CLIMATE VARIABILITY AND ECOSYSTEM RESPONSE AT LONG-TERM ECOLOGICAL RESEARCH SITES

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Climate Variability and Ecosystem Response—Synthesis

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At the outset we identified the theme of this book as how ecosystems respond to climate variability. We have examined this theme at a variety of LTER sites and at a variety of timescales. The subject matter of the book was also to be focused on a series of framework questions. We noted that the theme of climate variability and ecosystem response is inherently deterministic and implicitly carries with it the notion of climate cause and ecosystem result. The analyses in this volume demonstrated that this is a valid and fruitful working assumption. However, the idea of a simple single climate cause and effect might be true in some cases, but it is obviously simplistic. More realistically, the effects of climate variability cascade through ecosystems. In almost all cases there is the probability of many secondary and associated effects accompanying the primary effects. As an example, the possible results of potential warming in the Pacific Northwest forests include changes in global carbon dioxide input, nutrient cycling between the plants and the soil, and feedback links between the plant and soil organisms (Perry and Borchers 1990).

In general there seem to be at least three broad classes of interaction between climate and ecosystems. First, the ecosystem simply responds to individual climate events or episodes that exceed some threshold for response. Second, ecosystems may buffer climate variability. In this sense they are filtering the effect of the climate event or episode. The same component in an ecosystem can sometimes act as a buffer and sometimes not, according to the nature of the climate event. Thus a riparian environment might provide soil moisture that acts as a buffer to a drought, but the whole environment might be destroyed by a large flood event. Third, we hypothesize that the ecosystem may move into resonance with the climate variability with positive and negative feedbacks that produce a strong ecosystem response. The relationship between fire and the Southern Oscillation indicates that the Southwest United States (Swetnam and Betancourt 1990) may provide an example of such resonance. Other examples of resonance, discussed subsequently, may exist in the forests of Interior Alaska and Puerto Rico. If there is indeed an ecosystem response to climate variability, the response tends to occur in cascades. The cascades and intermediate cascade elements may act as gateways, filters, and/or catalysts in response to the climate signal. The senses in which we use these terms will be explained here.

In this concluding chapter, we will develop these themes within the context of the framework questions with which we embarked. Emerging from this discussion are some general propositions that seem to hold for our examples from LTER sites and could be tested in other contexts and in later LTER studies.

The Framework Questions Revisited

The framework questions (figures 1.3, 1.4) have proved useful in making comparisons between the climate variability and ecosystem responses of all the LTER sites considered in this volume. The framework first called for an identification of the type of climate variability involved. The framework then poses the following questions, stated here in abbreviated form. What preexisting conditions will affect the impact of the climate event or episode? Is the effect direct or cascading? Is the effect completed by the time of the next event or episode? Does the event or episode return to an original state? Does the event or episode have an upper or lower limit? Does the climate and/or ecosystem exhibit chaos?

Identification of the Climate Variability

On first consideration, the identity of climate variability is clear in most of the studies in this book. Sometimes not so clear is the interaction of climate events at some timescales in relation to events and episodes at other timescales. Also, it is helpful to attempt to distinguish between process, which occurs at a particular timescale, and pattern, which represents how a process manifests itself in space.

A wide variety of climate variability has been addressed. Specific hurricane and drought periods and processes are both considered in part I on short-term climate events. A study of the frequency of storms in the twentieth century (chapter 14) identifies the pattern of some areas such as those of the western U.S. LTER sites (CAP, JRN, SEV, NWT, SGS), where large increases in storm frequency have occurred. Our investigations at the quasi-quintennial timescale (part II) focus almost exclusively on the process of the ENSO events. ENSO gives rise to important geographical patterns of climate response across the world. ENSO events in the Western Antarctic Peninsula occur within the context of an almost 60-year warming trend. In this example, two timescales and processes must be considered simultaneously. Periodicities at the quasi-triennial timescale appear in LTER site growing-season mean and maximum temperature data (McHugh and Goodin, chapter 11). The Pacific Decadal Oscillation (PDO) is the principal process of climate variability considered in part III on the interdecadal timescale. Juday et al. (chapter 12) have established climate regime shifts for Interior Alaska that extend back over 200 years and are most likely related to the PDO. However, the interdecadal-scale studies display linkages to both the quasi-quintennial scale and the century scale. Indeed, El Niño events in Interior Alaska are seen as amplifications of PDO-related episodes as far as reproduction of white spruce is concerned (Juday et al., chapter 12). Investigators at the Sevilleta LTER site identify a 55- to 62-year periodicity in precipitation values (chapter 15). McHugh and Goodin (chapter 11) also confirm a 50-year periodicity in maximum temperature records from some LTER sites. The processes behind these periodicities are not yet clear. The studies at the century to millennial scale in part IV focus on the last 25,000 years in the Colorado Rockies and the Dry Valleys of the Antarctic and further into the Pleistocene for southern New Mexico. This time period includes the episodes of the Late Glacial Maximum and the return to warmer periods in the Holocene. It also includes the colder Younger Dryas period, as well as the Holocene Altithermal and Medieval Warm and Little Ice Age periods of the last thousand years. It is becoming clear that the pattern of the effects of some of these events may not be as globally homogeneous and intense as once was thought (Mann 2001). In all of these cases, we are more concerned with the climate signal that arises from these phenomena, such as ENSO and PDO, than the mechanisms of the phenomena themselves.

Many of our studies show that it is rare that an ecosystem is dominated by climate variability at one specific timescale. More likely, ecosystems are responding to a suite of climate variability occurring at a variety of timescales. For example, Goodin et al. (chapter 20) have identified several different timescales that affect the prairie ecosystem at the Konza Prairie, Kansas. Occasionally, the events at one timescale are clearly dominant, but even in these cases climate variability at longer and shorter timescales is still important. In addition, Goodin et al. (chapter 20) point out that the juxtaposition of climate events at different timescales may be as important as the strength of any single process because of their potential to either augment or offset each other. Ideally, we would like to have a climate record and a record of responses so we can distinguish variation in driver signal from the responder signal. This variation might involve lags and dampening or amplification of the driver signal. Rarely do we find such a clear-cut situation in the real world.

In some instances the identification of climate variability and the time and space scales at which it is operating poses some difficulty (McHugh and Goodin, chapter 11). The first area of difficulty is in distinguishing trends and discontinuities. At issue are how fast the trend is and when a shift in trend becomes a jump. The answer is scale-dependent. Also, of course, a cycle with a periodicity of two decades or more could be said to be composed of a series of alternating trends. The second difficulty arises because the interpretation of climate at one point (e.g., an LTER site) is dependent partially on the operation of climate at distant locations and the multiple interactions existing in the climate system as a whole. The third difficulty is that two, or more, timescales may be important to the same type of climate event. Storms, for example, primarily act at a daily timescale, but both the extratropical storms (chapter 14) and hurricanes (chapter 2) display interdecadal variation of frequency at a timescale of a century.

Bryson (1997) pointed out that climate is multidimensional, a vector property as opposed to a scalar datum. Thus we should recognize that climate variability seldom occurs in one climate variable alone. Brazel and Ellis (chapter 7) illustrate this point when they establish that, at the Central Arizona and Phoenix LTER site, an El Niño event is likely to be accompanied by change in the values of at least eight climate-related variables. Similar situations exist with climate variability at other LTER sites.

We should also point out that negative results may often be as interesting as positive findings. It is important, for example, to note that McHugh and Goodin (chapter 11) find no important periodicities in growing-season precipitation at LTER sites. Growing season precipitation is a critical variable for ecosystems, as shown by Gage (chapter 4). However, the absence of any periodicity in precipitation totals does not necessarily mean an absence of periodicity in drought occurrence—particularly in months that are very important to crop growth, as shown by the work of Gage (chapter 4). Another example is storm frequency. Hayden and Hayden (chapter 14) find no change in storm frequency nationally during the last century. Certain subregions of the country do, however, manifest some very important climate changes in terms of an increase of storm frequency over the century—sometimes by as much as 300%. Similarly, those authors also note no substantive difference between storminess during El Niño or La Niña years and an average year for the entire period of record.

