EVOLOGY

ECOLOGISTS USED TO THINK THAT EVOLUTION WAS TOO SLOW TO AFFECT THEIR STUDIES. THEY WERE WRONG.

BY RACHAEL LALLENSACK

The coloration of stick insects such as this *Timema bartmani* help it to hide, but might also affect the local ecology.

MORITZ MUSCHICK

It took Timothy Farkas less than a week to catch and relocate 1,500 stick insects in the Santa Ynez mountains in southern California. His main tool was an actual stick.

"It feels kind of brutish," says Farkas. "You just pick a stick up off the ground and beat the crap out of a bush." That low-tech approach dislodged hordes of stick insects that the team easily plucked off the dirt.

On this hillside outside Santa Barbara, there are two kinds of bush that the stick insect (*Timema cristinae*) inhabits. The creature comes in two corresponding colorations: green and striped. Farkas and his fellow ecologists knew that the stick insects had evolved to blend in with their surroundings. But the researchers wanted to see whether they could turn this relationship around, so that an evolved trait — camouflage — would affect the organism's ecology.

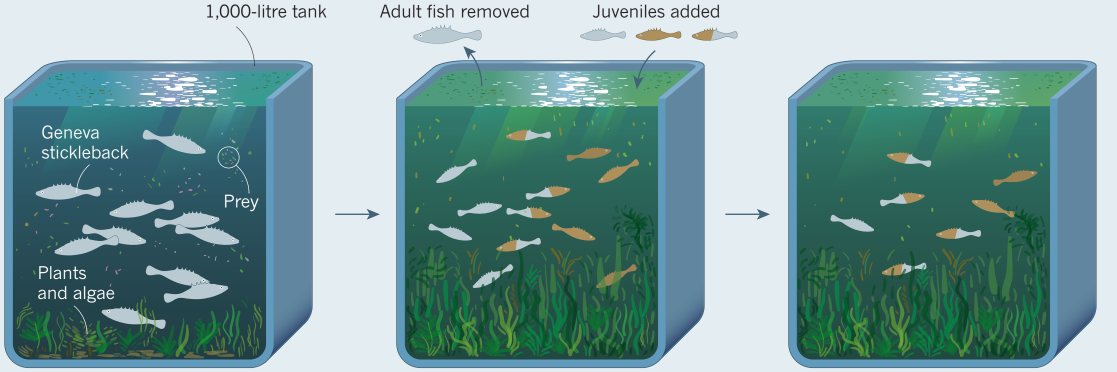
To find out, the team relocated mixtures of green and striped insects to different plants, so that some insects' coloration clashed with their new home. Suddenly maladapted, these insects became targets for hungry birds, and that caused a domino effect[1]. Birds drawn to bushes with mismatched stick insects stuck around to eat other residents, such as caterpillars and beetles, stripping some plants clean. "That this evolutionary force can cause local extinction is striking," says Farkas, an ecologist at the University of New Mexico in Albuquerque. "It affects the entire community." All this happened because of an out-of-place evolutionary trait.

Ecologists have generally ignored evolution when studying their systems; they thought it was impossible to test whether such a slow process could change ecosystems on observable timescales. But they have come to realize that evolution can happen more quickly than they assumed, and a wave of studies has capitalized on this idea to observe evolution and ecology in unison.

Such eco-evolutionary dynamics could be important for understanding how new populations emerge, or for predicting when one might go extinct. Experiments suggest that evolutionary changes alter some ecosystems

FISHY FEEDBACK

Researchers use model ecosystems to test how the evolutionary traits of one generation of a species can affect the environment and, in turn, the next generation. In this example, tanks are stocked with sticklebacks (*Gasterosteus aculeatus*) from either Lake Constance or Lake Geneva.



Altered ecology

Adult fish change their ecosystems in different ways. Geneva fish, for example, eat more of the larger prey and leave more algae growing.

Fish switch

The adults are removed, and the changes to the ecosystem are measured. Then, lab-raised juveniles from both the Geneva and Constance lineages are introduced, along with hybrids.

