

Second, these finds also address the question of provenance. Rehren and Pusch (2) convincingly show that the Egyptians were making their own glass in large specialized facilities that were under royal control. At Qantir, production was linked specifically to the use of copper to color the glasses either red or blue, and glass was manufactured in the form of ingots to be reworked elsewhere.

The production of ingots at Qantir, presumably for export, shows that at this period, Egypt exported rather than imported glass. The chemical composition of fully formed vessels, inlays, and plaques from other high-status sites throughout the Mediterranean and particularly the Aegean, at least in the case of cobalt blue glass, is

indistinguishable from that of the ingots, indicating that it was produced from Egyptian glass (10). Hence, elites in other societies were supplied with raw glass from Egypt for reworking. The location of glass manufacturing at the royal sites of Amarna and Qantir suggests that it was a controlled activity, which is not surprising, because glass was a “royal” medium used to enhance power, status, and political allegiances.

The evidence from Amarna and Qantir suggests that in the Late Bronze Age there was an Egyptian monopoly not just on the exchange of luxury glass but also on the diplomatic currency that the control of such technologies offered the elite. The evidence from Qantir presented by Rehren and Pusch (2) reinforces and reappraises the role of

glass both within Egyptian society and as an elite material that was exported from Egypt to the Mediterranean world.

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## MACROEVOLUTION

# Seeds of Diversity

Douglas H. Erwin

In a simple logistic growth model, the size of a population expands until further growth is limited by resource availability and the population size reaches a plateau. Robert MacArthur and E. O. Wilson extended these ideas to account for the effect of resources on species diversity in their model of island biogeography (1). Over the short term, competition for resources generates an equilibrium level of species diversity through a balance between immigration and extirpation. Over the longer term, equilibrium diversity reflects a balance between speciation and extinction, but in all cases the available resources control the equilibrium diversity. Now, Emerson and Kolm, in a recent paper in *Nature*, suggest that species diversity itself plays an important role in species diversification. They considered patterns of species diversity among plants and arthropods in the Hawaiian and Canary islands (2) and, after carefully controlling for island age, area, altitude, and nearest neighbor proximity through multiple regression analysis, concluded that species diversity itself promotes speciation. Simply put, the reason the tropics have so many species is that they have so many species.

What processes drive this positive feedback, and is it congruent with the MacArthur and Wilson model? There are explanations in which resource availability

still limits maximal diversity. Perhaps new species are continuing to subdivide resources as part of an adaptive radiation, or geographic differentiation is producing ecologically redundant species. A more interesting alternative is Emerson and Kolm's proposal that greater community structural complexity may drive greater diversity. Many organisms provide a habitat for a myriad of other species, either by serving as hosts for parasites or by modifying the environment through burrowing, nest building, or other activities. Issues of how species modify their own niche [niche construction (3)] and physically modify the environment to facilitate the production of niches for other species [ecosystem engineering (4, 5)] have received growing attention. The genesis of these ideas extends back to Richard Dawkins' *The Extended Phenotype* (6) and a paper by Richard Lewontin (7), each of which argues for a more expansive view of the selective interplay between organisms and their environment.

Niche construction involves activities of organisms that modify their environment and consequently modify the selective forces they experience. Many of these modifications may last for generations (think of the burrowing of earthworms or the multiple generations that may use a beaver dam), and these have been described as ecological inheritance. Laland and colleagues (3) have suggested that ecological inheritance represents a challenge to natural selection as the major driver of evolution. In a recent criticism of niche construction, Dawkins (8) observed that

the critical issue is the pattern of covariance between external, organismically induced factors and underlying genes: He would limit niche construction as a special case of the extended phenotype to settings where such covariance exists, a far more restricted view than that presented in (3). The by-products of life Dawkins calls “niche change,” and he would include oxygenation of the atmosphere and soil formation. Ecosystem engineering is often lumped with niche construction, but this is not limited to a species modifying its own environment. Modifications of the physical environment by one species affect, either positively or negatively, resource availability for other species. A termite mound may modify the selective forces facing the termites, but it also creates habitats for other species.

Missing from these discussions has been a sense of time and scale—a recognition that the most important episodes of niche generation may be during major evolutionary transitions, or recoveries from mass extinctions. Some of these are probably analogous to adaptive radiations, where ecological release in the face of underused resources allows a clade to diversify into a variety of more specialized forms. But many paleontologists have long expressed the view that the opening of new niches is an important component of such transitions, invoking “new adaptive zones,” “empty ecospace,” and similar concepts. For example, the diversification of multiple class- and ordinal-level invertebrate clades during the Ordovician established the marine communities of the Paleozoic, dominated by such sessile, filter-feeding forms as articulate brachiopods, bryozoans, and stalked echinoderms (9). Here new resources were provided by an expansion of the plankton (10) and through increased community com-

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plexity. The rapidity of the diversification and the ecological interactions between species suggests that, as in the plants and insects of the Hawaiian and Canary islands, species begat species. In terms of MacArthur and Wilson's model, these macroevolutionary events should be limited by the extent to which new resources increased the carrying capacity of the environment. But if there is feedback between diversifying species, and a total potential diversity that is not limited by resources, then we may need a class of models in which future diversity is a function of current diversity.

