

The Role of Climatic Change in the Design of Biological Reserves: The Paleoecological Perspective for Conservation Biology

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The design of areas (refuges, reserves, or preserves) to conserve the biological diversity of terrestrial ecosystems in the face of unprecedented habitat destruction has primarily been based on the equilibrium theory of island biogeography (MacArthur & Wilson 1967). The equilibrium models and others such as the passive sampling, random placement, and habitat heterogeneity hypotheses (for discussion see Boecklen & Simberloff 1986:250) are designed for the climatic and environmental conditions of the region today. They do not take into consideration the potential response of the biota to future long- and short-term climatic changes, although there have been some exceptions (Hamilton 1981; Peters & Darling 1985). Hunter et al. (page 375) use a paleovegetational perspective to address specific recommendations for the design of nature preserves. Specifically, they emphasize the individualistic responses of taxa to past environmental changes rather than a community, or holistic, response.

The significance of including contingencies for climatic change in designing biological reserves is clearly illustrated by the Holocene archeological and paleontological record of the eastern Sahara. Today, this area is one of the largest hyperarid expanses on Earth. During the early Holocene (8,000–10,000 years ago), "climatic conditions supported extensive vegetation, a Sudanic biome, perhaps, which would have had many microenvironmental zones [with a parkland megafaunal] available for exploitation by [widespread] pre-Neolithic and Neolithic [human] groups" (McHugh et al. 1988:30–31). In fact, during the middle Neolithic (ca. 6,200 years B.P.), the Nubian desert supported organized human villages, which subsisted on hunting and gathering as well as agriculture (Wendorf, Close, & Schild 1985). Al-

though this is a fairly long span of time (thousands of years), many of the significant environmental changes may have happened within shorter time spans (hundreds of years).

As illustrated in the hypothetical model by Peters & Darling (1985:709, Fig. 2), biological preserves designed for this area under early Holocene conditions would have been completely obliterated by climatic changes in the latter part of the Holocene. The late Holocene environmental changes may appear extreme and, perhaps, serve as a worst-case scenario, but large-scale environmental changes, coincident with a major extinction event, have occurred in North America and other parts of the world during the last 12,000 years (Martin & Klein 1984). The paleoecological record of the late Quaternary provides a baseline against which predictions for the future can be measured.

There are two divergent theoretical ways to model the response of biotas to climatic and environmental changes. If groups of organisms ("communities") respond to environmental changes as intact units, then the communities we observe today might be quite old geologically, allowing for extensive coevolution. Planning for the preservation of the communities would be quite straightforward — appropriate areas would be set aside as reserves and these communities would merely track environmental change.

The Pleistocene refuge model (e.g., Haffer 1969; Moreau 1963; Simpson & Haffer 1978; Vuilleumier 1971), in which areas were postulated to have harbored mesic communities during periods of regional aridity in the tropics, is primarily based on the premise of the community response concept. These models have been broadly applied to the design of biological preserves.

Although the refuges are widely accepted as being established "by virtue of an approving view (Simpson & Haffer 1978) and a massive symposium volume (Prance 1982)" (Simberloff 1986:171), they have yet to be documented by paleoecological data in spite of attempts to locate them (Colinvaux 1987; Leyden 1984:4,858). Similarly, there is no paleontological evidence (Graham 1979) for the proposed North American Pleistocene refugia for "warm-adapted" species in Florida and northern Mexico as proposed in some models (Blair 1958, 1965). These facts and other arguments (see Simberloff 1986) call into question the validity of using refuge models for the design of biological preserves.

The individualistic concept suggests that individual species respond to environmental changes by migrating in different directions, at different rates, during different times. Thus, our modern communities are ephemeral associations of species without any geological longevity and consequently little coevolution. More importantly, predicting the response of the "community" to environmental change is complicated because individual species must be considered.

Paleovegetational evidence supports an individualistic response to past environmental fluctuations (e.g., Davis 1976; Webb 1987). In fact, paleoecological data suggest that other organisms such as mammals, lower vertebrates, beetles, and terrestrial mollusks have responded the same way (for a summary see Graham & Lundelius 1984:224). Late Quaternary mammal distributions (Graham & Mead 1987; Graham, Semken, & Graham 1987) indicate that our modern mammal communities are, in part, the result of individualistic responses of species to climatic fluctuations (Fig. 1). In some cases during the Pleistocene, species, such as the collared lemming (*Dicrostonyx torquatus*), may have resided thousands of kilometers outside of their modern range (Fig. 2). As a result, late Pleistocene biotas do not have modern analogs, or stated another way, our modern communities and biomes are less than 10,000 years old (Graham 1986).