Several factors require investigators to use a degree of caution when studying climate variability in the context of ecosystem response. These include the interactive hierarchy of time and space scales at which climate variability occurs, the multiplicity of climate variables, and the potential for some types of climate variability to be defined without sufficient rigor. Climatologists working in the LTER program also sometimes note that ecologists occasionally award climate data more accuracy than is warranted. Among other issues calibration drift in instrumentation can sometimes be a problem. Occasionally this is related to the dynamics of the ecosystems themselves. Changing tree cover around meteorological observing sites is a common problem in the forested LTER sites. Still, in most of the studies in this book, the climate variability under discussion is fairly clear.

Preexisting Conditions

Whether a climate event or episode exceeds the threshold to produce an ecosystem response, as well as the degree of buffering to the climate signal the ecosystem may provide, both depend on preexisting conditions in the ecosystem and, sometimes, the climate system. Certainly, we see frequent examples of preexisting conditions themselves acting as gateways, filters, and even catalysts of ecosystem response to a climate driver. Many of the studies presented in this book contain examples of the importance of preexisting conditions to later ecosystem response.

A straightforward, simple example concerned the windthrow events in winter in the northern Cascade Range of Oregon. Such events were found to occur particularly when winds were from the east after a period of dry weather. High-pressure conditions in winter gave rise to icing on the branches of trees, setting the stage for some windthrow events (chapter 19; Sinton and Jones 2002). Another straightforward example involves the white spruce in Interior Alaska, which must have a sufficient level of growth reserves as a precondition to a successful seed production event that itself would be triggered by a climate episode and the consequences thereof (chapter 12). A second example from Oregon shows that one climate event can act as a preexisting condition for a second climate event that, in turn, gives rise to an important ecosystem response. This is the case of the bark beetle outbreak following a drought that was preceded by a windthrow event. In these examples the preexisting conditions act as gateways to permit additional ecosystem response. The existence of ice on the trees might be regarded as a third element that acts as a catalyst and makes the windthrow event worse than it might otherwise have been. The other two elements present in this case are dry conditions and wind.

Other examples of the importance of preexisting conditions are less straightforward. For example, the previous disturbance and land-use history are very important in determining the exact effects of a new hurricane storm event (chapter 2). In another case, some preexisting conditions can increase the certainty that plants will suffer adverse effects, but there are also situations when the adverse effects can occur anyway if a detrimental climate event occurs. This is shown in the example of drought in the North Central Region (chapter 4). Low corn yields occurred in 1988 because of a high heat/precipitation value in July. But in this case the stage had virtually been set for low yields because of the physiological stress that had occurred in the previous May and June. On the other hand, in Michigan in 2001, May and June precipitation values were well above normal, but an exceptionally dry July and August period led to low yields for this year as well. Shallow roots for corn and soybeans were unable to make use of preexisting soil moisture at the lower level of the soil. In these agricultural examples the preexisting conditions could be said to be acting as filters to further ecosystem response.

In general, the effect of preexisting conditions is more marked at the shorter timescales, as in the previous examples. When dealing with decadal and longer timescales, the climate and related biophysical conditions become part of the preexisting conditions for the next climate episode. In the Palmer LTER example, the 60-year warming trend itself becomes part of a preexisting condition on which quasi-quintennial variation is superimposed (chapter 9). A similar pattern is seen at the Arctic LTER in Alaska, except that in this case an interannual variation is superimposed on an 11-year (so far) warming trend (chapter 5). An extreme example of how preexisting conditions do play an important role at the longer scale is at the McMurdo Dry Valleys LTER site. Here, in Taylor Valley (77.5° S), Fountain and Lyons (chapter 16) observe a strong climatic legacy whereby past climate conditions strongly imprint current ecosystem structure, function, and biodiversity. Specifically, shifting precipitation and temperature patterns caused the Ross Ice Shelf to enter Taylor Valley and impound a valley-wide lake beginning about 27,000 years ago. Ice sheet retreat, again due to changes in precipitation pattern, about 9,500 years ago caused the lake to drain. Relic benthic algal mats from the ancient lake locally increase the organic carbon content of the Taylor Valley soils. Fountain and Lyons believe the current soil communities depend on this organic carbon matter as a primary carbon source. At the longest timescale considered in this book, Monger (chapter 17) describes how climate variability between glacial and interglacial periods for the area around the Jornada LTER site can actually give rise to new geomorphic surfaces on which ecosystems develop. During times of higher precipitation in the southern New Mexico area, erosion and sedimentation markedly altered the surfaces of both river valley and piedmont areas. In addition, at this timescale, climate and vegetation actually work together to control erosion rates on piedmont slopes.

Some conceptual, as well as real biophysical, elements can be considered as preexisting conditions. We consider three examples. First, as was found in some of the ENSO cases (chapter 6), there must be a specific plant physiological linkage available for plants to respond to unusual extreme climate conditions. The rooting depth of species is a recurrent example of a physiological linkage. Such a linkage could, in some ways, be considered a preexisting condition. Second, preexisting conditions may also be thought of as a set of nonclimate-related processes that form a backdrop on which climate variability operates, or the opposite is equally true. For example, in the Konza Prairie such factors or processes include fire, nutrients, grazing by large ungulates, soil characteristics, and topography (chapter 20). Another example relates to the timing of preexisting conditions. For some tree species at Coweeta, the degree of effect of a drought is in part determined by the stage of the cycle of the Southern Pine Beetle population (chapter 3). Third, we should also consider the issue of preexisting conditions in terms of the fact that most of our ecosystems are chaotic systems. It is an inherent characteristic of chaotic systems that a small change in initial conditions may lead to large changes in subsequent conditions. With respect to climate warming, Shaver et al. (2000, p. 880) point out that "the same temperature change applied to different ecosystems will illicit different responses depending on initial position on the temperature response surface . . . and on initial biogeochemical conditions and composition. . . ." Analogous situations are found throughout the natural world and in the examples given in this volume.

System Cascades

Of all the guiding questions for this book, research on cascades in systems has been the most fruitful. This is because it strikes to the heart of explaining how the systems operate. Indeed, the cascades are the ecosystem responses of our title. The more we know about system operation, the more we will understand the true nature of the system. The complexity and extent of cascades in ecosystems caused by climate impact is due especially to process connections between the living components of ecosystems. In some cases abiotic components also affect the cascades. Initial and intermediate cascade elements may act as gateways, filters, and/or catalysts to the climate signal. Gateways can be open or closed. They can either permit, or not permit, the passage of material, energy, or information. Filters may pass a variable amount of material, energy, or information along through the cascade. The amount varies from all to none and includes all the possibilities in between. Thus, the filters in the system provide a buffering function to a climate disturbance. Catalysts occur where the presence of one component greatly enhances the interaction of two or more other system components. Another consideration is that the climate event or episode having a potential effect on an ecosystem is often itself a part of a cascade in the climate system. For example, the variability in the values of many surface climate variables at the CAP LTER during ENSO events (chapter 7) occurs at the end of a cascade that started with anomalous sea surface temperatures (SSTs) in the equatorial Pacific Ocean. These SST anomalies entered a series of atmospheric processes that altered the upper part of the atmospheric flow and eventually affected the surface in the Southwest United States.

