

Effects of Global Climate Change on the Patterns of Terrestrial Biological Communities

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Recent paleobiological research has shown that late-Quaternary global warming caused individual species distributions to change along environmental gradients in different directions, at different rates, and over different periods. The individualistic responses of the biota created new community patterns. Individualistic changes can be anticipated in the future and if, as predicted, the rate of warming caused by the 'greenhouse effect' is greater than in past events, then the individualistic responses may be even more profound.

The accumulation of 'greenhouse' gases in the atmosphere may cause rapid warming of Earth's climate in the near future. Understanding the response of biological communities to this warming is of fundamental importance, but obviously we cannot conduct experiments at a global scale to predict the nature of this response. However, rapid global warming at the end of the Pleistocene performed a 'natural experiment' from which we can learn about the responses of terrestrial organisms to an abrupt global climate change.

Two alternative models define the spectrum of possible community responses to climate change¹. One hypothesis – a static community model – proposes that large groups of species (i.e. 'communities') shift as tightly linked and highly coevolved assemblages. The other hypothesis, an individualistic or dynamic community model, suggests that individual species respond differentially.

The biological consequences of these two hypotheses are very different. The static model predicts that communities are stable and remain as units through long periods of geologic time. This model would suggest that communities maintain their compositional integrity and track environmental changes by shifting their geographic distributions as tightly linked and highly coevolved groups of species.

Conversely, the dynamic model suggests that communities are loosely organized collections of species whose coexistence is dependent upon a host of physical, biological and historical variables.

Rather than directing evolution of the community as a whole, environmental changes cause species to respond individually, to migrate in different directions and to assemble into new species associations². Therefore, species associations ('community' composition) may appear ephemeral in geologic time and our modern communities may be less than 10 000 years old. This model also implies that many ecosystems are not highly coevolved. The paleoecological evidence clearly demonstrates that the individualistic model is closer to the truth.

Phytogeographic evidence

Paleobotanists have long recognized the individualistic response of plants to environmental change, as well as the existence of non-analog plant communities (contemporary co-occurrence in paleocommunities of species that are allopatric today) in the late Quaternary³⁻⁵. The large number of pollen sites in Europe and eastern North America permits the production of contour maps of pollen percentages – 'isopoll' maps – for different periods. These maps document the past distribution of tree populations and powerfully illustrate the individualistic behavior of different species through time⁶⁻¹⁰. The continental ranges of species shift, expand and contract in various and chronologically unique patterns.

Taxa are seen to have been sympatric at some times and allopatric at others. Excellent examples are the past distributions of beech (*Fagus*) and hemlock (*Tsuga*) in eastern North America. Today these two taxa have essentially congruent ranges and are important elements of the hemlock–white pine–northern hardwood forest¹¹. Following the maximum Wisconsin glaciation, these taxa first appeared in any appreciable abundance about 12 000 years ago, but had separate ranges – beech on the southeastern Coastal Plain and hemlock in the southern Appalachians⁷ (Fig. 1). During the next 4000 years, hemlock migrated

northward up the Appalachians, while beech moved north along the Coastal Plain. For the next two millennia, both taxa moved westward through the Great Lakes region, establishing their essentially modern overlapping ranges and their importance as forest dominants. Thus, the close range congruency of these two taxa has existed for only the last 6000 years.

In montane regions, studies show that intact vegetation zones do not move up and down the slopes in response to vegetation change, but that taxa migrate individually, some more than others. In the southwestern United States, the analysis of radiocarbon-dated macrofossils from packrat (*Neotoma*) nests clearly shows the individualistic altitudinal shifts of plant taxa^{12,13}. Similar altitudinal adjustments of individual plant taxa have also been documented by palynological studies in the mountainous regions of Africa¹⁴.

