Bridge species drive tropical engine of biodiversity

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The University of Chicago's David Jablonski is presenting new evidence that most evolutionary lineages started in the tropics and expanded outward in a process driven by what he and his colleagues call "bridge species." Credit: NASA Visible Earth

Although scientists have known since the middle of the 19th century that the tropics are teeming with species while the poles harbor relatively few, the origin of the most dramatic and pervasive biodiversity on Earth has never been clear.

New research sheds light on how that pattern came about. Furthermore, it confirms that the tropics have been and continue to be the Earth's engine of biodiversity.

By examining marine bivalves (two-shelled mollusks including scallops, cockles and oysters), a model system for large-scale ecological and evolutionary analysis, the study shows that most evolutionary lineages started in the tropics and expanded outward.

"This 'out of the tropics' dynamic is the major process that shapes the latitudinal pattern of biodiversity that we see today on land and sea," said lead author David Jablonski, the William R. Kenan Jr. Professor in Geophysical Sciences at the University of Chicago. His team focuses on marine bivalves because they combine a wealth of important biological patterns with a large but manageable number of living species (about 8,000) and a rich fossil record.

The new research will be published this week in the online Early Edition of the *Proceedings of the National Academy of Sciences* presents evidence that the "out of the tropics" process is driven mainly by bridge species, a new term referring to evolutionary lineages that straddle the boundary between the tropics and cooler neighboring regions.

"We thought the 'out of the tropics' process would be driven by the formation of new species at the edge of the tropics, but that doesn't seem to be true," Jablonski said. "Whether bridge species really are the conduit, 'out of the tropics' for all those lineages still needs to be confirmed. We'll tackle that next, by examining molecular data on species within these lineages, inside and outside the tropics, to see how they're related."

As with the *PNAS* study, this follow-up research would require examining data on both fossils and living organisms. "Alas, it's still rare for paleontologists to integrate the fossil record with data on present-day organisms, but for large-scale biodiversity studies like this, it's a very powerful approach, often an essential one," Jablonski said. "Biodiversity is a product of origination, extinction and immigration, and when the

fossil record is adequate, as it is with bivalves, it provides the most robust window into the dynamics that produced present-day patterns."

Surprising findings

The new research corroborates the "out of the tropics" model that Jablonski and others introduced in a 2006 publication. In fact, the new research documents this dynamic over the past 12 million years—even during the Ice Ages, when the temperature differences between the equator and the poles became more severe. That runs counter to the broadly accepted principle of "niche conservatism," which suggests that related species tend to retain the ecological limits of their ancestors, Jablonski said. "Most species we studied do adhere to that principle, but the ones that do not are crucial to the deployment of biodiversity on Earth."

There are many such bridge species but each evolutionary lineage generally has only one or two. Therefore, bridge species are widespread in an evolutionary sense but rare in terms of overall biodiversity, according to the research. And the fossil record shows that most of today's bridge species started as tropical species. "Somehow they left their tropical cradle, adapting to the colder temperatures and more variable climates of the temperate zones," said Jablonski. "It's impressive that they apparently expanded their ability to tolerate these harsher conditions."

Another surprise is that the most widespread species of bivalves are not the ones with the broadest temperature tolerances. Rather, they are often the ones with limited temperature tolerances that have specialized on temperatures that are the most widespread. "This is important because broad geographic range is one of the most reliable estimates of the extinction-resistance of a species," Jablonski said. "What surprised us is that the most widespread temperatures—and therefore many of the most

widespread bivalve species—occur in the tropics."

Homo sapiens is even more impressive than the bridge species in this study, he added. Humans have not only immigrated out of the tropics but throughout the Earth. Only a handful of marine species range all the way from equator to poles, Jablonski has found, but humans are as widespread as any species known today. "As a species we're pretty extinction-resistant, but even widespread tropical species may be at risk today," said Jablonski.

As research on both living and fossil species has shown, broad geographic ranges buffer species from extinction when pressures are local, such as from hurricanes, pollution or overexploitation. But when—for marine species—those pressures alter global ocean temperatures, circulation patterns or chemistry, a broad geographic range is less likely to help, Jablonski said.

"That's what happened at the end-Cretaceous mass extinction 65 million years ago, and that could be looming today."

More information: "Out of the Tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient" Early Edition of *Proceedings of the National Academy of Sciences*, week of June 10, 2013: www.pnas.org/cgi/doi/10.1073/pnas.1308997110

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