The complexity and extent of the cascades of climate effects within ecosystems is best illustrated through a detailed case study. The example selected here deals with the cascade of events in the hydrologic system of the Andrews LTER site following a large rain, or rain on snow, event such as that which occurred in February 1996. This is an interesting example for many reasons. First, it is well documented. Second, not only does the example deal with the abstract concept of a cascade, but it also is a very real cascade of water working in a real time sequence over a series of spatially linked channel and topographic components arranged on the landscape from higher to lower elevations. Third, the example focuses on how different processes may display some sequential linkage. Identification of the sequencing of different processes in a cascade is very important. Within the context of a global-scale temperature increase, Shaver et al. (2000) note that the dominant controls over ecosystem response will change over time as different processes change at different rates. Furthermore, the changing sequence will not necessarily be the same in all ecosystems. The following description of what the authors call a "disturbance cascade" is derived from the analysis by Nakamura et al. (2000).

The Andrews precipitation-forced disturbance cascade is a parallel cascade consisting of two initial drivers. The first is small, rapid debris slides from hillslopes. The second is large, slow-moving earthflows. In the first path, debris slides move into steep, headwater stream channels and move through the channels as debris flows. The movement delivers sediments and logs to larger streams. On entering fourth- and fifth-order channels, the debris can be entrained and float along on rafts of coarse woody debris (CWD) or can cause jams at the confluence with larger channels. The jams may break during floods, causing a surge that pushes the debris further downstream. The CWD transport may terminate in areas of accumulations of wood or may be dissipated gradually, as wood levees, along stream banks. In the second path, slow earthflows gradually constrict stream channels. This increases the potential for stream bank erosion and stream side slides during high-flow events. The slides can deliver sediment and trees that form temporary dams. The breakup of the dams triggers flood surges downstream. Associated CWD may move in a congested manner sometimes disturbing riparian vegetation.

The sequence of processes may be interrupted at any point along the flowpath. Sometimes preexisting conditions, such as a change in the channel slope, may halt or alter the nature of the sequence. Roads may intersect the cascade flow path and act as filters or have other effects (Wemple et al. 2001). Occasionally, the cascade sequence will not occur at all. Streamside slides may merely alter a channel location with few downstream consequences. Similar outcomes, such as flood surges, may result from different processes. These disturbance cascades were found to produce a gradient of decreased overall severity of impact on the ecosystem and increased variability of severity of stream and riparian disturbance in the downstream direction. For the February 1996 event, instances of changing processes from one to another and halting in particular parts of the cascade were quantified. Especially noteworthy is that only a very small fraction of all the initial mass movement events resulted in the full cascade sequence. Thus, filtering in this cascade was strongly marked.

This example suggests a case in which the climate event had to pass through a geomorphological cascade before beginning an ecosystem cascade affecting the flora and fauna. The immediate ecosystem effect varied from complete removal of alluvium, soil, and vegetation on steep, narrow, low-order channels to localized patches of toppled trees.

We learn much from the comparison of system cascades identified at the various LTER sites discussed in this book. To start with, cascades can be short or long, intuitively obvious or less obvious, linear or nonlinear. Some short cascades are found in the Antarctic. The remarkable responses of fauna in the glacial lakes of the McMurdo Dry Valleys LTER site to the freezing of the lake surface and the extreme low temperatures represents some extraordinary cascades through the aquatic ecosystem, as described by Fountain and Lyons (chapter 16). Although the responses are extraordinary, the cascades are short because the food chains are short. Fountain and Lyons (p. 334) point out that "the low biodiversity and short food chains make the ecosystem directly dependent on the physical environment such that few buffers exist and the response of the ecosystem to slight climate change is immediate." Short cascades are also seen at a daily timescale at the Arctic LTER, where there is approximately a direct response in Net Ecosystem Production (NEP) to an increase of photosynthetically active radiation levels, among other things (chapter 5). Cascades on agricultural crops also tend to be short (chapter 4). Many of the other cascades described in the preceding chapters are long ones. Often the more we learn about the way the ecosystem operates, the longer the cascades become. So, for example, LTER investigations have shown that a simple relation between high water flow events and increase productivity in the lakes of the arctic tundra actually involves changes in the degree of mixing of lake water and variations in available nutrient content (chapter 5).

Some cascades are simple and intuitively obvious such as the increase of glacial meltwater and streamflow in response to higher radiation input values at the McMurdo Dry Valleys LTER site (chapter 10). Others, such as the increase of traffic accidents in and near Phoenix initiated by a La Niña event, gene switching and the production of new phenotypes in species at the Coweeta LTER site in response to drought (chapter 3), or the hurricane-initiated increase of forest fire danger and possible extensive logging that itself can create huge ecosystem effects (chapter 2), are certainly not intuitively obvious. Neither is the fact that some ecosystem processes may respond in different ways to a given climate episode, in the case of NEP levels in Oregon forests in relation to summer precipitation values (chapter 19).

Many cascades are linear, but we have also recognized nonlinear responses. For example, because summer temperatures are close to freezing point at MCM, the change between liquid and solid water in the hydrologic systems is delicately balanced. Welch et al. (chapter 10) report that small changes in temperature and radiant energy are amplified by large, nonlinear changes in the hydrologic budgets that can cascade through the system. Another example is the response at Luquillo, Puerto Rico, where 75% of the sediment export occurs during the 1% of the days that have the greatest rainfall (chapter 8). Such a nonlinear response can be exacerbated even more when the heavy rain events give rise to debris flows that course down hillslopes and through streams, as sometimes happens both at Luquillo and at the Andrews LTER site in Oregon. In an entirely different environment, the Sevilleta LTER site of New Mexico, another surprising, nonlinear response to decadal-length drought is hypothesized to be economic collapse and a large number of changes of landownership toward the end of a drought (chapter 15). We learn something new about climate variability and ecosystem response from almost every different cascade. Drought in the corn crop ecosystem may lead to a cascade in which the plant system suffers mortality or becomes weakened and susceptible to insect herbivory or disease (chapter 4). A lesser recognized cascading effect, pointed out by Gage, for agricultural systems subjected to drought is the establishment of more irrigation systems with their subsequent effect on local and regional water tables. In these two last examples, the cascades existing in the ecosystem represent catalysts for later major changes in the human dimensions of local and regional change.

Scientists at the Palmer LTER site believe they have identified an important cascade in their ecosystem. Pygoscelid Penguins are representatives of the higher trophic level in this ecosystem. Population variations at quasi-quintennial and decadal timescales in Pygoscelid penguins have to be understood via a cascade that starts with an entrainment of phytoplankton in newly forming sea ice of the previous autumn. In some senses this could be regarded as a preexisting condition. The cascade continues with the growth of sea ice communities during the winter and the spring release of a potential bloom inoculum of particulate organic matter in the water column. These events are related, in turn, to the survival of larval krill that depend on the algal food source in the sea ice. In summary, there are strong linkages among sea ice, phytoplankton, and krill. The foraging ecology of the penguins is dependent on krill recruitment and abundance, indirectly through habitat changes that mediate the availability of krill (Smith et al. chapter 9). This type of cascade best illustrates the concepts of gateways and filters. Because the sea ice is necessary for phytoplankton development, the sea ice extent represents a gateway. Whether this gateway is open depends on the delicate balance of the sea water temperatures near freezing point. If the sea ice exists, it acts as an open gate. If sea ice is not present, its absence acts as a closed gate and does not permit the development of the phytoplankton that are the first level of the cascade. If the cascade is established then each step in the food chain filters the passage of chemical energy to subsequent steps in the cascade.

