As predicted, year-to-year concordance in species abundance increases with increasing environmental variability (Fig. 3b). The environmentally variable systems have the most predictable relative species abundances year after year. Given this relationship, species richness has no effect on year-to-year concordance.

The effect of environmental variability, though in accord with predictions, may seem counter-intuitive. It is the highly variable systems that show the greatest consistency in structure. In these duck surveys, the greater the year-to-year concordance in relative abundances, the greater the relative variability in the total density of all the duck species. (This requires some special pleading – the elimination of an obvious statistical and geographical outlier and a one-tailed test is justified because it follows from the relationships derived in Fig. 1.) 'Stability' of relative abundances comes at the expense of 'stability' of the total numbers.

That species richness does not affect concordance is perhaps to be expected, given the complications I discussed above. There is a more fundamental problem, however. As noted earlier, there is an asymmetry in plotting summaries of data *over time* at individual points in *space* as I do in Fig. 3. Such a view cannot enjoy logical supremacy. The data in the analyses could easily be the individual years, each datum summarizing the distributions in space. Bethke and Nudds come to the same conclusion from considering the ducks' behaviour.

The ducks migrate northwards in the spring, reaching the productive southern prairies first. Only if these prairies are unusually dry will some of the species continue to move northwards. The duck numbers present in the relatively constant northern wetlands are not just a consequence of the local conditions, but of those elsewhere. Local duck numbers are linked across millions of square kilometres. In addition, numbers in one year will depend on the numbers in the previous year, and, for species as long-lived as ducks, for many of the previous years.

Spatial and temporal challenges

To be unpleasant, we might conclude that the data sample is taken from one place and one time. Thus, there is only one data point, no replication and so no possible inferences. So let's dismiss the analyses as being clouded by extensive pseudo-replication in time and space. Let's go back to our comfortable, well replicated, year-long, single-species experiments on ten hectare plots. Bethke and Nudds shouldn't have ventured into the unfashionable area of research space in the first place. Though others may scurry back into the safety of the fashionable, tenure-securing research space, I am left worried.

My first concern is that understanding how species' numbers change over large scales is important to our masters, who, by definition, control the purse strings. They have an unfortunate habit of demanding immediate answers to questions on heroic scales. Even more badmannered is their refusal to fund our requested long-term study of the problem and to make decisions without waiting for its results. (Bethke and Nudds continue their collaboration with an analysis of the impact on duck numbers of land use changes against a background of varying hydrological conditions. The problem, its timing and its answer of a deficit of three million ducks caused by the changes is typical of our masters' concerns.)

Secondly, I feel challenged by the spatial and temporal problems. Just how far apart need the sampling strata be in order to be independent? How do we draw inferences against this background of spatially and temporally linked data? And where are the models that describe variation in time *and* space? These are clearly difficult questions and they don't lend themselves to experiments.

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Multi-century regional western spruce budworm outbreak patterns

Dendrochronology's rich tradition has foundations rooted in the works of da Vinci and Malpighi[1]. Although the main stem of principles was developed by A.E. Douglass (see Ref. 1), one branch of dendrochronology actually pre-dates his work. The association between narrow tree rings and damage by insects, hail and frost was recognized by Hartig in Europe at the end of the last century[1]. The impact of spruce budworm (*Choristoneura fumiferana*) feeding on the anatomy of tree rings was first described by Bailey[2] in 1924. But it was not until the middle of this century that this branch of dendrochronology flowered and bore fruit for population dynamicists. Blais[3] exploited these techniques in developing and extending a description of the long-term regional population dynamics of the spruce budworm in eastern North America back to the 17th century. More recently, Alfaro *et al.*[4] correlated observational records of western spruce budworm (*C. occidentalis*) outbreaks with reduced tree growth in British Columbia. The most recent flowering of this branch of dendrochronology is described in a paper by Swetnam and Lynch[5].

Spruce, fir and budworm

Swetnam and Lynch exploited the longevity of trees growing in the American southwest, and used the elegant methods of dendrochronology (also pioneered by Douglass in the southwest[1]) to develop extremely long western spruce budworm outbreak chronologies. The principal host of this insect species is Douglas fir (*Pseudotsuga menziesii*), but it also feeds on white fir (*Abies concolor*). Rocky Mountain Douglas fir (*P. menziesii* var. *glauca*) is known to live for over 700 years[6]. White fir is not as long-lived; trees in this region seldom live beyond 275 years[7]. Swetnam and Lynch were able to sample several stands, which permitted the study of chronologies back to the 16th century. One chronology, though not subjected to statistical analysis, was 790 years long. This must be a record for the oldest known Rocky Mountain Douglas fir. Most significantly, their chronology covers the entire period of Anglo-American settlement of the area. In fact, the beginning of this record pre-dates Coronado's expeditions to New Mexico by over 200 years. Most tantalizingly,

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the earliest years of this record extend back to the period when Pueblo Bonito in Chaco Canyon was abandoned by the Anasazi[8].