Evo effects

With large prey depleted, Geneva juveniles are at a disadvantage. Other fish, and especially hybrids, fare better in the altered ecosystem — perhaps the effect of selection favouring diversity.

just as much as shifts in more-conventional ecological elements, such as the amount of light reaching a habitat. "Eco-evolutionary dynamics is the dragon lots of people are chasing right now," says Troy Simon, an ecologist at the University of Georgia in Athens.

Rapid evolution can sometimes offset some of the detrimental effects of a warming climate and other known drivers of change; in other cases, it can worsen those effects. Even for the most common processes, such as changes in population size or food chains, ecologists must take evolution into consideration, researchers say. "Everybody realized rapid evolution was occurring everywhere," says evolutionary ecologist Andrew Hendry of McGill University in Montreal, Canada.

DARWIN IN REVERSE

It all goes back to Charles Darwin's finches. When the naturalist visited Ecuador's Galapagos Islands in 1835, he documented some variation in the beaks of finches living on different islands and eating different foods. Years after the voyage, he hinted in his *Journal of Researches* that this variation suggested a tight relationship between the birds' ecology and their evolution.

Darwin never imagined seeing this in action, because he thought that evolution occurs only at the "long lapse of ages". But by the late 1990s, ecologists had started to realize that evolution could be observed within a few generations of a given species — a timescale that they could work with.

Organisms that live and die quickly provided some of the early data demonstrating how evolution influences ecology. A key study[2] published in 2003 focused on algae and rotifers, microscopic predators that feed on algae; both species can tick through up to 20 generations in the course of a couple of weeks. The study mixed the organisms together in tanks and showed that when algae evolve rapidly, they throw off normal predator–prey population dynamics.

Usually, the two species play out a cycle between 'boom' and 'bust'. The algal population grows; the rotifers then gobble them up and their own population explodes. When the predators have depleted the algae, their numbers crash. The algae then rebound and the pattern starts again. But when the researchers introduced different algal varieties — seeding some genetic diversity — the algae began to evolve rapidly and the cycle changed completely. The algal population remained elevated for longer, and the rotifers' own boom was abnormally delayed because the new algae were more resistant to predation.

Similar studies in aphids[3] and water fleas[4] have confirmed that rapid evolution can affect characteristics of populations, such as how fast they grow. These ecological changes can alter future rounds of evolution and selection. Seeing such rapid evolution in action has changed ecologists' picture of what they thought was a predictable and fundamental ecological process, and showed how important it is to consider evolution when studying how populations interact. "Everything about ecology has to be re-examined in light of the fact that evolution is more important than we thought," says Stephen Ellner, an ecologist at Cornell University in Ithaca, New York. "This changes everything."

FAKE LAKES

After these initial lab studies, ecologists started to think bigger. Experiments conducted indoors at small scales can't reproduce the intricacies of natural ecosystems, so researchers have been testing their ideas in grander, less artificial set-ups.

Working out whether eco-evolutionary dynamics affect the real world is one of the field's biggest challenges, says Rebecca Best, an evolutionary ecologist at Northern Arizona University in Flagstaff, because so many uncontrollable factors can affect wild ecosystems.

She has found a middle ground by incorporating natural elements into a tightly controlled experiment. At a site overlooking Lake Lucerne in Switzerland, she and her team set up 50 miniature lakes: large plastic tanks each holding 1,000 litres of water, plus a slurry of sediment, plant life, algae, invertebrates and water collected from three lakes — Geneva, Constance and Lucerne. Once these 'mesocosms' were settled, with plankton reproducing and plants taking root, the team introduced into each tank one of two genetically distinct lineages of adult threespine sticklebacks (*Gasterosteus aculeatus*): one lineage from Lake Constance and the other from Lake Geneva. A few weeks later, the researchers removed the fish and replaced them with a mixture of lab-raised juveniles from both locations, plus some hybrids of the two lineages.

They found[5] that how the adults had manipulated their environments affected the survival of the next generation of fish (see 'Fishy feedback'). If the adult fish removed prey of a certain size, for example, younger fish that shared characteristics with the adults — in this case, mouth size — went hungry. Juveniles that were different from the former occupants fared better. The study showed that the traits of the adult fish shaped the environment for the next generation — enough to dictate the evolutionary trajectory of those that followed.