The concept of gateways existing in cascades has been developed very explicitly by Juday et al. (chapter 12) in the case of white spruce reproduction in Interior Alaska. These workers identify five climate-mediated gateways in the overall white spruce reproduction cascade. The first gateway is the preexisting condition of the need for a sufficient level of growth reserves. The second gateway is the need for a drought stress signal at the time of the formation of the bud primordia, which occurs at the end of vegetative shoot elongation. A third gateway is the requirement of a lack of severe pruning of reproductive shoots by wind and canopy snow loading in the fall and winter of the first year of seedling growth. A fourth gateway is the requirement of high growing degree-day heat sums to promote the maturation of the pollen and cone buds in time for the remainder of the steps to be completed before frost ends the growing season. Finally, a double fifth gateway requires both the survival of pollen and cone buds in early stages (e.g., lack of killing frost) and a heavy pollen flight (e.g., lack of persistent rains) to ensure high levels of cross pollination. In this example a suite of different aspects of climate variability plays a role in the final successful, or otherwise, species reproduction.

There are at least two temporal elements implicit in the concept of gateways. The first is sequencing. Second, the timing of the open gate must match the timing of other possible constraints. The gate will be open or closed at certain discrete times, and the timing of the opening is important if the ecosystem cascade is to be followed. So, for example, as mentioned previously in the context of preexisting conditions, in the Coweeta forest whether a drought has an effect related to the population dimensions and impacts of the Southern Pine Beetle (SPB) depends on the stage of beetle population. The drought has to coincide with the open gateway of a high SPB population for the cascade that ends in tree mortality to be completed.

The diversity of LTER sites presents a huge variety of potential cascades and the events occurring in these cascades. Nowhere is this more true that in the urban Central Arizona–Phoenix (CAP) site. Brazel and Ellis (chapter 7) list multiple resulting cascades and effects that are strongly driven by ENSO-related climate episodes. Some of the effects are very surprising. A case in point is the increase of traffic accidents associated with the frequent dust storms of La Niña years. ENSO events also partially control the intensity of the Phoenix urban heat island. Even more importantly, Brazel and Ellis point out that many of these cascading effects feed back into the urban ecosystem. The multiple effects of both El Niño and La Niña events on the CAP urban ecosystem suggest an extension of the cascade concept. Much of our attention in this book has been directed to a single cascade in the ecosystem following a climate event or episode. The ENSO climate driver establishes parallel cascades through its precipitation and temperature signals. The analysis in chapter 6 shows that sometimes the temperature effect results in an ecosystem response and sometimes the precipitation effect does. The CAP (chapter 7) case makes us recognize that there can be multiple, separate, parallel cascades to a single climate driver. Indeed, the reality is most likely that multiple climate drivers produce multiple parallel cascades, some of which interact and some of which do not. The MCM case (chapter 10) also identifies several parallel cascades. These relate first to algal mats and stream nitrogen uptake, second to salinity and stability of lake water columns as well as the type of phytoplankton species that are dominant, and third to soil invertebrates. The salmon catch case (chapter 13) refers to parallel cascades that can occur in both coastal and deep-sea ocean waters. The hurricane case (chapter 2) also can have parallel cascades associated not only with wind damage but also possibly to related primary effects such as river floods or salt water inundation, or secondary impacts such as landslides or fires. It is the task of the LTER, and other, researchers to identify the strands of the cascades and their interactions. This is particularly important because Shaver et al. (2000) suggest (in other words) that the longer the time of operation of the ecosystem the greater will be the chance of interaction of parallel cascades. In the case of ecosystem warming, these authors note many changes that will only take place during very long time periods. Such changes include soil profile development, organic matter accumulation, changes in fire regimes, or long-distance movement of herbivores or timberlines. Many such changes will be due to the interaction of parallel cascades.

An inherent characteristic of cascades is the temporal dimension. The importance of timing on the degree of effectiveness of the Southern Pine Beetle in killing trees at the Coweeta LTER site was mentioned in the context of cascade gateways. At the same site shoestring root rot fungus also has a greater impact during drought stress than at times of other climate conditions. The cross-site ENSO study (chapter 6) made it clear that the timing of a climate episode or event is critical if a subsequent cascade of events is to follow. Also the occurrence of hurricanes in New England in October and November when a minimum number of leaves is on the trees makes the forest less prone to hurricane damage (chapter 2). Thus, the timing of an event or episode may also act as a gateway. Studies at the North Temperate Lakes LTER (Robertson et al. 1994) clearly show that a difference of one month in the timing of an El Niño signal can be critical in determining whether that signal will have an effect on the ecosystem. In another example Gage (chapter 4) shows how important early growing-season precipitation is to the eventual corn yield of the North Central Region. The critical importance of the timing of snowmelt at the Arctic site and development and decay of sea ice at Palmer are additional examples (chapters 5 and 9). Whether the ecosystem response gateway is open often depends in these cases on the timing of the climate driver. An extension to the cascade principle and its temporal element is that an ecosystem response may be driven in sequence by two, or presumably more, climate drivers. For example, KNZ NPP is most highly correlated to air temperature in the early part of the growing season, whereas later in the growing season it is better correlated with precipitation values acting through soil moisture conditions (chapter 20).

The geography of the LTER network is important. Geographical considerations demonstrate the importance of cross-LTER site studies. The same initial climate driving function may have totally different effects in different areas. This is especially true when large-scale diving factors such as ENSO or PDO variability are considered. In the case of ENSO, the climate precipitation signal in the Pacific Northwest (PNW) is opposite that of the Southwest. This appears to be the case throughout the twentieth century at the decadal timescale (Schmidt and Webb 2001). In another example, McHugh and Goodin (chapter 11) give an analysis of the way in which the climate, particularly growing-season mean, maximum, and minimum temperature, is inversely associated between the Andrews and the Bonanza Creek LTER sites, respectively located in the Pacific Northwest and Alaska. Times of higher than average values of growing season maximum and minimum temperature in interior Alaska tend to correspond with times of lower than average growing season maximum and minimum temperatures in the Pacific Northwest. This is quite consistent with the salmon catch data referred to in chapter 13 and relates to the distinct manner of operation of the PDO. Intersite comparisons raise exciting new questions. A possible linkage between cone production in the PNW (chapter 19) and Interior Alaska (chapter 12) and the relation to the state of the PDO demands more investigation. In another geographical contrast, the same climate variable ENSO has a larger effect in the SW than in the PNW. In the PNW the difference in precipitation values between El Niño and La Niña years is not so significant as in the SW because the variation is around a higher mean value. As noted previously, the dry, forest-grassland types of vegetation in the SW seem to be "tuned" to ENSO variations, which stimulate grass and fuel production during wet phases and burning during dry phases (Swetnam and Betancourt 1998; chapter 15). Fuel variation is not so dynamic in the PNW conifer forests.

Yet another dimension to the consideration of cascades is exhibited at the Sevilleta LTER site (chapter 15). Here it is hypothesized that an increase in creosote bush shrub is somewhat self-enforcing because the shrubs emit nonmethane hydrocarbons that act as local greenhouse gasses, keeping minimum temperatures as much as 4°C higher than they would be without the shrubs. Our discussion of cascades so far has been in unidirectional terms. This example shows that we must also consider the possibility of the cascade turning back on itself with a positive feedback. Cases of negative feedback are also conceivable. Yet, we tend to see the cases of cascade elements acting as catalysts in the situations of positive feedback.

Completion of Ecological Response

Our framework question asks, Is the ecosystem effect or response completed by the time of the start of the next climate event or episode? This question can be asked in different ways such as in the three questions posed by Boose (chapter 2) in his hurricane study. The question can also be posed implicitly in different contexts. For example, Parmesan et al. (2000, p. 446) have stated "the initial resistance, trajectory of response, and extent to which a system returns to original conditions (resilience) after a disturbance depend on the frequency, intensity, duration, and extent of disturbance, as well as the inherent properties of the biological system, including evolutionary history. . . . " LTER studies confirm this in many cases of climatological or meteorological disturbance.