As opposed to mapping individual taxa through time, Huntley¹⁵ carried out a cluster analysis of pollen spectra for 1000-year intervals from sites throughout Europe. He then mapped the quantitatively derived vegetation units. These maps clearly show the ephemeral nature of vegetation types as they appear, disappear, and sometimes reappear at different times and places. The clear paleoecological message is that plant taxa respond differentially to changing climate; intact vegetation 'zones' do not move in response to changing climate, but taxa reassemble into different vegetation types following a major climate change.

Zoogeographic evidence

Animals also document an individualistic response to late-Quaternary climate changes^{1,16}. For example, around 17 000 years ago the northern pocket gopher (Fig. 2a) inhabited southwestern Wisconsin, more than 600 km east of its modern distribution, and it persisted in western Iowa until at least 14 800

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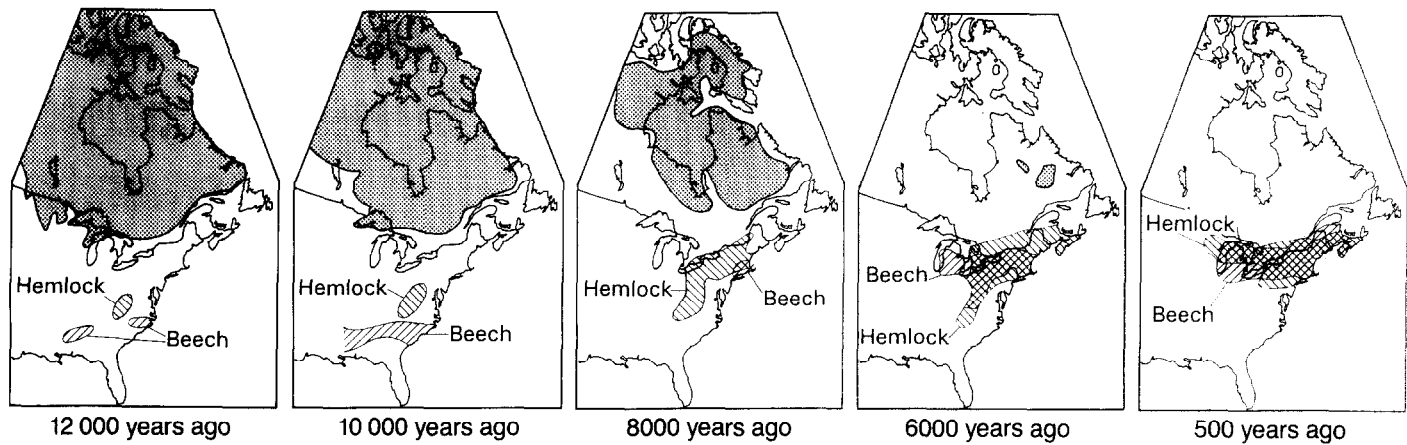


Fig. 1. Time series of the 5% isopolls for beech (*Fagus*) and hemlock (*Tsuga*) in eastern North America. The stippled area represents the Laurentide ice sheet. Adapted from Ref. 7.

years ago. Late-Wisconsin climate changes caused this species to shift its range further west. Conversely, the same climate changes caused the distribution of the least shrew to shift eastward (Fig. 2b). The collared lemming, widespread south of the Laurentide ice sheet during the Wisconsin (Fig. 2c), retreated almost 1600 km farther north in response to climate warming. These differential responses are characteristic of mammalian faunas throughout most of the world, but especially in North America, Europe, Asia and Australia¹⁶. Birds have shown similar range adjustments during the late Quaternary¹⁷, but the significance of these changes is problematic because of their extreme mobility.

Late-Pleistocene terrestrial molluscan communities have not been extensively studied in North America in recent decades, but the few studies that have been conducted tend to support the concept of an individualistic response to environmental fluctuations. Miller¹⁸ documents the occurrence of non-analog associations, presumably owing to individualistic responses, in Pleistocene molluscan faunas from southwestern Kansas.

