

in stickleback. The study by Barrett *et al.* points to the great promise for connecting molecular genetics with phenotypic variation and fitness in the wild, a synthesis that would have made a pleasant gift for Darwin on his 200th birthday next February.

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- I thank S. Bassham, J. Snodgrass, and C. Hulslander for comments. W.A.C. is supported by grants from the NSF (IOS0642264 and IOS0818738) and NIH (R24GM79486).

10.1126/science.1165663

ECOLOGY

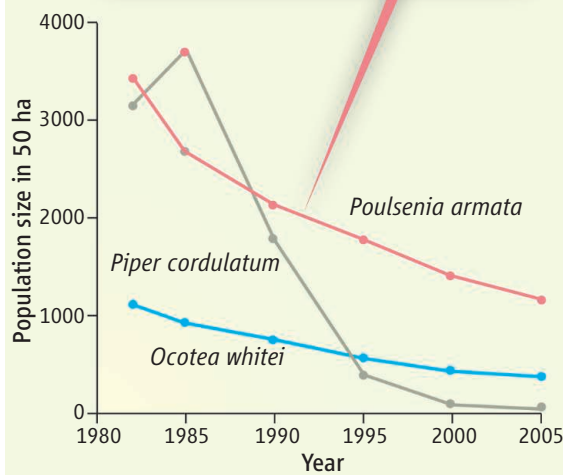
Biodiversity in a Warmer World

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There is ample evidence that 20th-century warming has shifted ranges of temperate and arctic species, but on page 261 of this issue, Moritz *et al.* (1) provide an exceptionally thorough example: They take advantage of a well-documented study from a century ago (2) to demonstrate contractions and expansions of elevation range among small mammals in Yosemite National Park, California, USA. In contrast, there have been few attempts to even address the tropics' sensitivity to global climate change (3). Also in this issue (page 258), Colwell *et al.* (4) use a novel conceptual approach to analyze climate shifts in tropical ecosystems.

Colwell *et al.* explain that weak latitudinal temperature gradients in the tropics will make it difficult for species to track suitable climatic conditions by migrating through the lowlands; instead, short-distance upslope migration to cooler mountains is what we should expect. The authors note three ways in which global warming may cause extinction. First, the tropical lowlands may experience biotic attrition: Warming drives species out of the lowlands, but no source of species adapted to higher temperatures is available to compensate the losses. The two additional risks for tropical mountain species are range-shift gaps (where species' current altitudinal ranges do not overlap climatically suitable ranges of the future) and mountain-top extinction (where warming pushes climatically suitable conditions off mountain peaks). These latter risks are also relevant outside the

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Steep decline. In a complete census of trees above 1 cm diameter in 50 ha of forest in Panama, the largest population declines are associated with drought, not temperature change (13).

A new framework helps to understand how species ranges change under global warming.

tropics (5); indeed, Moritz *et al.* document the contraction of ranges of high-elevation species in Yosemite.

Colwell *et al.* then analyze ranges of 2000 species of plants and insects along a 2900-m altitudinal transect on Volcán Barva, Costa Rica, and relate these to expected upslope climate shifts. They find that a 3.2°C warming threatens 53% of the species with lowland extinction and 51% with range-shift gaps. Only a minority of species would face mountain-top extinction.

These numbers suggest large risks. However, the figures are likely to be controversial, because there are substantial uncertainties in our understanding of the sensitivity of tropical species to climatic warming. Notably, the prediction of heavy lowland extinctions is based on the assumption that species will be unable to tolerate temperatures higher than today's. Yet, many extant species evolved when climates were warmer (6) and may retain this warmth tolerance. Climatic limits within lineages often remain remarkably stable over millions of years (7, 8). On evolutionary time scales, there is little evidence that warming is detrimental in the tropics: Neotropical plant diversity peaked in the period of maximum warmth between 35 and 55 million years ago (9), and high tropical diver-

sity may be the product of the greater extent of warm areas in the past (10). On the other hand, extreme warming may have caused tropical extinctions or vegetation die-offs (11). Hence, the heat sensitivity of tropical lowland species is an open question.

