prairie Dogs

The seasonal timing of productivity has also influenced the distribution and activity cycles of a group of smaller herbivores characteristic of steppes, the prairie dogs. Figure 5 shows the geographic range of the black-tailed prairie dog (*Cynomys ludovicianus*), superimposed upon the map of steppe vegetation presented in figure 1. Notice that the range of the black-tailed prairie dog coincides with the steppes characterized by summer precipitation, that is, the region where photosynthetically active forage is available throughout the summer. In this connection, it is interesting to note that black-tailed prairie dogs are active throughout the year unlike ground-dwelling sciurids that inhabit the steppes of the Intermountain West, such as the Columbian ground squirrel (*Spermophilus columbianus*) and the white-tailed prairie dog (*Cynomys leucurus*), and avoid the summer drought that characterizes this region by undergoing seasonal torpor. Although hibernation in prairie dogs, ground squirrels (*Spermophilus* spp.), and marmots (*Marmota* spp.), is often thought of as an adaptation to reduce energy requirements during cold weather, Bintz (1984) has argued that water stress during summer also promoted the evolution of seasonal torpor.

I suggest that the availability of succulent forage throughout the warm season, combined with this species' relatively good physiological mechanisms for water conservation, may have influenced the seasonal cycle of the black-tailed prairie dog by allowing individuals to maintain year-long activity. In contrast, the congeneric white-tailed prairie dog (*C. leucurus*), which occurs in intermountain steppes, is an obligate hibernator; this underscores the association between summer drought and seasonal torpor among prairie dogs.

Furthermore, black-tailed prairie dog coteries display a high degree of social integration (King 1955) and the ability of black-tailed prairie dogs to maintain year-long activity is thought to have influenced the evolution of social behavior in this species. Michener (1983) has shown that among ground-dwelling sciurids, cohesive social behavior occurs in species in which different age and sex classes are active above ground simultaneously. She suggests that temporal overlap between age classes is a necessary condition for the evolution of social tolerance and space sharing in this group. In some ground-dwelling sciurids, the annual activity period lasts only a few months and different age and sex classes are active at different times. Under these circumstances, opportunities for cohorts to interact are severely limited because they encounter each other infrequently, and cohesive social behavior is unlikely to evolve.

In black-tailed prairie dogs, however, year-long activity allows for a prolonged period of interaction between different age and sex classes, thereby setting the stage for the evolution of highly social behavior. In contrast, hibernating white-tailed prairie dogs exhibit a low degree of seasonal coincidence between age and sex classes and lack the highly cohesive social behavior seen in black-tailed prairie dogs. Among prairie dogs in western North America, the species that occurs in regions with summer drought is a hibernator, with low overlap in the activity periods of different age and sex classes, and relatively asocial behavior.

However, the species that inhabits regions with summer rains is active throughout the year, experiences a high degree of overlap in the activity periods of different cohorts, and is highly social.

Like bison, black-tailed prairie dogs have a significant impact on the vegetation and associated fauna of the midwestern steppes (Agnew et al. 1986). Because of their wide distribution and high densities, prairie dogs are capable of significantly modifying soils, vegetation, and associated fauna through their feeding and burrowing activities. The absence of a pronounced summer drought in the Great Plains steppes appears to have influenced both the distribution and the annual cycle of black-tailed prairie dogs, allowing them to be active throughout the year and to form highly social, dense aggregations; thus, acting as a significant agent of biotic disturbance.