Fossil Coleoptera (beetle) communities have received considerable study in both Europe¹⁹ and North America²⁰. Climate change has significantly altered the geographic ranges of many species. For example, *Aphodius holdereri*, the most common large dung beetle in Britain during certain parts of the late Pleistocene, is now confined to the high plateau of Tibet and adjacent northwestern China¹⁸. Again, beetle distributions changed individually. As was succinctly stated by Morgan (Ref. 20, p. 362), during the late Pleistocene in North

America 'conditions were such that individual species (which today are often separated by large geographic distances) were able to live as part of a single assemblage'. Coope¹⁹ has documented the same pattern for European late-Quaternary beetle assemblages.

In contrast to vegetation, mollusks, beetles, birds and mammals, most herpetile species in the northern hemisphere apparently did not undergo such dramatic range shifts during the late Quaternary. Consequently, most middle-latitude herpetile communities of the United States²¹ and Europe²² do have modern analogs, although non-analog associations occur in some sites in the southern United States²³. The reasons for the paucity of non-analog herpetile associations are unclear, but this is one of the more intriguing questions in late-Quaternary vertebrate paleoecology.

Heterochrony, climatic equability and historical effects

The interpretation of late-Quaternary non-analog assemblages as viable paleocommunities is dependent upon the contemporaneity of the fossils found in an assemblage. A number of natural taphonomic processes can produce fossil assemblages with non-analog associations of species, by mixing of assemblages of different ages and environments. Obviously, these heterochronic assemblages do not have any biological meaning. However, despite potential problems of temporal mixing in certain situations, widespread occurrence of non-analog associations in different depositional systems, for different organisms, and for many Pleistocene biotas throughout the world, makes a strong case for non-analog

life assemblages. Moreover, the lack of non-analog associations in Holocene sites²⁴, with taphonomic settings similar to those of the Pleistocene¹, also strongly suggests that the mixing problem is slight.

Until recently, it was difficult to date non-analog associations directly because specimens such as seeds, needles and insect parts were too small for conventional radiocarbon dating methods. The Accelerator Mass Spectrometer (AMS) now allows the direct dating of extremely small samples. New techniques for isolating and radiocarbon dating specific amino acids from bone samples²⁵ not only improves the accuracy of bone dates, but also permits the dating of objects as small as individual rodent teeth. Therefore, radiocarbon dating can now determine the contemporaneous association of many macrofossil assemblages.

In some cases, AMS analyses have shown mixing to be a problem, but in other cases they have clearly demonstrated contemporaneity of non-analog associations. Based on AMS dating of various insect taxa, Elias and Toolin²⁶ have tentatively interpreted a late-Pleistocene 'non-modern-analog' insect assemblage from Colorado as heterochronic, but they acknowledge the need for further investigations into this problem at the site. On the other hand, AMS dates on rodent teeth from an Arkansas cave deposit have documented the contemporaneity and sympatry in the late Pleistocene of two rodent species that are today allopatric²⁷.

The association in paleocommunities of species that are allopatric today and that appear to be ecologically incompatible has been explained, in part, by the climate

equability model²⁸. This model assumes that the geographic distributions of organisms are controlled by seasonal extremes in climate rather than by mean annual variations. Specifically, the southern limit of a northerly distributed taxon – such as spruce (*Picea*) or collared lemmings – is controlled by summer temperature maxima. If summers become cooler, then the southern limit of distribution for these taxa will expand farther south; but if summers become warmer, then their southern limit will be restricted farther north. Conversely, the northern limit of a southerly distributed taxon – such as elm (*Ulmus*) or least shrews – is limited by winter temperature extremes. Therefore, the past co-occurrence of taxa with disparate modern distributions (e.g. spruce with elm, collared lemmings with least shrews, etc.) may have resulted from reduced seasonality: a more equable climate. These community patterns were disrupted by more-continental climates at the end of the Pleistocene (about 10 000 years ago), when seasonality was enhanced by solar radiation forcing²⁹. In fact, these changes in climate and community patterns have been implicated in the late-Pleistocene extinction event¹⁶.