Furthermore, Colwell *et al.* assume that temperature alone sets range limits. Although temperature is clearly a limiting factor for some tropical species at high altitudes, most studies on the distributions of lowland species focus on precipitation as limiting, because moisture has such an obvious impact (see the figure) (12, 13). As an example of moisture precedence, 30% of Panama's tree species limited to above 600 m above sea level on the dry Pacific slope occur near sea level on the wet Caribbean slope (14). Even where temperature is an important limiting factor, it is unlikely to be operating alone (15): The idiosyncratic range dynamics of small-mammal species at Yosemite (1) warn against the assumption that ranges simply reflect temperature tolerances. Finally, range limits estimated from small samples gathered at one location can

only be underestimates (16); predictions of extinction risk will be overestimated if ranges are underestimated.

Colwell *et al.* provide an important illustration of the potential risk posed by global warming to tropical diversity. In fact, even bleaker predictions have been made. One general circulation model predicts loss of Amazonian forest by the middle of this century due to drought stress (17). But forecasts of the impact of global warming on tropical diversity are hampered by uncertainties about what causes range limits. Even in temperate communities, little direct evidence of such factors goes into models; most models are based on correlations between current range and climate.

A key research focus should thus be to find direct evidence of how species respond to relevant environmental variables. The framework outlined by Colwell *et al.* can then be used more accurately, and will also be relevant outside the tropics. Even lowland attrition may occur here, because climatic shifts are likely to exceed species' migration capacities (18, 19).

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10.1126/science.1164542

GEOPHYSICS

Volcanic Symphony in the Lab

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Like philharmonic orchestras that perform symphonies with different musical instruments, active volcanoes produce a mix of seismic signals (earthquakes) that vary in their periodicity. Because each type of signal is associated to different physical processes, seismic monitoring can be a powerful tool for eruption forecasting, especially when combined with geochemical data (such as composition of escaping gases) and ground-deformation monitoring (1). The key issue is how to associate volcanic processes—which include fracture and dike propagation, magma feeding, and degassing—with each type of earthquake (2, 3). One approach is to recreate volcanic conditions with small laboratory samples, and then extrapolate the experimental signals (sonic to ultrasonic waves) to the scale of volcanic features. On page 249 of this issue, Benson *et al.* (4) measured acoustic emissions (AEs) in a basalt sample from Mount Etna

during loading and fracturing, and then on a rapid decompression of fluid. The AE signals recorded during the pore fluid decompression are similar to those detected during low-frequency earthquakes associated with volcanoes, which suggests that some natural quakes also originate from the rapid release of pressure in fluids (melts, gas, and supercritical fluids) flowing in fractures.

The seismic signals from volcanoes include high-frequency waves similar to those detected during tectonic earthquakes as well as low-frequency or long-period earthquakes and very-long-period earthquakes; tremors (continuous low-frequency ground vibration) and hybrid events that can mix these signals are also observed (2). Several theories have been proposed that connect volcanic with different seismic signals (3), but lab experiments potentially can allow observation of each physical mechanism separately—just as a clarinet passage is easier to recognize in a symphony performance if you have first heard the clarinet playing alone. Benson *et al.*, using the tools typical of passive seismology (which looks at seismic signals and includes three-dimen-

Analysis of acoustic signals from lab samples links rapid pressure drops of pore fluids with low-frequency volcanic earthquakes.

sional earthquake location, waveform analysis, and computation of focal mechanisms), interpreted volcanic seismicity on the basis of experiments that reproduce variation of the physical conditions (such as pressure drop in a conduit) occurring in volcanic environments.

In rock deformation experiments, AEs are elastic waves produced by local strain events such as microfracturing, interaction of fluids with the crack walls, etc. (5, 6), although only rarely are emissions transmitted at audible frequencies (20 to 20,000 Hz). Following the pioneering work of Obert and Duvall (7), who used geophones to measure these signals, the use of arrays of piezoelectric transducers has enabled researchers to pinpoint the source of the AE and follow the evolution of sample damage (6, 8, 9).

To what extent can we link these lab studies and data from volcanoes? Experimental and natural waveforms can be similar in shape but can differ by orders of magnitude in frequency and amplitude (see the figure). Earthquakes are detected by seismometers and accelerometers that record ground motion and acceleration, whereas AEs are detected by

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