Best says that her mesocosm experiments are more sophisticated and realistic than lab studies, but less easy to control. Ideally, she says, the team would run the experiment in the field, but that would come with its own obstacles, such as having to factor in the evolution of other species in the ecosystem, or the risk of events such as extreme storms.

Experiments such as Best's are "vastly easier and more controlled than anything you can do in nature", Hendry says. But they might not reflect what happens in real ecosystems. "That's the watershed moment we're at right now. Does this actually play out in the real world?"

In the messy real world, it can be difficult to pinpoint the impact of a single feature, either an ecological attribute (such as rainfall) or an evolutionary one (such as a change in camouflage).

A few intrepid ecologists are trying anyway. Last year, a study[6] on guppies in Trinidad demonstrated that the fish's evolution can drive an ecological change as strongly as an environmental factor: the amount of light available.

The study focused on two populations of guppies (*Poecilia reticulata*) in the northern part of the island. Their habitats differ in several ecological characteristics, including how much shade they receive from the forest canopy, which affects how many algae grow in the streams.

The team moved populations of guppies — which differed in evolved traits such as body proportions and colour — between eight rivers in the watershed, and measured the canopy above the water. In some of the study sites, introducing a new kind of guppy altered algal populations as much as allowing 20% more light to stream onto the water did. Even a natural ecosystem, say the researchers, is a product of evolution as well as ecology.

This experiment did use a more natural setting than many others, but Trinidadian guppies are ecological celebrities that have appeared in hundreds of studies, and the rivers they inhabit have been highly manipulated already. Researchers want to know whether the forces at work in the guppy populations also play out in species that are not necessarily famous for evolutionary dynamics, says McGill ecologist Gregor Fussmann. "We need systems that are generic," he says.

LIZARD LIMBS

That's exactly what Thomas Schoener, an evolutionary ecologist at the University of California, Davis, and his team have set out to do with two populations of lizard in the Bahamas. Their project is part of an ongoing multigenerational study, begun in 1977. They have been attempting to simulate accelerated evolution by catching curly-tailed lizards (*Leiocephalus carinatus*) and moving them to a string of tiny islands inhabited by brown anoles (*Anolis sagrei*), to see how the ecosystems change as a result.

Curly-tails are natural predators of the smaller brown anole, so when the team first moved the curly-tails onto islands with the anoles, populations of the latter dropped[7]. Spider populations increased when anoles — their main predator — took a hit, and the excess spiders then ate more springtail insects (*Collembola*). Researchers spotted surviving anoles fleeing to the trees to escape their new predator, and that triggered damage to plants. The team knew from previous work[8] that anoles adapt fairly quickly to tree climbing by favouring shorter-limbed offspring.

But then something unexpected happened. Hurricane Irene hit the islands in 2011, followed by Hurricane Sandy in 2012. Populations of both anoles and curly-tailed lizards crashed. On some islands, anoles were completely wiped out after the storm.

"The hurricanes are a mixed blessing because on the one hand, they give us all kinds of interesting data about disturbance," Schoener says. "But on the other hand, it can slow down what might be a normal progression of evolution."

The team has managed to keep its project on track, and is observing evolutionary changes in leg length and the lizards' re-colonization of the islands after the hurricane.

Surprisingly, the anoles that survived the storm have longer limbs than the pre-hurricane population[7] — the opposite of the team's prediction, but perhaps better for holding on to branches tightly during a storm. The team has just received funding to study how this evolutionary change will affect the ecosystem.

> **"EVERYTHING ABOUT ECOLOGY HAS TO BE RE-EXAMINED IN LIGHT OF THE FACT THAT EVOLUTION IS MORE IMPORTANT THAN WE THOUGHT."**

The hurricanes certainly complicated Schoener's study, but other researchers appreciate the unplanned intervention because it provides a chance to study the consequences of real events and watch the lizards recolonize the islands. Even in the absence of a natural disaster, any number of dynamics could also change the course of an organism's evolution, says Best. "Those potential interactions are going on for everything in the ecosystem."