It is also likely that different parts of an ecosystem will have different recovery times. The example of the February 1996 flood at the Andrews LTER site is interesting because the range of recovery times for different parts of the ecosystem have been documented for this event (Swanson et al. 1998). The recovery times ranged from less than 3 months for aquatic algae, through 1–3 years for cutthroat trout, to more than 30 years for coniferous trees. Boose (chapter 2) recognizes an important caveat to our thinking on recovery times when he points out that some adaptive responses, such as the creation of new foliage and branches following a hurricane, cannot be repeated indefinitely at short intervals. In contrast to an individual flood or hurricane event, suggested ecosystem process and component response times to decade- to century-long temperature increases have a wide range. The range extends from one day for leaf photosynthesis and respiration, through a decade for litter mass change, to over 1000 years for soil organic matter development and plant migration and invasion processes (Shaver et al. 2000).

LTER studies reveal some cases where the ecological response to a drought is completed and other cases where the response is not completed by the time the next drought occurs. Gage (chapter 4) points out that the effects of a one-year drought, such as that of the 1988, on annual rotational agronomic systems are minimal. However, the same 1988 drought had long-lasting, documented effects on some of the natural vegetation species at the Cedar Creek LTER site in southern Minnesota. Citing Tilman and Downing's (1994) work, Gage notes that the effects of the 1988 drought were evident in the oak savanna complex 5 years later. About 30% of the pin oaks and 19% of bur oaks died. As a result of such episodes, some parts of the ecosystem may return to their original state, whereas other parts are affected for many years to come or even permanently. It is certainly true that the landscapes of most LTER sites exhibit long-term legacies after a severe, relatively short-term, climate episode. This raises the question, What is it that determines which parts of the ecosystem will be most negatively affected? Based on our small number of examples, it seems that vegetation with longer life spans such as trees, as opposed to grasses, is most vulnerable.

The Cedar Creek finding is reminiscent of the fact that dead junipers still reside on the landscape at the Sevilleta LTER site, the result of La Niña-related droughts of the 1950s (chapter 15). However, studies based on tree rings, which provide information for almost 400 years at the Sevilleta site, place this result in an even more surprising context. Sevilleta researchers hypothesize that the 1950s drought was one of a series of droughts that recur at an interval of 55–62 years. Partly due to the fact that it was accompanied by the introduction of cattle ranching, the ecosystem has not yet, and possibly never will, recover from the previous cyclic drought of the 1890s. At both Sevilleta and the Jornada LTER site in southern New Mexico, shrubland took over from grassland, and there is no sign of a return before the beginning of the next drought period. Thus, although in some senses, these semiarid ecosystems may return to "normal" in terms of biomass productivity levels, for example, after an El Niño–related season or two of above average winter and spring precipitation, they still may not be returning to "normal" at the multicentury timescale.

Cross-timescale considerations are also important at the Palmer Antarctic site, where ENSO-scale events govern key biophysical interactions and many of the interactions are complete by the time of the next ENSO event. However, the circa 60-year warming trend at this location complicates matters such that Palmer researchers find it difficult to envisage an "end scenario" (chapter 9). Nevertheless, it is very interesting that the 600-year fossil record at Palmer shows the current presence of chinstrap and gentoo penguins to be unprecedented and that the site was dominated throughout most of the 600 years by Adélies. In some cases, long-term trends, or their operation in association with oscillatory climate phenomena, can set new "preexisting" conditions for each cycle of "cyclic" climate variability as in the case of variability in PNW salmon abundance at the decadal timescale.

Two of the studies in this book extend to the timescale of 25,000 years. Beetle assemblage evidence from Elias (chapter 18) suggests that certainly at this timescale the ecosystem has made its necessary adjustments by the time of the next ice advance or return to warmer climates. However, these "adjustments" in the insect assemblage are to a "lowest common denominator." As Elias (p. 381) expresses it, "the current group of species in the alpine ecosystem may not be the best fit for the environment—they are simply the best fit among those species able to persist regionally through the last glacial cycle." In this case we have a climate filter acting at the millennial timescale. Furthermore, Elias (p. 381) believes ". . . that at the century to millennial timescale, the response of major components of the vegetation in high altitude ecosystems of the Colorado Front Range lags behind major temperature changes." The lag is in the order of 500–1000 years. Analogous, lagged responses are described by Monger (chapter 17) for the arid environments of the Southwest as they change between glacial and interglacial times. In the Antarctic Dry Valleys, however, the ecological response to warming conditions is still dependent on events that started at least 24,000 years ago, as described previously and in chapter 16. In this case, even at these large timescales, the ecological response to Holocene warming cannot be said to have been completed. This is because it remains to be seen what would happen to the current soil communities if the carbon source derived from relic benthic algal mats were ever to be completely depleted. Indeed, Fountain and Lyons (p. 334) suggest "given the extremely slow cycling of nutrients and the pace of geomorphic change, we suspect that ecosystem responses are overprinted on each other and are not completed before the next event occurs."

Return to Original State of Climate Variable and Ecosystem Response

We have asked, Does the climate event or episode and the ecosystem response return to an original state? Many of the issues that fit appropriately in this section have been discussed in the previous section on "Completion of Ecological Response" concerning whether the ecosystem will return to its original state before the onset of the next climate event. We have not, however, addressed the manner of return. The nature of the return to the original state is important. In some cases, whether the cascade reverses depends largely on whether some component of the system has been destroyed, such as in the complete removal of topsoil, or simply made temporarily unavailable, such as the temporary absence of phytoplankton under certain conditions in the PNW coastal ocean. We also acknowledge that some would argue that the concept of "return to original climate and ecosystem conditions" is misleading because the systems do not operate in those ways. For example, a "return to an original condition" might occur only in the most superficial of senses. Some of this debate is a matter of discipline. For example, palynologists have little sense of returning to an original position. On the other hand, the language and metric of dendrochronological studies of fire history sometimes seem to assume cyclic system behavior and a return toward predisturbance conditions. We certainly agree with the available evidence that suggests that the longer the timescale being considered, the less likely it is that one will find a perfect analog to the current or any single past or suggested future condition. Despite these considerations, we believe that it is worthwhile to examine the concept of "return to original climate and ecosystem conditions" using the information provided by the case studies of this volume.

If we assume there is a return by the atmosphere and ecosystem to an original state, what is the manner of return? We have examples where the return seems to be rather smooth. The case of the oscillating salmon catch in the Pacific Northwest (chapter 13) or grassland NPP levels (chapter 20) are good examples. A relatively long life span sometimes helps a somewhat smooth return to original conditions. For example, the grayling in the Arctic aquatic ecosystem benefit from their 20-year life span. This longevity helps to filter out and dampen the effects of interannual climate variability on their population numbers (chapter 5). In other cases, the return to some original state by no means follows the path of the original change and sometimes is dependent on the timescale involved. The cases of dead trees resulting from drought periods on the landscapes of the Cedar Creek, Sevilleta, and Coweeta LTER sites suggests that the ecosystem did not immediately return to its original state following the climate event. The relatively slow growth rates of juniper, for example, render it impossible to replace the dead trees with mature new trees in a decade or two. A longer term perspective on the issue is that intermittent drought and standing necromass, are, to a certain extent, part of the long-term original and natural state of these ecosystems.

We have also seen examples where the ecosystem does not return to its original state after a climate disturbance. The Palmer Antarctic ecosystem appears to be under a strong directional change driven by warming, and at the decadal and century timescales shows no sign of returning to the state found by LTER researchers when they began their studies in the early 1990s. Interior Alaska also seems to be experiencing a marked warming at the century timescale. Of interest here is the suggestion that, although the white spruce may be adapted to decadal-scale climate variability, a continued warming trend might lead to this species losing its sensitivity to the relationship between summer temperature values and growth rate (chapter 12). Increasingly, a smaller amount of growth is exhibited for a given increase in temperature. One possible reason for this increasing lack of sensitivity might be that the environment of the white spruce is moving closer to the upper cardinal temperature limit for the species.