The methods employed were simple. By measuring tree-ring widths from increment cores taken from several living trees in a stand, a time-series of tree growth for the stand was obtained. Similar measurements made on non-host trees, such as the long-lived limber pine (*Pinus flexilis*), piñon (*P. edulis*) and ponderosa pine (*P. ponderosa*), enabled Swetnam and Lynch to identify and account for climatic effects in the budworm host species time-series. Calibration of the resulting series against historic observational records of weather and budworm outbreaks (beginning in 1924 in the area), enabled them to identify the defoliation signature in the tree-ring record. The proportion of trees showing depressed growth during an outbreak was used as an index of outbreak intensity. The result was a long-term proxy data set of western spruce budworm population behaviour in New Mexico that could be subjected to statistical analysis. In combination with knowledge of forest management history and the proxy data on climate, Swetnam and Lynch could assess the association between climate and forest management practices on the one hand, and budworm population behaviour on the other.

Twenty western spruce budworm outbreaks were identified in the longest record examined. This is the best evidence available that the western spruce budworm co-exists with Douglas fir in a stable relationship. The fact that the white-fir chronologies were significantly shorter suggests that this host is unable to survive repeated outbreaks and must rely on its shade-tolerant habit to persist in stands dominated by old Douglas-fir trees on which western budworm populations can pullulate. Swetnam and Lynch suggest that the insect population may, in fact, be regulating stand productivity in a manner described by Mattson and Addy[9]. Stand composition, determined by the superior survival of the principal host (Douglas fir) and the superior recruitment of the more vulnerable host in the absence of fire (white fir), is modulated by western spruce budworm feeding. Similar relationships exist between the spruce budworm (*C. fumiferana*) and its principal host (white spruce, *Picea glauca*) and its more vulnerable host (balsam fir, *Abies balsamea*)[10]. In each case, pure and mixed stands of the principal host sustain outbreak populations for periods that exceed a decade[5,10], whereas extensive mortality is common in pure balsam fir stands after a few consecutive years of defoliation[11]. (Where white fir occurs in pure stands, it is often attacked by *C. retiniana*.) Thus, there are remarkable similarities in the host relationships between the western species (*C. occidentalis*) and its boreal analog (*C. fumiferana*).

Parenthetically, these associations point to an incongruence in the common names of the two species. The spruce budworm is adapted to white spruce and its range largely coincides with the boreal transcontinental range of its principal host. This common name is appropriate. The western spruce budworm, by contrast, seldom attacks spruce and is mainly distributed within the range of Douglas fir, to which it is adapted. Although the species does have a western distribution, Swetnam and Lynch's work documenting the long-term coexistence of Douglas-fir and western spruce budworm provides additional justification for a change of its common name to 'Douglas-fir budworm'.

Outbreak dynamics

Swetnam and Lynch subjected chronologies dating back to the 1600s to statistical analysis. Their results give a fairly complete representation of the temporal variation in outbreak behaviour. Outbreaks appear to be pseudo-periodic with periods of defoliation ranging from five to 25 years. What is more, the dynamics appear complex, resulting in phase-forgetting cycles in which population phase shifts with respect to the previous cycle. Nevertheless, western spruce budworm populations do not appear to be chaotic. The region-wide synchrony of many of the outbreaks suggests that exogenous factors play a significant role in regulating outbreaks. Spring precipitation may be the factor driving population change, with wet springs associated with release and outbreak years. Evidence was also provided for endogenous control of the system; possibly through mechanisms involving the response and recovery of forest canopies subjected to defoliation. The holy grail of forest entomology has always been to determine what causes outbreaks of forest insects. It is now clear from this and other work[12] that for the spruce budworms, at least, observational studies will have to span several decades. The validity of short-term experimental work may also be seriously questioned.

Land use

Perhaps the most interesting findings relate to budworm outbreaks in relation to recent changes in land use. There is little question that outbreaks in the 20th century are more synchronous regionally than in previous centuries. Swetnam and Lynch noted that logging, fires and grazing pressures reduced the density and coverage of forests in the region in the early Anglo–American settlement era. The relaxation of these pressures resulted in the regeneration of fairly dense and continuous mixed-conifer forest canopies containing substantial proportions of suitable western spruce budworm hosts. These conditions, in contrast to those prevalent in pre-settlement times, have provided the insect population opportunities that resulted in more extensive and intense synchronous outbreaks in the 20th century. It would appear that forest fragmentation of the pre-settlement era contributed to the spatially and temporally heterogenous populations in which outbreaks were not as severe. Synchronous outbreaks have been noted in other forest insect species of North America. Recent changes in outbreak patterns of the Douglas-fir tussock moth (*Orgyia pseudotsugata*)[13] and the jack pine budworm (*C. pinus*)[14] are also suspected to be due to historic changes in regional land use patterns.

Swetnam and Lynch provide a unique insight into the long-term population behaviour of one forest-insect species. The implications of these findings are manifold because Swetnam and Lynch have integrated elements of climatology, ecology (including landscape ecology), archeology and history to forge their synthesis. Perhaps the seeds they sow in this paper will spur others to invest in the acquisition and analysis of long-term population data. More importantly, the paper implies a warning: profound anthropogenic-induced landscape changes, and possibly global changes, have created conditions that altered the dynamics of a native forest pest dramatically. Indeed we might take note, ponder these changes and behave adaptively lest we, like the Anasazi, be forced to abandon this beautiful village.

