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

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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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Uncertainty in Hurricanes and Global Warming

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

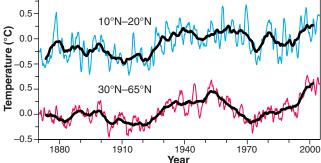
Hurricane activity generally occurs over the oceans in regions where sea surface temperatures (SSTs) exceed 26°C (2). In the Atlantic, SSTs and hurricane activity (see both figures) vary widely on interannual and multidecadal time scales. One factor in the year-to-year variability is El Niño: Atlantic 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).

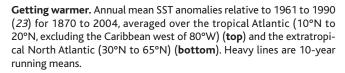
In addition to interannual and multidecadal variability, there is a nonlinear upward trend in SSTs over the 20th century. This trend is most pronounced in the past 35 years in the extratropical North Atlantic (see the first figure). It is associated with global

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).



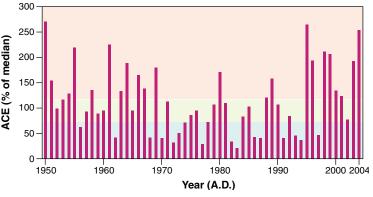
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Higher SSTs are associated with increased water vapor in the lower troposphere. Since 1988, the amount of total column water vapor over the global oceans has increased by 1.3% per decade (12); the variability and trends in water vapor are strongly related to SST anomalies. This behavior is similar to that expected theoretically (13) and supports model projections (14) suggesting that relative humidity remains about the same as temperatures increase. Both higher SSTs and increased water vapor tend to increase the energy available for atmo-



A measure of regional storm activity. The ACE index reflects the collective intensity and duration of tropical storms and hurricanes during a given hurricane season. Values are given as percentage of the median from 1951 to 2000; the white band indicates normal conditions, the blue is below normal, and the pink is above normal, according to NOAA. [Adapted from (1)]

spheric convection, such as thunderstorms, and for the development of tropical cyclones (9, 15). However, the convective available potential energy (15) is also affected by large-scale subsiding air that increases the stability and dryness of the atmosphere, and is often associated with wind shear throughout the troposphere (16). The convective available potential energy appears to have increased in the tropics from 1958 to 1997 (17, 18), which should increase the potential for enhanced moist convection, and thus—conceivably—for more hurricanes.

An important measure of regional storm activity is the Accumulated Cyclone Energy (ACE) index (see the second figure) (1). Since 1995, the ACE indexes for all but two Atlantic hurricane seasons have been above normal; the exceptions are the El Niño years of 1997 and 2002. According to the National Oceanic and Atmospheric Administration (NOAA), the hurricane seasons from 1995 to 2004 averaged 13.6 tropical storms, 7.8 hurricanes, and 3.8 major hurricanes, and the ACE index was 169% of the median. In contrast, the hurricane seasons during the previous 25-year period (1970 to 1994) averaged 8.6 tropical storms, five hurricanes, and 1.5 major hurricanes, and the ACE index was 70% of the median. In 2004, ACE reached the third-highest value since 1950 (1); there were 15 named storms, including nine hurricanes.

Despite this enhanced activity, there is no sound theoretical basis for drawing any conclusions about how anthropogenic climate change affects hurricane numbers or tracks, and thus how many hit land. The environmental changes that are under way favor enhanced convection and thus more thunderstorms. But to get a hurricane, these thunderstorms must first be organized into a tropical storm (which is essentially a collection of thunderstorms that develops a vortex). Model projections of how wind shear in the hurricane region responds to global warming caused by increased carbon dioxide in the atmosphere tend to differ (14), and it is not yet possible to say how El Niño and other factors affecting hurricane formation may change as the world warms.

However, once a tropical storm has formed, the changing environmental conditions provide more energy to fuel the storm, which suggests that it will be more intense than it would otherwise have been, and that it will be associated with heavier rainfalls (14). Groisman et al. (19) found no statistically significant evidence that precipitation associated with hurricanes increased along the southeastern coast of the contiguous United States during the 20th century; however, their analysis did not include years after 2000, and there was a distinct increase in hurricane precipitation after 1995. Groisman et al. found a linear upward trend in precipitation amount by 7% in the 20th century in the contiguous United States; the increases in heavy precipitation (the heaviest 5%) and very heavy precipitation (the heaviest 1%) were much greater at 14% and 20%, respectively (19). Such trends are likely to continue (20).

Thus, although variability is large, trends associated with human influences are evident in the environment in which hurricanes form, and our physical understanding suggests that the intensity of and rainfalls from hurricanes are probably increasing (δ), even if this increase cannot yet be proven with a formal statistical test. Model results (14) suggest a shift in hurricane intensities toward extreme hurricanes.

The fact that the numbers of hurricanes have increased in the Atlantic is no guarantee that this trend will continue, owing to the need for favorable conditions to allow a

vortex to form while limiting stabilization of the atmosphere by convection. The ability to predict these aspects requires improved understanding and projections of regional climate change. In particular, the tropical ocean basins appear to compete to be most favorable for hurricanes to develop; more activity in the Pacific associated with El Niño is a recipe for less activity in the Atlantic. Moreover, the thermohaline circulation and other climate factors will continue to vary naturally.

Trends in human-influenced environmental changes

are now evident in hurricane regions. These changes are expected to affect hurricane intensity and rainfall, but the effect on hurricane numbers remains unclear. The key scientific question is not whether there is a trend in hurricane numbers and tracks, but rather how hurricanes are changing.

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