The concept of returning to an original state tends to lose its meaning at the millennial timescale. Changes between glacial maxima and minima in the Quaternary defy the definition of an original state. In addition, the time spans start to be so long that evolutionary processes begin to make their mark on flora and fauna. However, knowledge of climate variability and ecosystem response at this timescale can have important implications. For example, the fact that the paleorecord shows the existence of arid desert shrub in the middle Holocene (presumably unimpacted by intense human activity) before grasses developed in the later Holocene is vital (chapter 17). This fact greatly informs the debate on the possible causes of the change over the last 150 years from grassland to shrubland at the Jornada LTER site and in other places in the Southwest.

The return period of climate events is an important factor in determining whether the ecological response has been completed by the time of the next event. In addition, the fact that some climate features have characteristic return periods of ecologically important events is related to the concept of the ecosystem entering into resonance with the climate variability. Resonance seems to exist at a variety of timescales. For example, at shorter timescales, it is fairly easy to see that agriculture resonates closely with seasonal and interannual climate variations (chapter 4). Similarly, in natural ecosystems resonance is clear. See, for example, the close relationship between net ecosystem production (NEP) for acidic tundra at Toolik Lake and photosynthetically active radiation (PAR) (figure 5.7). However, we have only just begun to hypothesize that resonance also exists at the longer timescales.

Let us first reexamine the case of the tropical rainforest LTER site at Luquillo, Puerto Rico. In this forest, stream water export of potassium and nitrate ions increased following the disturbance caused by Hurricane Hugo and remained elevated until the canopy leaf cover returned (chapter 8). We might speculate that the response of this part of the ecosystem to the hurricane event will depend on how long it is before the next hurricane passes over this site. Interestingly, in other Luquillo studies, it has been noted that the time for maturity of a tabonuco forest stand is approximately the same as the 60-year average recurrence interval of category 4–5 hurricanes in Puerto Rico (Scatena 1995). Boose (chapter 2) quotes a similar time period (50 years for category 3 storms). Boose also identifies one of the negative feedback processes at work during the forest recovery, noting that because of their reduced stature, heavily damaged stands are naturally protected from subsequent wind damage for a period of years or decades. This represents another example of the ecosystem moving into resonance with the period of climate variability. The example of Pacific Northwest salmon catch is clearer than the case of Puerto Rico forests. Because the life span of the Coho salmon—about 3 years—is much shorter than the decadal-scale climate regime shift of about 20–30 years, the immediate ecosystem response, in terms of population numbers, should be complete before the next climate episode occurs. However, we should be aware that some demographic models suggest that population systems have a memory. Whether the memory, in this case, would extend beyond 20–30 years requires further investigation. Also requiring more research is the question of whether the decadal- scale variation of climate and Coho salmon population represents the latter moving into resonance with the former.

Another possible example of resonance is in the U.S. Southwest. There is a strong fire response to the El Niño–Southern Oscillation (ENSO), with wet times leading to fuel buildup and dry times associated with a higher frequency of fire. The fires cause the release of nutrients that encourage growth/fuel buildup in the next wet episode. Thus, the fuel-fire cycle can operate well within the pace of the ENSO (climate) dynamic and without long lags. Swetnam and Betancourt (1990) noted a close relationship between ENSO and the fire regime in the U.S. Southwest. We can speculate that the resonance in the ecosystems of this region may operate at both the quasi-quintennial timescale and at the circa 52-year periodicity identified in chapter 15.

Yet another possible example of an ecosystem moving into resonance with cli-

mate variability is that of white spruce reproduction in Interior Alaska. Here, the episodic cone production of the species is suggested as an evolutionary adaptive strategy to a climate regime with a decadal variability. Juday et al. (chapter 12, p. 245) write "it appears that the described reproductive timing of white spruce maximizes the odds that seeds will be released into a landscape in which fires have occurred recently." The fire has usually removed a thick organic mat that otherwise prevents seed success, and the reproductive timing of white spruce maximizes the odds that seeds will be released into a landscape in which fires have occurred recently. Other biotic elements may play roles in ecosystems moving into resonance with the climate, but more investigation is needed to identify the subtleties. For example, irregular seed crops may protect a plant from a high level of seed predation. It would be interesting to see whether there is a linkage among climate variability, seed crop production, and seed predator population numbers.

Four more concepts and issues emerge. First, if ecosystems come into resonance with climate variability, then what are the processes they use to do so? Second, if it is possible to identify the timescales and processes at which the resonance takes place, then we can identify other potential climate and other disturbances that might have an even larger impact on an ecosystem because the system is not in resonance with them. Human insults to ecosystems are the best example of this. Management, or other human activities, may well interrupt natural resonance. However, natural examples exist as well, such as the stochastic nature of earthquakes, volcanic eruptions, tsunamis, and meteorite impacts. Third, the pace and magnitude of ecosystem response in a "resonating" system will be important. If the frequency of climate variability and that of ecosystem response is well matched, the magnitude of the response will be at its most efficient. Conversely, if the frequency of the climate variability becomes higher or lower over time, then the magnitude of the ecosystem response may be muted because feedback mechanisms may not act effectively. Fourth, we must recognize the difference between the ecosystem response to a single disturbance on one hand and the response to a disturbance regime on the other. Cascades of effects may be fairly easily identifiable in the first case, whereas in the second case we must consider the timing, severity, and spatial patterning of one or more disturbance processes over time. Consideration of disturbance regimes raises questions of how frequency and severity affects species composition at a site. The concept of resonance might be more difficult to apply in the case of disturbance regimes.

Greenland (chapter 6) introduces the concept of a "characteristic timescale" for an ecosystem. Identifying such a timescale would help address the questions related to completion of ecosystem response and return to original state. It also raises the interesting issue of whether there is such a thing as a characteristic timescale for an ecosystem. At least for "simple" biological responses to a climate event or episode, both Clark (1985) and Woodward (1987) have provided quantitative analyses. Some of our studies indicate what the characteristic timescale may be. Boose (chapter 2, p. 28), for example, proposes "long-term impacts of hurricanes on forests can be understood only at a scale of centuries." On the other hand, the reality is that ecosystems are made up of many different components, and each component will have its own characteristic timescale of response. Using the concept of recovery times, Swanson et al. (1998) and Scatena (1995) have documented this for temperate and tropical rainforests, respectively. Yet perhaps some characteristic timescales, such as those related to cases where the ecosystem moves into resonance with particular types of ecosystem variability, dominate over other potential characteristic timescales for a particular ecosystem and are a fundamentally important part of the nature of that ecosystem. If this is the case, then the characteristic timescale is another way of describing the resonance between the climate and the ecosystem.

Limits of Climate Variability and Ecosystem Response

Few authors in this volume attempted to explicitly address the question of whether the climate event or episode and the ecosystem response had identifiable upper and lower limits. This is because it is important to study climate events that cause severe ecosystem change so the limits of the ecosystem response are clearly bounded. Not all of the subject matter of our chapters meets this criterion. In retrospect, the reason for the lack of consideration of limits is that the subject is partially timescale-related. If an individual investigator is not familiar with all the timescales at which their ecosystem operates, he or she will not have all the information needed to answer this question. The interdisciplinary approach of LTER research is often helpful in extending an individual's knowledge of an ecosystem, so we can expect more answers to this question to appear as the LTER program further matures.