She and others say there is plenty more to do, both in the lab and in more-elaborate field studies. Some researchers want to add genetic data to their work, to understand what is driving evolution in the first place. This would tell them whether a particular trait — growth rate, for example — is truly heritable and evolving, rather than a characteristic that can be directly affected by an animal's environment. Genomic data could also help to find hidden characteristics — those harder to observe than body size or growth rate — that might affect ecology.

In a study[9] of algae and rotifers, Lutz Becks, an evolutionary ecologist at the Max Planck Institute for Evolutionary Biology in Plön, Germany, and his colleagues watched several cycles in which populations waxed and waned as the algae clumped together and dispersed. But when the team looked at individual genes underlying clumping behaviour, they found that their expression varied wildly from one cycle to the next, even though the clumping looked the same. They have since observed co-evolution of three species at once — algae, rotifers and a virus — and found[10] that the rotifers slowed the rate at which the algae and virus co-evolved. The team plans to repeat this type of experiment, analysing genome data to see how specific details of the algal and viral genes change over time. "We'd like to get to a point where we can actually predict what genomic architecture might be needed for rapid evolution," says Becks.

Rapid evolution can offset — at least partially — the damaging effects of climate change and other ecological disturbances. In 2011, for instance, a group led by Ellner reanalysed[11] 35 years of data from dormant eggs of *Daphnia* water fleas, exhumed from a sediment core in Lake Constance. The data represented periods before, during and after a time when the lake was affected by blooms of cyanobacteria, a microbe with low nutritional value for *Daphnia*. The team found that as the *Daphnia*'s food became less nutritious, juvenile fleas grew poorly and ended up as smaller adults. But after several generations, evolutionary changes caused the growth rate of juveniles to return to normal. And the adults regained some of their lost stature, although they didn't reach the same size as they had before the blooms. The researchers suggest that rapid evolution is likely to occur most often when the environment is changing, but the effects are hidden because they pull in opposite directions. "Evolution is going to be part of how the biosphere responds to climate change," Ellner says.

Farkas has these questions about evolution and ecology at the front of his mind as he beats the bushes around Santa Barbara and sorts his stick insects. He and his team are planning even more elaborate schemes. They want to catch a full feedback cycle unfolding — ecology affecting evolution affecting ecology once more — all while collecting genetic data. "Comparing how large these effects of evolution will be and understanding when and where evolution is happening is going to be important," says Farkas. "To me, it's the final frontier. But it's going to take a really long time." ■

Rachael Lallensack *is a journalist based in Washington DC.*

1. Farkas, T. E., Mononen, T., Comeault, A. A., Hanski, I. & Nosil, P. *Curr. Biol.* **23,** 1835–1843 (2013).
2. Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F. & Hairston, N. G. Jr *Nature* **424,** 303–306 (2003).
3. Turcotte, M. M., Reznick, D. N. & Hare, J. D. *Am. Nat.* **181** (Suppl. 1), S46–S57 (2013).
4. Van Doorslaer, W. *et al. Glob. Chang. Biol.* **15,** 3046–3055 (2009).
5. Best, R. J. *et al. Nature Ecol. Evol.* **1,** 1757–1765 (2017).
6. Simon, T. N. *et al. Copeia* **105,** 504–513 (2017).
7. Schoener, T. W., Kolbe, J. J., Leal, M., Losos, J. B. & Spiller, D. A. *Copeia* **105,** 543–549 (2017).
8. Kolbe, J. J., Leal, M., Schoener, T. W., Spiller, D. A. & Losos, J. B. *Science* **335,** 1086–1089 (2012).
9. Becks, L., Ellner, S. P., Jones, L. E. & Hairston, N. G. Jr *Ecol. Lett.* **15,** 492–501 (2012).
10. Frickel, J., Theodosiou, L. & Becks, L. *Proc. Natl Acad. Sci. USA* **114,** 11193–11198 (2017).
11. Ellner, S. P., Geber, M. A. & Hairston, N. G. Jr *Ecol. Lett.* **14,** 603–614 (2011).