It is, therefore, reasonable to assume that species will respond individually to future environmental fluctuations and that new biotic assemblages may appear. Climatically or environmentally static models of reserve design do not take this into consideration. When the concepts of long-term climatic change and the individualistic response are superimposed on either the equilibrium (MacArthur & Wilson 1967) or nonequilibrium (see Boecklen & Simberloff 1986) models, they offer a new dimension for the contingencies of designing reserves. In fact, this more dynamic approach might view these reserves as merely holding stations for species through time and might suggest that their survival will be dependent upon mobility or dispersal. Western and Ssemakula (1981) have used the term "faunal enclaves"

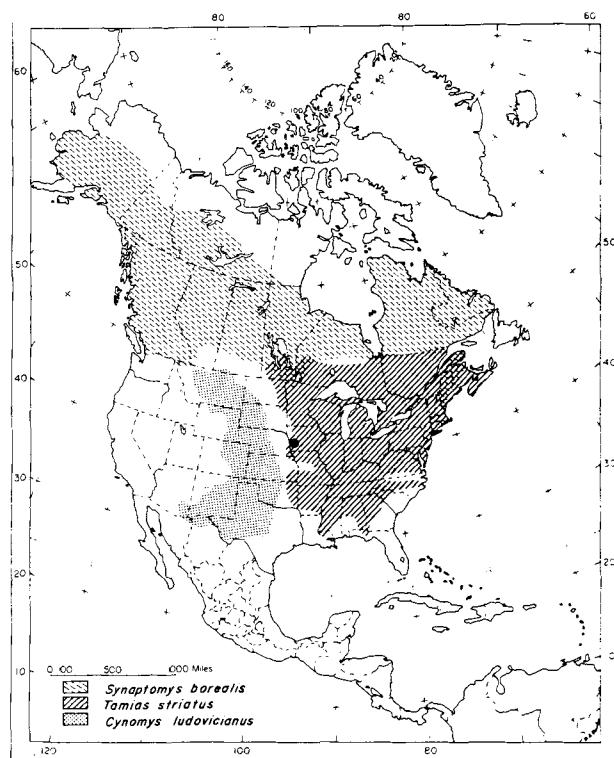


Figure 1. The modern distribution (shaded areas) of three rodent species (prairie dog [*Cynomys ludovicianus*], eastern chipmunk [*Tamias striatus*], and northern bog lemming [*Synaptomys borealis*]) that occurred contemporaneously in the 23,200-year-old Craigmire local fauna (Rhodes 1984), which is located by the dot. Adapted from Graham (1986). The disjunct nature of these distributions clearly illustrates the individualistic response of mammalian species to environmental changes. These types of distributions are typical of late Pleistocene mammal faunas (Lundelius et al. 1983).

to refer to similar processes in the savannah reserves in eastern Africa.

Large size of the reserve and connecting corridors are important features in promoting dispersal of species. However, as succinctly pointed out by Boecklen & Simberloff (1986), as well as Western & Ssemakula (1981), size, in and of itself, is a poor predictor of the number of species an area will support. They suggest that the number of habitat types within an area is a better indicator. This is consistent with the suggestion by Hunter et al. that nature reserves should contain a range of environments to allow organisms to adjust their local distribution in response to environmental change. Likewise, corridors, or "avenues of migration," between reserves must contain a wide array of habitat types for these will be the extinction filters, or "bottlenecks," of the future.