Although the answer to this question of limits is partially related to the timescale for which we have information, it is also related to the physics or biophysics of the climate event and ecological response in question. This is well demonstrated for white spruce in Interior Alaska (chapter 12), where the gateways in the suggested model are specifically related to certain limiting values of climate variability (e.g., summer temperature and its relation to drought) and ecosystem response or preexisting condition (e.g., growth reserves). In another case, Schaefer (chapter 8, p. 154) states "although there is no fixed upper limit to the amount of rain that can fall within a 24-hour period, there are no records that . . . it has exceeded 600 mm in Puerto Rico." A longer record might produce a higher 24-hour record. Particular wind velocities are used to define the strength category of a hurricane, but the highest category, 5, is open ended at a wind velocity exceeding 69 m/sec (155 mi/hr). It should be possible to use physical principles and information on sea surface and air temperature extremes, as well as maximum and minimum storm wind velocities, to make a fairly good estimate of the maximum possible precipitable water for the location. Alternatively, the theory of extreme statistics could be applied. Neither of these approaches has yet been used much at LTER sites. One sense of a limit to ecosystem response to a hurricane is implicit in chapter 2, where Boose describes a range of responses from partial defoliation to complete blowdown of a mature forest. The latter might be taken as the upper limit of ecosystem response in the hurricane context.

The Palmer LTER site (chapter 9) shows some situations where climate variability and ecosystem response display limits and other cases where it does not. The limits are clearly shown in the ENSO-dominated timescale, but they are completely unknown in relation to the multidecadal warming trend because it is not possible to say where and when this warming trend will end. In an analogous fashion, the limits of climate (precipitation) variability seem to be well established at the quasi-quintennial scale and, to some extent, at the century scale at the Sevilleta site. But we know less about them at the millennial scale. Additionally, where the ecosystem is subject to alteration by human activity, the response to a particular climate event may be quite different from one event to another. This was shown by the emerging dominance of shrubland over grassland in the southwestern LTER sites partly related to cattle grazing in the 1890s.

The millennial timescale, which here is taken to be the Holocene but which also can involve the Pleistocene and some of its preceding geological epochs, does not play such an important role for present-day ecosystem managers. But it does help to be aware of changes at this timescale for two reasons. First, changes at the millennial scale can give information concerning the extremes to which the system can move and/or give some feel for its degree of homeostasis. The millennial-scale changes set the "limiting values" on the natural system changes in a practical and hierarchical sense. It is conceivable that human influence can help exceed these limits, but it is useful to have some idea of where the limits are or have been in the past. Second, it is also important to recognize that many of the floral and faunal species presently found in the ecosystem, or close relations of current species, have survived throughout all these extremes. This helps us to understand the degree of resilience of the ecosystem to natural changes. Third, it helps to recognize that many atmospheric phenomena that are important today have been present for a long time. For example, radiolarian records from the Santa Barbara basin indicate that El Niños have been occurring for at least 5.5 million years (Casey et al. 1989).

There have been warmer and cooler periods throughout the Pleistocene. Yet the extreme climates from the Last Glacial Maximum (LGM) 20,000 years ago to the warmer climates of the Holocene treated in chapter 18 may, in many ways, be regarded as representing, or approaching, limits of values of climate variables that modern Rocky Mountain and semiarid southwestern ecosystems may have to withstand in the absence of human influences. One suite of ecosystem responses to these changes is the varying assemblages of beetles. Elias (p. 370) argues that "ecological changes take place at many timescales, but perhaps none is more significant than the truly long-term scale of centuries and millennia, for it is at these timescales that ecosystems form, break apart, and reform in new configurations." Vegetation response in the Colorado Front Range took the form of a change from alpine tundra to subalpine forest and a decrease of the tree-line elevation of 500 m during the colder times of the mid-Pinedale glaciation. Elias' statement is also applicable to the ecosystem changes described by Monger for southern New Mexico.

Chaos

Only one author in this volume elected to address the question of whether chaos is exhibited in the climate or ecosystem. We believe this is due to a number of reasons. First, most investigators in climate and ecosystem sciences are unprepared to address the topic rigorously. Second, in many cases, the quantitative understanding of our systems is not yet advanced enough to apply large parts of chaos theory to LTER study sites.

We believe, however, that we should endeavor in future years to position ourselves to be able to apply chaos theory to our systems to discover new insights. Calls by the National Science Foundation for investigations into ecosystem complexity are consistent with this. Phillips (1999) has pointed to ways in which a qualitative analysis of partially specified dynamical Earth surface systems (ESS) can be made. In addition, virtually all that he says about ESS applies to ecosystems. We have mentioned previously, for example, that it is the very nature and definition of a chaotic system that small changes in initial conditions will often give rise to large changes in subsequent effects.

McHugh and Goodin are the sole authors who address the topic of chaos and complexity (chapter 11). Among other things they emphasize the large number of nonlinearities in the climate system. Other parts of LTER literature, such as the development of desertification theory at the Jornada LTER site (Scheslinger et al. 1990), suggest that nonlinearities are plentiful in our ecosystems. Sooner or later we will have to address the presence of nonlinearities, complexity, and chaos directly because these aspects are part of the real nature of our systems. We speculate that one or two decades from now a future LTER meeting on climate variability and ecosystem response will be couched in a framework of chaos theory.

We also note that ecosystem science is not alone in its failure to address chaos theory. Although Lorenz (1963) established a major part of the theory of chaos in atmospheric science, meteorologists have not pursued the theory with much vigor. On the other hand, Lorenz' discovery led to a paradigm shift in atmospheric science, which stemmed from the realization that because the atmospheric system was chaotic we could never hope to realize the dream of making a perfect weather forecast. We wonder what comparable paradigm shift, or shifts, await the field of ecology when we examine our systems with a focus on their nonlinear nature.

Emerging Concepts and Principles of Climate Variability and Ecosystem Response

In this synthesis, the following recurrent principles begin to emerge:

Issues of time and space scale are pervasive throughout the field of climate variability and ecosystem response. It is not always possible to separate the effects on ecosystems of climate events and episodes of different timescales.

At each LTER site climate events and episodes operate at different timescales. Consequently, these scales cannot be viewed in complete isolation.

Some timescales, like that on which the ENSO operates, show patterns with a broad spatiotemporal coherence that therefore encompass responses across a wide range of ecosystems.

Most LTER sites show evidence on their landscape of some past climate event or episode.

Timescales of climate variability and ecosystem response determine, in large part, whether the response is complete by the time of the next climate episode or event.

Some ecosystems return to an original state following climate disturbance, whereas others do not. When ecosystems return to an original state, sometimes the return is linear and sometimes it is nonlinear.

For a climate event or episode to be effective, there must be some identifiable, usually physiologically related, link to the flora and/or fauna of the ecosystem. Some proportion of climate variability will not have an effect on the ecosystem.

In some cases, for a climate event or episode to be effective it may involve a nonlinear amplification in forcing that later has an impact on the ecosystem.

Most ecosystem responses to climate events and episodes are not simple, single-cause, single-effect responses. Rather, the response takes the form of a cascade of effects.

The response cascades may be short or long, intuitively obvious or not, and linear or nonlinear or both. The nature of the cascade often depends on the complexity of the ecosystem. The LTER network includes some relatively simpl ecosystems such as MCM and some very complex ecosystems such as LUQ

Response cascades may take place both in time and space. Shaver et al. (2000 point out the need for improved models of the temporal sequence of ecosystem response because long-term responses may be very different from initia responses and responses will not be uniform in space.

Cascades that result from climatic impact in ecosystems often take time to manifest themselves and can result in legacies within ecosystems that conditio subsequent climate impacts. Because cascading climate-driven impacts withi ecosystems are often lagged in time, efforts to identify fixed time correlation are sometimes ineffective.

An initial climate driver may cause parallel cascades acting through several dif ferent climate variables.