Diversity cannot continue to increase forever, and ultimately resource availability must play a role, but perhaps a smaller one over evolutionary time than has been

thought. Paleontologists, taking their cue from ecologists, have generally assumed that resource limitation controls the diversity of a community, but some have wondered whether changes in diversity might come from periodic disturbance. There have been few explicit considerations of this possibility, but Stanley (11) suggested that the apparent periodicity of mass extinctions and biotic crises reflected prolonged environmental disturbance and lengthy rediversification, not a periodic external forcing factor (such as periodic meteor bombardment). If periodic disturbance does provide a major control on diversity, then niche generation may be an ongoing process, more rapid during macroevolutionary transitions, but providing a regular source of new adaptive possibility until the next crisis occurs.

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## CLIMATE

# Uncertainty in Hurricanes and Global Warming

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**D**uring the 2004 hurricane season in the North Atlantic, an unprecedented four hurricanes hit Florida; during the same season in the Pacific, 10 tropical cyclones or typhoons hit Japan (the previous record was six) (1). Some scientists say that this increase is related to global warming; others say that it is not. Can a trend in hurricane activity in the North Atlantic be detected? Can any such trend be attributed to human activity? Are we even asking the right questions?

In statistics, a null hypothesis—such as “there is no trend in hurricane activity”—may be formed, and it is common to reject the null hypothesis based on a 5% significance level. But accepting the null hypothesis does not mean that there is no trend, only that it cannot be proven from the particular sample and that more data may be required. This is frequently the case when the signal being sought is masked by large variability. If one instead formulates the inverse null hypothesis—“there is a trend in hurricane activity”—then the 5% significance level may bias results in favor of this hypothesis being accepted, given the variability. Acceptance of a false hypothesis (a “type II” error) is a common mistake. Rather than accept the hypothesis, one may be better off reserving judgment. Because of the weak-

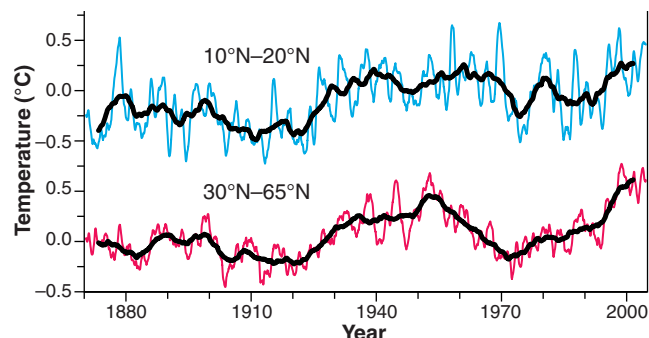
ness associated with statistical tests, it is vital to also gain a physical understanding of the changes in hurricane activity and their origins.

Hurricane activity generally occurs over the oceans in regions where sea surface temperatures (SSTs) exceed 26°C (2). In the Atlantic, SSTs and hurricane activity (see both figures) vary widely on interannual and multidecadal time scales. One factor in the year-to-year variability is El Niño: Atlantic hurricanes are suppressed when an El Niño is under way in the Pacific (3, 4). The decadal variability is thought to be associated with the thermohaline circulation and is referred to as the Atlantic multidecadal oscillation. It affects the number of hurricanes and major hurricanes that form from tropical storms first named in the tropical Atlantic and the Caribbean Sea (5–7).

In addition to interannual and multidecadal variability, there is a nonlinear upward trend in SSTs over the 20th century. This trend is most pronounced in the past 35 years in the extratropical North Atlantic (see the first figure). It is associated with global

warming and has been attributed to human activity (8). In the tropical North Atlantic—the region of most relevance to hurricane formation—multidecadal variability dominates SSTs (see the first figure), but the 1995–2004 decadal average is nonetheless the highest on record by >0.1°C. Hence, although the warming in the tropical North Atlantic is not as pronounced, it is probably related to that in the extratropical North Atlantic.

SSTs are not the only important variable affecting hurricanes (2, 9, 10). Other factors that have influenced the increase in hurricane activity in the past decade (11) include an amplified high-pressure ridge in the upper troposphere across the central and eastern North Atlantic; reduced vertical wind shear over the central North Atlantic [wind shear tends to inhibit the vortex from forming (2)]; and African easterly lower atmospheric winds that favor the development of hurricanes from tropical disturbances moving westward from the African coast. Atmospheric stability is also important (4).



**Getting warmer.** Annual mean SST anomalies relative to 1961 to 1990 (23) for 1870 to 2004, averaged over the tropical Atlantic (10°N to 20°N, excluding the Caribbean west of 80°W) (top) and the extratropical North Atlantic (30°N to 65°N) (bottom). Heavy lines are 10-year running means.

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