A host of physical, biological and historical variables other than climate may control the distributions

of species, and differences in these variables probably contribute to the individualistic response.

In addition, analyses of beetle communities have documented another important dimension of the individualistic concept shaping biological communities. Coope¹⁹ suggested that lag effects have created 'anomalous' assemblages. These are not the same as the non-analog assemblages that we have previously discussed. The geographic distributions of the plant and insect taxa that compose these anomalous assemblages may overlap today, and thus have modern analogs, although their interactions may have changed. Also, in contrast to a non-analog assemblage, which may be in steady state with climate, an anomalous assemblage is characterized by beetles with an environmental signal incongruent with the vegetation. An excellent example given by Coope¹⁹ is the sudden post-glacial warming that allowed a diverse suite of temperate insects to move rapidly into Britain whilst the only trees on the landscape were birches (*Betula*). Particularly notable is the beetle *Calosoma inquisitor*, which today preys almost exclusively on caterpillars that defoliate oak (*Quercus*) trees; this beetle species presumably utilized birch trees in Britain during the late Pleistocene.

Apparently, beetles responded to climate change more rapidly than plants and consequently inhabited new areas before the vegetation had adjusted. This differential response time has two very important ramifications for future warming events and evolutionary biology. First, because of their rapid response rate, beetles might be a sensitive biological monitor (an 'early warning system') for global warming. Secondly, some beetles may not be as highly coevolved and dependent upon vegetation patterns as modern distributions might suggest.

Implications

The individualistic reorganization of communities in response to environmental changes has important implications for understanding the biotic response to 'greenhouse' warming. Probabilities of extinction must be of primary concern. At the end of the Pleistocene, many large terrestrial mammals went extinct throughout the world. The proposed causes of this extinction are greatly debated³⁰, but several hypotheses implicate the individualistic reorganization of biotic communities. Graham and Lundelius¹⁶ have argued that the emergence of new vegetation communities at the end of the Pleistocene forced herbivorous mammals to select new diets. The high rate and magnitude