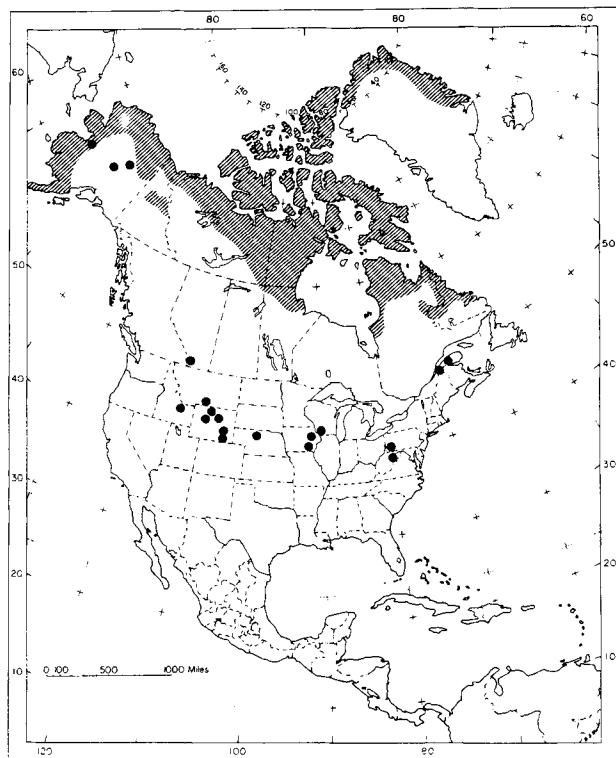


Figure 2. Modern distribution (shaded area) and Pleistocene fossil localities (dots) for *Dicrostonyx* spp. in North America. Adapted from Graham (1986).

In fact, more thought and effort must be directed to the conceptual design of corridors. As stated by Hunter et al., these corridors should be developed on a continental scale. Although relatively narrow, the extensive and intertwined network of railroad right-of-ways that are rapidly being abandoned might serve as effective corridors. Also, the margins of interstate highway systems should be considered.

Corridors are especially important for highly mobile vertebrate species. Today, thousands of African mammals are dying because their avenues of escape from severe but localized climatic conditions are blocked by fences. Constructing future reserves as habitat islands without avenues of migration would probably result in an analogous situation. The utility of these corridors would not be restricted to large migratory mammals but would also facilitate the dispersal of small mammals and other terrestrial vertebrate species as well as plants.

Hunter et al. suggest that decisions about where to locate nature reserves should be influenced by the distribution of particular physical environments. This is a critical point for a variety of logistical and biological reasons, as they discuss. However, like biotas, landscapes have not been static in the past. They continually

evolve, as exemplified by extensive prehistoric and historic fluctuations in lake levels, fluvial discharge, sea level, and alpine glaciation. All of these climatically induced changes can cause significant alterations in the landscape and physical environment. This underscores the importance of considering corridors in designing nature reserves so that organisms can adjust to these changes.

The direction of future climatic changes further compounds the issue. Naturally induced climatic changes caused by astronomical forcing suggest cooling for the future. However, the greenhouse effect caused by CO₂ enrichment of the atmosphere by human pollutants will result in climatic warming. Furthermore, climatic models suggest that the effects of global climatic changes will be expressed with various magnitudes in different areas (tropics vs. arctic, continental margins vs. continental interiors). Therefore, biological preserves must be designed for a variety of complex climatic fluctuations in time rather than a simple directional change.

The oscillations of climatic change are particularly relevant for communities that presumably are inhabiting "marginal" environments. Two examples from North America may be boreomontane species living on isolated mountain peaks in areas with arid environments (e.g., in the southwestern United States) or species restricted to modern tundra environments in the arctic. Continued climatic warming could theoretically eliminate both of these environments and locally cause the extinction of endemic species (Peters & Darling 1985). However, all of these species survived the previous interglacial period, which was significantly warmer than the current one. The mechanisms of survival are not known but the ability to migrate to suitable microenvironments was probably a key factor.

Perhaps the most prophetic message paleoecology has to offer conservation biology is that we *must* plan to facilitate climatic change in the future. It is futile to assume that the species associations ("communities") that we observe today and that we are trying to capture in our reserves will be the same over long spans of time, perhaps less than hundreds of years. As metaphorically stated by Hunter et al., "Today's distribution of species and communities is from one frame of a movie recording continuously changing distributions and associations of taxa." Obviously, many important issues must be considered in designing biological reserves, but future climatic and environmental changes are inevitable.