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Arctic and alpine biodiversity: patterns, causes and ecosystem consequences

As human populations expand, two general environmental concerns have arisen: (1) that human activities are altering the functioning of the Earth System; and (2) that these activities are causing species extinctions at a rate and magnitude rivaling those of past geologic extinction events. However, these concerns have been largely independent of each other, with little concern for the environmental causes or the ecosystem consequences of changes in biodiversity. The Scientific Committee on Problems in the Environment (SCOPE) and the United Nations Environment Programme (UNEP) have recently initiated a Global Biodiversity Assessment. An important component of this assessment is a series of studies on the causes and consequences of biodiversity in 14 major biomes.

A recent meeting in Kongsvold, Norway, initiated this activity by considering the patterns, causes and consequences of biodiversity in arctic and alpine ecosystems. These ecosystems were selected as critical because (1) high latitudes are predicted to undergo more pronounced warming than other regions of the globe, (2) the ecological consequences of climatic warming could be most significant in cold regions, (3) high altitudes, due to reduced pressure, are regions where CO_2 should be particularly limiting and could alter species interactions, (4) arctic ecosystems with their large frozen pools of carbon and methane may have strong feedbacks to global climate, and (5) due to their relative simplicity, these ecosystems may show clear effects of species on ecosystem processes. Hence, arctic and alpine ecosystems provide unique insights into causes and consequences of diversity in general. In this report, we summarize the major conclusions of that meeting and the recommendations for future research. (The full results of the meeting will be published in a book by Springer-Verlag.)

Paleoecology

Arctic and alpine ecosystems underwent dramatic historical changes during and after glacial periods (L. Brubaker, University of Washington, Seattle, USA) and low temperature stress constitutes a filter that eliminates many organisms. Consequently, there are only about 1500 arctic species and about 10 000 alpine species (about 4% of known vascular plant species; C. Körner). Each major temperate alpine flora, such as that of the Alps or the Rocky Mountains, has a similar number of species to the Arctic but these species are concentrated in a smaller area. The high mountains of Central Asia were an important source region for arctic and alpine floras and faunas as a result of migration into the Arctic and then back to other temperate alpine regions during the Quaternary (D. Murray, University of Alaska, Fairbanks, USA). Equatorial and southern hemisphere mountain regions are generally more distinct, being derived from different local floras. These tropical alpine floras often have fewer species than the temperate alpine, perhaps because they are surrounded by low-elevation tropical vegetation with few species that are 'pre-adapted' to alpine conditions. Thus, history plays a crucial role in defining patterns of diversity in arctic and alpine ecosystems.

There are striking relationships between local and global diversity. Arctic species that dominate widespread communities generally have a circumpolar distribution, whereas rare species occur in more restricted habitats such as mountain slopes and have a narrower geographic range (M. Walker, University of Colorado, Boulder, USA). Thus, species extinctions are more likely to affect those processes such as herbivory that are concentrated in these specialized habitats than processes such as trace-gas flux where wide-spread communities are more important. At the local scale, species richness is concentrated in areas of moderately unstable substrate, whereas habitats with stable substrate develop peat and have low species diversity in both the Arctic and the alpine. The Arctic has relatively few narrowly distributed endemics. By contrast, in the alpine, many taxa appeared to remain isolated on mountain tops during glacial advances and retreats, leading to a high degree of endemism, particularly in the southern Alps where glacial events were less extreme (B. Ammen, University of Bern, Switzerland; P. Ozenda and J-L. Bores, Université Joseph Fourier, Grenoble, France). During the warming trend of the past few decades, many alpine species appear to have advanced upward in elevation (G. Grabherr, University of Vienna, Austria). Thus, taxa restricted to narrow alpine zones at the tops of mountains may disappear, if the climate continues to warm.

Responses to climate change

Experimental studies provide a strong basis for predicting how arctic and alpine communities may respond to climatic change. At high latitudes, experimental increases in air temperature cause large changes in growth, reproductive output and clonal expansion, whereas in the mid- and low-Arctic, changes in other factors, such as nutrient supply, are more important (T. Callaghan, Merlewood Research Station, Grange-over-Sands, UK; S. Jonasson, University of Copenhagen, Denmark). In the high Arctic, temperature seems to operate directly on the vegetation rather than through soils processes, at least over the first years of experimentation. CO_2 enrichment has little effect on plant growth in arctic tundra in the short term, perhaps because other factors more strongly restrict growth.

In both the Arctic and alpine, human impact will be the greatest source of environmental change in the coming decades (O. Young, Dartmouth College, Hanover, USA). Although there have been substantial direct impacts associated with resource extraction in the Arctic and tourist developments in the alpine, changes associated with arctic haze, nitrogen deposition and altered fire and grazing regimes may have greater impact on biodiversity and ecosystem processes. For example, air pollution from industrial Europe has dramatic effects on the species composition and ecosystem effects of arctic mosses. Human impacts depend strongly on economic and social forces outside the Arctic and alpine, and, therefore, feedback loops involving people do not respond strongly to changes within these ecosystems.

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