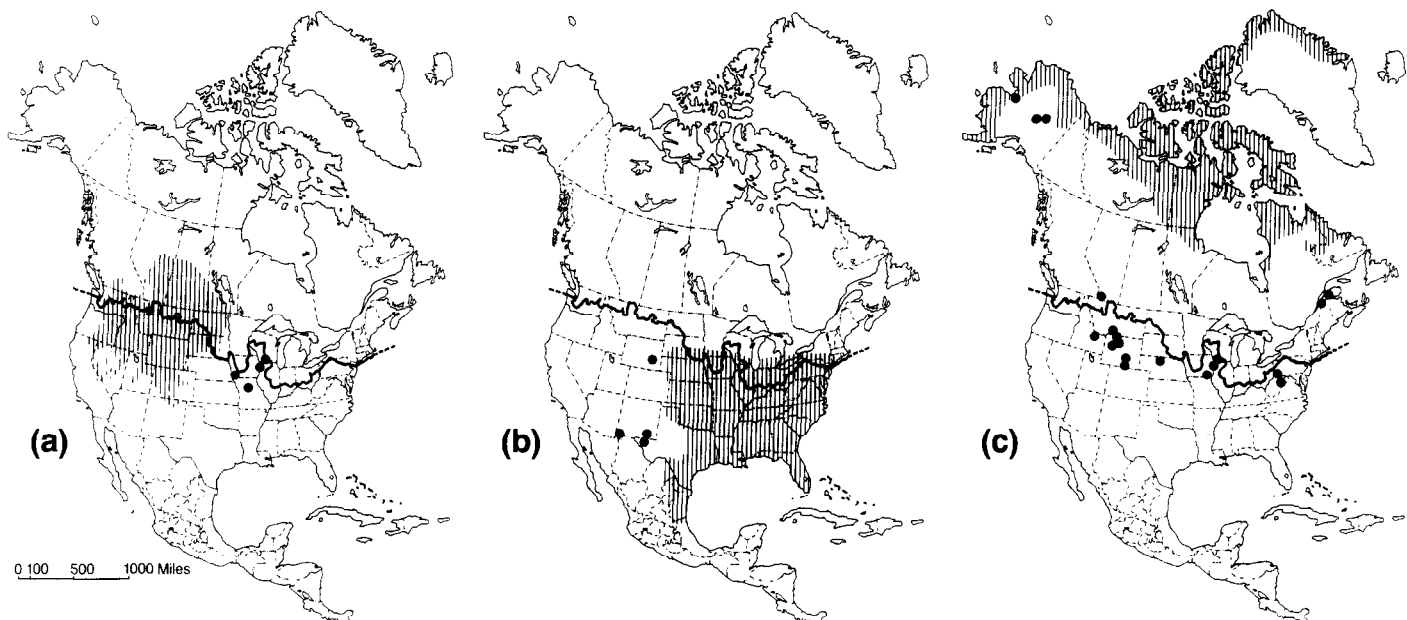


Fig. 2. Changes in the late-Quaternary distributions of (a) northern plains pocket gopher (*Thomomys talpoides*), (b) least shrew (*Cryptotis parva*), and (c) collared lemming (*Dicrostonyx* spp.). The solid line represents the southern limit of the glacial maximum during the Wisconsin glaciation. Shaded areas are modern distributions of taxa, and filled circles denote late-Pleistocene fossil localities of taxa. Adapted from Ref. 35, with permission.

of these vegetation changes⁷ may have heightened competition even for the mixed feeders at this time. Likewise, Guthrie³¹ has suggested that the new vegetation mosaics may have had lower effective nutritional value (reduced abundance of edible and palatable plant species), which would have lowered carrying capacity. In addition, environmental patchiness may have decreased, thus limiting the geographic distribution of some species and thereby significantly increasing their probability of extinction. In reality, all of these changes, and perhaps others, may have had a synergistic effect. All of these possibilities must be considered for future climate change.

The dynamic community model is highly relevant to the design of natural reserves. The individualistic response to climate change strongly underscores the significance of developing habitat corridors to link natural reserves³²⁻³⁴. Reserves designed as habitat islands will not allow species to track environmental change. In such a situation, species will either adapt to the new environments or become locally extinct. The individualistic concept is also important in modeling the response of whole communities to future environmental change. The paleobiological record suggests that merely shifting the location of entire ecosystems is unrealistic. Instead, the ecological requirements of individual species must be incorporated into models.

Finally, the paleobiological record is critical for testing the capability of computer-driven General Circulation Models (GCMs) to predict future climate changes. The validity of GCM results is tested by comparing model predictions of past climates with the observed paleobiological record (see Ruddiman, this issue). To this end, it is imperative to develop electronic databases of various paleoclimate proxies. The National Oceanic and Atmospheric Administration (NOAA) and European palynologists have begun such projects, and similar programs have been initiated for North American mammals. The use of multiple biological data sets (e.g. pollen, mammals, insects) is important for cross-checking interpretations as well as for providing

broader geographic coverage. For example, pollen records are abundant in eastern North America and throughout Europe; but in areas lacking pollen sites (e.g. the plains and desert regions of the United States, Eurasia and interior Australia), small mammals may offer an excellent alternative proxy record.

Predicting community response to greenhouse warming becomes particularly hazardous as the forecasted temperature increase exceeds that of any period of the last 120 000 years. The paleoecological record reveals that non-analog climates produce non-analog community assemblages, and our ability to predict community response to climate change diminishes as climate parameters move beyond the boundaries of existing climates. Future climates may lie outside not only the existing climate domain, but also outside our paleoclimate database and outside the climate to which existing species are evolutionarily adapted.

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