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Literature Cited

- Blair, W. F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. Pages 433–468 in C. L. Hubbs, editor. *Zoogeography*. American Association for the Advancement of Science, Washington, D.C.
- Blair, W. F. 1965. Amphibian speciation. Pages 543–556 in H. E. Wright, Jr., and D. G. Frey, editors. *Quaternary of the United States*. Princeton University Press, Princeton, New Jersey.
- Boecklen, W. J., and D. Simberloff. 1986. Area-based extinction models in conservation. Pages 247–276 in D. K. Elliott, editor. *Dynamics of Extinction*. John Wiley and Sons, New York.
- Colinvaux, P. 1987. Amazon diversity in light of the paleoecological record. *Quaternary Science Reviews* 6:93–114.
- Davis, M. B. 1976. Pleistocene biogeography of the temperate deciduous forests. *Geoscience and Man* 13:13–26.
- Graham, R. W. 1979. Paleoclimates and late Pleistocene faunal provinces in North America. Pages 49–69 in R. L. Humphrey and D. Stanford, editors. *Pre-Llano Cultures of the Americas: Possibilities and Paradoxes*. Washington Anthropological Society, Washington, D.C.
- Graham, R. W. 1986. Response of mammalian communities to environmental changes during the late Quaternary. Pages 300–313 in J. Diamond and T. J. Case, editors. *Community Ecology*. Harper and Row, New York.
- Graham, R. W., and E. L. Lundelius, Jr. 1984. Coevolutionary disequilibrium. Pages 223–249 in P. S. Martin and R. G. Klein, editors. *Quaternary Extinctions*. University of Arizona Press, Tucson.
- Graham, R. W., and J. I. Mead. 1987. Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America. Pages 371–402 in W. F. Ruddiman and H. E. Wright, Jr. *North America and Adjacent Oceans During the Last Deglaciation*. Geological Society of America, K-3, Boulder, Colorado.
- Graham, R. W., H. A. Semken, Jr., and M. A. Graham, editors. 1987. Late Quaternary mammalian biogeography and environments of the Great Plains and prairies. Illinois State Museum Scientific Papers 22.
- Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* 165:131–137.
- Hamilton, A. C. 1981. The Quaternary history of African forests: Its relevance to conservation. *African Journal of Ecology* 19:1–6.
- Leyden, B. W. 1984. Guatemalan forest synthesis after Pleistocene aridity. *Proceedings of the National Academy of Science* 81:4,856–4,859.
- Lundelius, E. L., Jr., R. W. Graham, E. Anderson, J. Guilday, J. A. Holman, D. W. Steadman, and S. D. Webb. 1983. Terrestrial vertebrate faunas. Pages 311–353 in S. C. Porter, editor. *Late Quaternary Environments of the United States*. University of Minnesota Press, Minneapolis.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Martin, P. S., and R. G. Klein. *Quaternary Extinctions*. University of Arizona Press, Tucson.
- McHugh, W. P., J. F. McCauley, C. V. Haynes, C. S. Breed, and G. G. Schaber. 1988. Paleorivers and geoarchaeology in the southern Egyptian Sahara. *Geoarchaeology* 3:1–40.
- Moreau, R. E. 1963. Vicissitudes of the African biomes in the late Pleistocene. *Proceedings of the Zoological Society of London* 141:395–421.
- Peters, R. L., and J. D. S. Darling. 1985. The greenhouse effect and nature reserves. *BioScience* 35:707–717.
- Prance, G. T., editor. 1982. *Biological Diversification in the Tropics*. Columbia University Press, New York.
- Rhodes, R. S., II. 1984. Paleoecology and regional paleoclimatic implications of the Farmlandian Craigmile and Woodfordian Waubonsie mammalian local faunas, southwestern Iowa. *Illinois State Museum Reports of Investigations* 40:1–51.
- Simberloff, D. 1986. Are we on the verge of a mass extinction in tropical rain forests? Pages 165–180 in D. K. Elliott, editor. *Dynamics of Extinction*. John Wiley and Sons, New York.
- Simpson, B. B., and J. Haffer. 1978. Speciation patterns in the Amazonian forest biota. *Annual Review of Ecology and Systematics* 9:497–518.
- Vuilleumier, B. S. 1971. Pleistocene changes in the fauna and flora of South America. *Science* 173:771–780.
- Webb, T., III. 1987. The appearance and disappearance of major vegetational assemblages: Long-term vegetational dynamics in eastern North America. *Vegetatio* 69:177–187.
- Wendorf, F., A. E. Close, and R. Schild. 1985. Prehistoric settlements in the Nubian Desert. *American Scientist* 73:132–141.
- Western, D., and J. Ssemakula. 1981. The future of the savanna ecosystems: Ecological islands or faunal enclaves. *African Journal of Ecology* 19:7–19.