There may be many parallel cascades, sometimes interacting with each othe and sometimes not interacting.

Many of our studies focus on a single process. A focus on cascades leads us t concentrate more on the sequential linkage of one process to the next.

Whether upper and lower limits of the values of climate events and episodes an resulting ecosystem responses can be identified depends on both the degre of our knowledge of the relevant biophysical processes and the amount c empirical data available.

Cascades or parts of cascades in the atmosphere and ecosystem may act as gate ways, filters, and catalysts to additional ecosystem response.

There seem to be at least three broad classes of interaction between ecosysten and climate:

1. The ecosystem buffers climate variability.
2. The ecosystem system simply responds to individual climate events an episodes that exceed some threshold for response. This threshold is ofte crossed or triggered by a nonlinear process.

3. We hypothesize that the ecosystem can move into resonance with the climate variability with positive and negative feedbacks that produce strong ecosystem response.

Future Research

From this discussion it is clear that the LTER program provides a platform from which a huge amount of information emerges on the topic of climate variability and ecosystem response. Based on the information in this book, many avenues of research on this topic will be important in the future.

1. We must continue to obtain more information at each LTER site on climate as a disturbance factor of ecosystems. Each new piece of information on this topic alters our perspective of the principles that emerge from this field. We need to develop tools that are sensitive to both atmospheric and ecosystem variability. In addition, we must attempt to anticipate the correct *combination* of system properties to be observed to be able to demonstrate in detail system resonance or another kind of behavior.

2. We must continue to be aware of the need for cross-site comparison. One corollary to this is that we must strive to design our experiments, and to collect our data, in such a manner to facilitate intersite comparison. The LTER network has a unique infrastructure for being able to make such comparisons as long as a certain amount of preplanning is accomplished. We have the potential to formulate hypotheses related to climate variability and ecosystem response for groups of LTER sites with common properties. The network has an ever-increasing number of site-years of sampling for different disturbance processes. The hurricane event is a case in point. Currently, nine LTER sites in the Caribbean and the East Coast of the United States are well positioned to observe the effects of tropical storms that make landfall. Four LTER, or former LTER, sites have been directly impacted by tropical storms. In 1938 an unnamed hurricane passed over the Harvard Forest LTER site. Hurricane Hugo passed over the Luquillo, Puerto Rico, LTER site and the North Inlet, South Carolina, former LTER site in September 1989 and Hurricane Opal passed over the Coweeta, North Carolina, site in October 1995. At the time of this writing, the subnetwork of hurricane-vulnerable LTER sites collectively represented about 160 site-years of direct, LTER-supported observation of both hurricanes and ecosystem responses and perhaps more than 2000 site-years of archival records of hurricane occurrence. This mininetwork is well configured geographically and temporally to obtain a good sample of large and extreme events and to consider questions about regional patterning of disturbance and ecosystem responses across a range of ecosystem types. Current sites provide opportunities for observation in ecosystems, including tropical and temperate forests, coastal barrier islands and wetlands, and an urban site.

Some scientists believe the U.S. East Coast is entering a period of several decades when the frequency of hurricanes making landfall will increase (Goldenberg et al. 2001). LTER scientists at potentially affected sites should make contingency plans to study new storms and their ecological impact by standardizing some of the methodologies that have been used in earlier studies. Preexisting conditions and common impact indicators should be carefully specified. Hurricanes are not the only possible focus of study. Other individual LTER sites or groups of sites may sample other climate disturbance processes. Diagrams such as figure 1.2 may be used to identify such groups of sites. As the LTER program extends into the future, it may also be possible to use available climate forecasts, such as those for the state of the ENSO, to design experiments that use the natural climate extremes of this quasi-quintennial phenomena. A visionary might even conceive of the ability to forecast the state of the interdecadal-scale PDO and its resulting ecosystem responses.

Another question related to cross-site comparison concerns the possibility that some sites might be more susceptible to climate variability than others. At first sight, the Sevilleta LTER site in New Mexico might be said to be more susceptible to an El Niño climate signal of a similar size than the Andrews site in the PNW. Could it be, for example, that the sites on the extreme outside edge of the cluster of LTER sites shown in figure 1.2 are likely to show a more marked response to climate variability than those sites near the center of the cluster? A related matter is the question of "redundance" of climate variability. There are many situations where the variability of a climate variable is of little importance to the ecosystem. For example, at the Andrews LTER, as long as no flooding occurs, greater than average January precipitation does little except run off from a system that is already fully charged with water physically and biologically. Where it is not already obvious, the identification of climate variability redundance would permit investigators to focus their resources on other parts of the ecosystem.

3. We must use our increasing knowledge at LTER sites and our cross-site comparisons to identify important generalities, often related to process, that are more specific in nature than our comments about the importance of scale. For example, we should pay more attention to critical thresholds such as those related to the ice/liquid boundary or to plant rooting depth. Other thresholds might include the precipitation duration-intensity necessary to trigger landslides or thresholds related to the phenology associated with achieving good seed crops. Another general concept has to do with the residence time of communities and individuals at a site and the sensitivity of a site to climate disturbance. One way to achieve the identification of these generalities is to hold workshops on them individually. Experience from some of the workshops that led to this volume has shown us that important concepts will emerge from such workshops.

4. We must start to develop multidimensional approaches to the issues of climate variability and ecosystem response. It is a rare case that there is only one aspect of climate variability occurring at any given time. At Coweeta, for example, both droughts and windstorms occur from time to time, but they each favor the development of different types of microhabitats. Drought effects, such as increased standing necromass, favor the development of some microhabitats, whereas windthrows favor others. The two situations exist simultaneously in the forest, and investigators must find ways to treat the parallel ecosystem responses and their possible interactions.

5. We must begin to confront the climate signal detection problem. The detection

of climate signals embedded in the ecosystem and realized as cascades of time-varying ecosystem properties is exceptionally complex. The problem requires the application of the full spectrum of analytical tools available to scientists and an ever-growing resource of long-term data, especially on ecosystem dynamics. Endeavors in this area will represent another fortunate congruence between climatologists and ecologists. This is especially so for paleoclimatologists, who have long used a wide variety of proxy ecological data such as tree rings. However, as difficult and sophisticated as the interpretation of tree rings is, we envision the problem of climate signal detection as being much more complex because it involves multiple levels in the ecosystem cascades. There is also the problem of the overprinting of a variety of climate impacts as one moves from shorter to longer timescales. Part of the task in climate signal detection is to gain a clearer picture of how phenomena at focal scales are affected by phenomena at adjacent or other scales. Hierarchy theory (Ahl and Allen 1996) will be one of the analytical tools for this task.

6. We must seriously consider how ecosystems may respond to global trends. In particular, we need to understand how ecosystem response may have either positive or negative feedback on a climate change. For example, shifts in polar ecosystems (melting of sea ice and permafrost, changes in snow cover, etc.) will, in turn, have an impact on climate. An understanding of such feedback mechanisms is of enormous ecological and social importance.

7. We must continue to refine the principles that emerge from the studies in this book. Quantitative modeling studies backed by carefully collected field data will help achieve this goal. More quantification will also help address some of the framework questions of this study that have been largely neglected.

8. At least as far as this list is concerned, one of the exciting realizations emerging from this volume is the possibility of ecosystems moving into resonance with climate variability at the quasi-quintennial and longer timescales. This seems to be a very fruitful idea worthy of further development and investigation. The growing maturity of LTER sites places researchers in a good position to examine the existence of such resonance in ecosystems other than those we have identified. In the cases we have already identified, the subtleties of the resonance may be examined more thoroughly. Such investigations exemplify the central core of the character of LTER research. This is true both in the sense of capitalizing on long-term research already completed and in the sense of opening up exciting new areas of investigation not envisioned when the LTER program began.

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