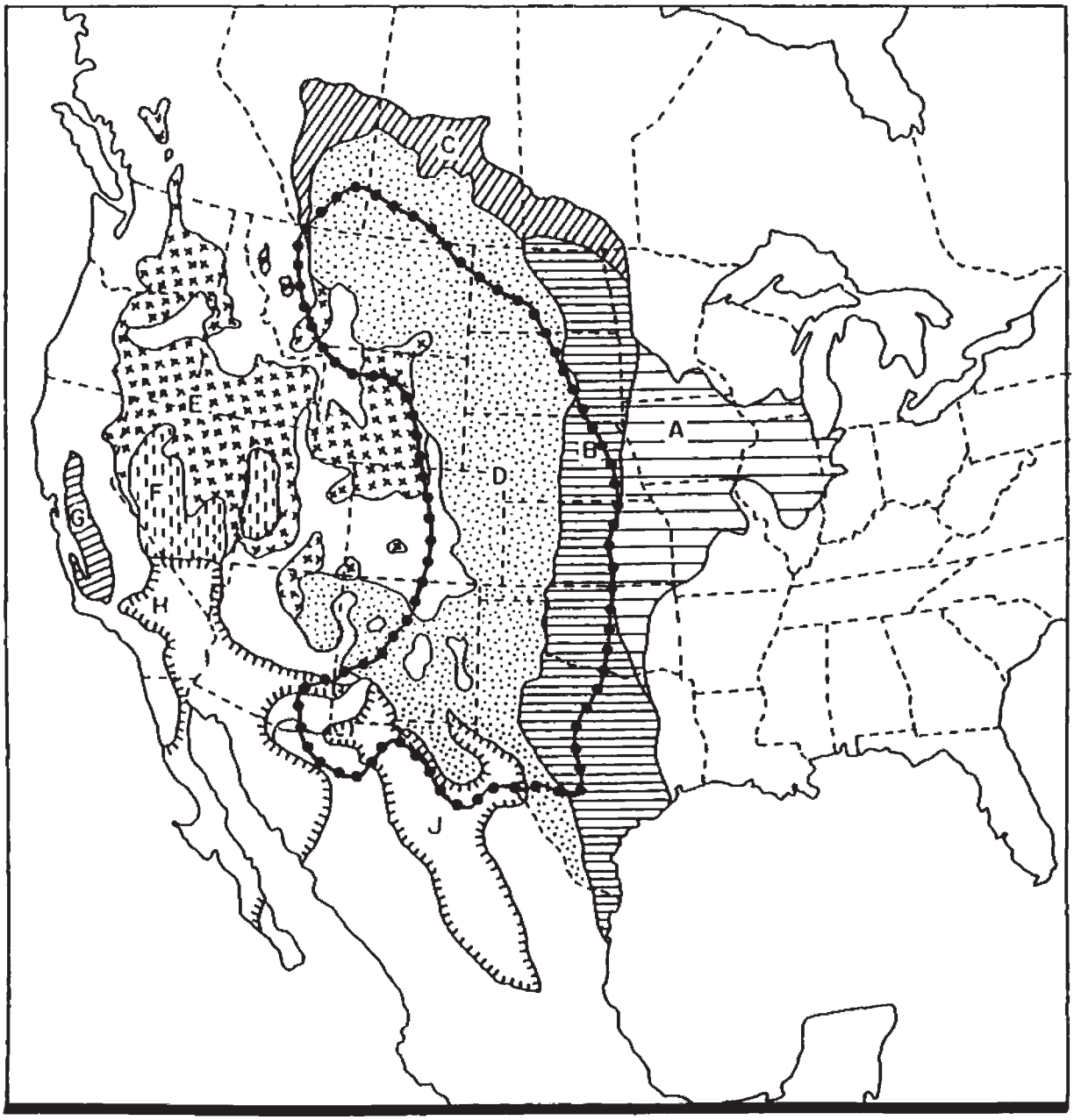

Figure 5. Distribution of the black-tailed prairie dog. B, C, D= Midwestern steppe; dotted line= outline of black-tailed prairie dog range.

VARIABLE PRECIPITATION IN DESERT ENVIRONMENTS

Life Cycles of Desert Plants

Because the amount and timing of precipitation in deserts are highly variable, strong selection pressure in this environment has favored adaptations that allow desert plants to take advantage of temporarily favorable conditions. These adaptations include the ability to endure long periods of unfavorable conditions as seeds or in a dormant vegetative state, and the ability to respond to appropriate environmental cues that signal the onset of favorable conditions by germinating or resuming growth (Louw and Seely 1982).

Timing of Reproduction in Desert Amphibians

Similarly, desert amphibians have evolved mechanisms that allow them to respond quickly to environmental cues signaling conditions favorable for reproduction. This characteristic makes them uniquely vulnerable to any disturbance that interferes with those environmental cues or causes them to be misinterpreted.

For example, desert amphibians often rely on acoustical cues, especially low-frequency sounds. Couch's spadefoot toad (*Scaphiopus couchi*) normally emerges from its burrows to breed in temporary ponds. This activity is cued by acoustical stimuli associated with thunderstorms. Off-road vehicles (ORVs) also produce low-frequency sounds and these travel long distances in desert air. Spadefoot toads exposed to motorcycle sounds respond by leaving their burrows; this could cause individuals that misinterpret ORV sounds to emerge at inappropriate times when temporary ponds are not available (Berry 1980). The reliance of this species on environmental cues that signal temporarily favorable conditions in a highly variable environment puts them at risk, resulting in an unusual vulnerability to novel disturbances that mimic those cues.

CONSEQUENCES OF CLIMATE CHANGE

Phenology and Persistence of Checkerspot Butterfly Populations

The examples presented above suggest that the ways in which an ecosystem's producers adapt to patterns of seasonality influence the distribution, abundance, and activity cycles of its consumers and that this coevolutionary history affects sensitivity to both biotic and abiotic disturbances. Because climate change has the potential to affect productivity and phenology, it has the potential to alter the frequency and intensity of disturbances. For example, it has been suggested that during the past two centuries increases in atmospheric CO_2 resulting from industrialization have contributed to increased cheatgrass productivity in intermountain steppe communities and a concommitant increase in fire frequency (Smith et al. 1987; Whisenant 1990; Mayeux et al. 1994).

It is difficult to retrospectively establish such connections between subtle changes in climate and changes in autecology and disturbance regimes. To clarify the effects of climate change it is necessary to switch to a finer scale of analysis. Studies of the Bay checkerspot butterfly (*Euphydryas editha bayensis*) in a western grassland ecosystem illustrate the mechanisms by which changes in phenology due to variation in climate determine population persistence for herbivores that are closely tied to the life cycles of their host plants.

These relationships between climate, plant phenology, herbivory, and population persistence have been demonstrated by Murphy and Weiss (1992). They draw on decades of data on the dynamics and ecology of Bay checkerspot populations to identify the mechanisms by which fluctuations in climate lead to local extinctions of Bay checkerspots.

The Bay checkerspot is restricted to patches of native grassland occurring on serpentine soils in California. For populations of this herbivore to persist, the development of larvae and host plants during California's moist, cool-weather growing season (figs. 1G and 3) must proceed synchronously. Eggs hatch in spring and larval growth and development depend upon the availability of succulent vegetation. Larvae must reach

fourth-instar size before they enter diapause during the summer drought.

Because the Bay checkerspot has a highly specialized diet and very limited powers of dispersal, populations are extremely vulnerable to unfavorable conditions that disrupt the tight phase relationship between larval development and plant phenology. Unusual climatic conditions do just that. Warm, dry weather accelerates development in both larvae and their host plants. However, rapid larval development does not compensate for early plant senescence and high larval mortality results because host plants sense before the larvae complete their development. As a result, droughts during the 1970s caused marked population declines and numerous local extinctions. Unusually wet weather also causes population declines because delayed plant development does not compensate for retarded larval development. Weather extremes result in high rates of extinction among Bay checkerspot populations and consequently in altered levels of host plant herbivory.

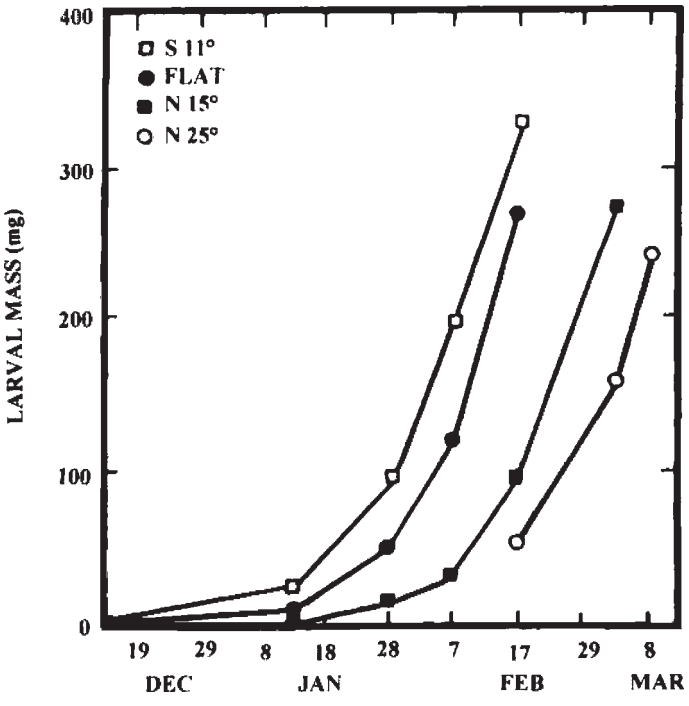

Figure 6. Growth of Bay checkerspot larvae on four slope exposures at Morgan Hill, 1987-88. From Murphy and Weiss. In: Peters and Lovejoy, *Global Warming and Biological Diversity*, 1992.

In unusually wet or dry years, checkerspot populations may persist only in areas of favorable microclimate provided by topographic refugia. During droughts, for example, larval survival is greatest on north-facing slopes, where the microclimate is cooler and wetter because larval development on these slopes lags behind south-facing slopes by about a month (fig. 6).

Accelerated global climate change can be expected to exacerbate this situation. The results summarized here pertain only to short-term responses of checkerspot populations to climate change. In addition, variations in temperature and in the amount and timing of precipitation affect the composition of plant communities further influencing the distribution and availability of larval host plants.

CONCLUSIONS: CLIMATE AND SUSTAINABILITY

What does all this have to do with sustainable use of grassland ecosystems? First, the grassland ecosystems of western North America are climatically diverse with differences in productivity, seasonality, and disturbance regimes. If we are to use grasslands sustainably, we must understand the climatic and evolutionary constraints operating in each ecosystem and the resulting differences in resilience. Sustainable use cannot exceed productivity, which is constrained by climate. Furthermore, organisms are adapted to the disturbance regimes typical of the regions where they evolved.

The consequences of failing to understand that are illustrated in the Intermountain West. In this region novel land uses led to irreversible changes because of a dramatic alteration in disturbance regimes. This occurred because of the introduction of livestock grazing and agriculture followed by invasions of exotic plants that had superior adaptations to the new disturbance regime. Disturbances created by resource use are likely to be sustainable if they imitate natural disturbance regimes in size, frequency, and intensity. Finally, rapid climate change has the potential to increase extinction rates for organisms adapted to current conditions that are unable to migrate elsewhere because of habitat fragmentation or poor powers of dispersal. In addition, rapid climate change has the potential to alter disturbance regimes.

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